PhD-dissertation reviews

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Source: Ardea, 99(2) : 243-252

Published By: Netherlands Ornithologists' Union

URL: https://doi.org/10.5253/078.099.0217

PhD-dissertation reviews

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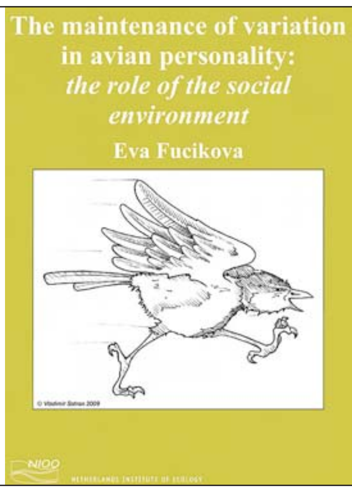
Fucikova E. 2010. The maintenance of variation in avian personality: the role of the social environment. PhD thesis. University of Groningen, The Netherlands. ISBN: 978-90-367-4703-5. Paperback, 113 pp. Available at http://irs.ub.rug.nl/ppn/331370018.



In recent years, considerable effort has been allocated to study the phenomenon of animal personality. The existence of animal personality is particularly intriguing because it implies that behaviours are less flexible than previously thought and raises the questions: why do personalities exist and how is variation in personalities maintained? There is growing awareness that consistent individual differences in behaviour can be adaptive. Therefore, identifying the mechanisms underlying personality variation in wild populations is needed to understand how personality can evolve under natural circumstances. In this thesis, Eva Fucikova bridges the fields of behavioural ecology and evolutionary biology to address the question of how personality variation in wild birds is maintained. More specifically, she investigates the role of local social environment and particularly the role of negative frequency-dependent selection in the maintenance of variation in personality in a population of Great Tits *Parus major* in Westerheide, The Netherlands. The general expectation is that selection should favour the rarer phenotypes in a frequency-dependent manner. She approaches the problem using two data-sets of avian personality and fitness: long-term descriptive data (2000–2006) and two-years of experimental data (2007–2008).

Fucikova's thesis contains five research chapters. In the first chapter she investigates the relationship between two individual fitness components and individual social environment. In the second chapter, she further investigates whether negative frequency-dependent selection contributes to maintain variation in adult personality. In the third and forth chapters, she moves on to the juvenile perspective and examines whether negative frequency-dependent selection also acts on juvenile personality. In the final chapter, she experimentally tests the hypothesis that negative frequency-dependent selection is a major mechanism that maintains variation in personality.

The first research chapter (Chapter 2) investigates whether individual fitness is linked to the individual's social environment using seven years of behaviour and fitness data. She used the mean exploratory behaviour of all males neighbouring a focal individual as a measure of their social environment, and adult local survival and number of recruited young per pair as proxy for fitness. She found that reproductive success but not adult survival was correlated with neighbour personality. The direction of this relationship differed between years but was not related to beech-mass crop or population density. She concluded that neighbour personality is an important factor influencing individual fitness. Interactions between the recruits of the focal pair and either neighbouring adults or juveniles may explain the observed pattern. In Chapter 3, using the same data, Fucikova examined yearly selection acting on personality with focus on negative frequency-dependent selection. She analyzed variation in adult annual survival, reproductive success and an integrative measure of fitness in relation to the three-way interaction between the individual personality trait, individual social environment and year or sex. She also examined whether fluctuating selection acts on the personality of males and females. The results revealed complex patterns. In the analysis of adult survival, she identified at the individual level various forms of selection that differed between years (positive/negative frequency-dependent, directional selection or no selection). She also found fluctuating selection acting on male and female personality. However, unlike a previous study in the same population, these patterns were not related to beech-mass crop or population density. She concludes that variation in personality is likely maintained by a combination of different selection mechanisms, including fluctuating selection caused by environmental heterogeneity and frequency-dependent selection.

In Great Tits, high juvenile mortality occurs within the first weeks of independence, thereby creating potential bias in the behavioural types of birds that are recaptured in winter. To circumvent this problem, Fucikova developed a new 'personality' test that can be assayed during the nestling phase, i.e. before selection takes place. She describes in Chapter 4 a new method in which 'handling stress' (breath rate) is measured repeatedly when birds are 14 days and 6 months old. She showed for laboratory and wild individuals that this trait was repeatable within individuals over time although the direction of change in the stress response was opposite for nestlings and adults. She also showed that the handling stress response correlated positively with individual exploratory behaviour, and concludes that handling stress can be used as a personality measure for nestlings and that this test provides a tool to assess personality variation within and between nests. However, because little is known about the relationship between handling stress and other behaviours and because this measurement is likely to be influenced by catching method, caution must be taken when using handling stress as a proxy for individual personality.

Chapter 5 describes the processes involved in selection on juvenile personality using data from the behavioural tests performed in the nestling phase. By using the same approach as for adults, Fucikova investigated whether frequency-dependent selection acts on juvenile personality. Surprisingly, she showed that the earlier found effect of parental social environment on brood survival was not apparent at the individual level: the individual juvenile survival probability was not related to the social environment of their parents but was correlated to their own personality instead. 'Responsive' birds were more likely to survive and were subject to positive directional selection. Hence this study revealed that handling stress was a predictor for local juvenile survival and that variation in adult and juvenile personality was maintained via different mechanisms that likely are tied to age-related differences in life-history.

In Chapter 6 Fucikova experimentally tested whether negative frequency-dependent selection underlies variation in animal personality. For two years, 25% of the birds from the two extremes of the personality range of exploratory behaviour were removed from the study area. By altering the frequency distribution of the personality types, the authors created a 'slow' and 'fast' environment, which left scope for negative frequency-dependent selection to act on individual personality. Rarer phenotypes were expected to perform better in each type of social environment. Counter to the prediction, frequency-dependent selection was only found in one of the two years and differed in direction between males and females: slow females and fast males survived better in a fast environment while fast females and slow males survived better in a slow environment. In concordance with the previous descriptive chapters, this study confirmed that negative frequency-dependent selection is not a major mechanism maintaining variation in personality. The maintenance of variation in animal personality probably involves various forms of selection in combination with habitat heterogeneity and differences in individual life-history.

In conclusion, this thesis faces the challenge of investigating which forms of selection act on animal personality with a focus on frequency-dependent selection. By using a long term data set and by performing a unique manipulation of local social environment, Fucikova's work shows that no single mechanism can explain the maintenance of personality variation in a wild animal population. Due to fluctuations in local environmental conditions, including local social composition, and differences in individual properties, the nature of the selection mechanisms acting on personality vary between years, between age classes and life-history stages. This work stresses the importance of collecting longitudinal individual behavioural data and integrating them in an ecological context. Further investigations into how selection depends on the ecological context, such as local social environment, will be important to increase our understanding of the evolution of animal personality in complex natural situations.

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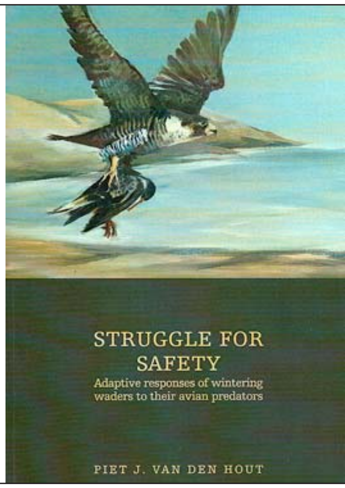
van den Hout P.J. 2010. Struggle for safety: Adaptive responses of wintering waders to their avian predators. PhD thesis, University of Groningen, The Netherlands. ISBN 978-90-367-4575-8. Paperback, 200 pp. Available at: http://irs.ub.rug.nl/ppn/330640917.



What comes to mind when reading 'waders' and 'predation' are studies on shorebirds (aka waders) and their invertebrate prey: what they eat, why, how much, what they do when there isn't enough, etc. Only a handful of studies have looked at shorebirds in their role as food for others. This is probably at least partly because it is very easy to observe a foraging shorebird but much harder to actually witness a shorebird being attacked by a predator. Nevertheless, predation – regardless of trophic level – has increasingly been integrated as a central concept of population ecology. The most obvious effect of a predator on its prey is the mortality inflicted by a successful predation event. But predators also have a somewhat more subtle, non-lethal, effect on their prey as individuals make behavioural and even physiological adjustments to reduce the risk of being eaten. As Piet van den Hout shows us, low predation mortality is no proof of low predation impact, but can instead be an indication that most individuals avoid being depredated by employing effective anti-predation behaviour.

In his dissertation, van den Hout examines how top-predators (those at the apex of the food chain) shape prey populations by assessing the costs of predation for shorebirds, and how and why these costs vary. This was done by combining experimental work at the Royal Netherlands Institute for Sea Research (NIOZ) with field observations at the Banc d'Arguin in Mauritania. The Banc d'Arguin is not only a major wintering site for millions of Arctic breeding shorebirds, but importantly, the high site-faithfulness and relatively small home ranges of shorebirds at the Banc d'Arguin proved to make systematic research on raptor-shorebird interactions much easier than in the Dutch Wadden Sea.

Chapter 1 provides a general introduction to the theoretical framework of predator-prey interactions, and to the study organisms and sites. The next two chapters are 'appetizers' and give examples of two predation-reducing behaviours, namely flocking and vigilance. Chapter 2 features Coots *Fulica atra* overwintering in Keoladeo National Park, India. While feeding on aquatic plants, Coots are vulnerable to falling prey to Ganges Soft-shell Turtle *Aspideretus gangeticus*. To dilute the individual risk of predation, they form flocks of dense flotillas that behave like a super-organism. Chapter 3 describes head-tilting in Baird's Sandpipers *Calidris bairdii* and Puna Plovers *Charadrius alticola* foraging on a salt plain in Chile. The benefits of this behaviour in terms of anti-predator vigilance are discussed.

Chapters 4–6 explore the effects of predators, both lethal and non-lethal, on shorebirds at the Banc d'Arguin. Chapter 4 examines the relative risk of predation for several shorebird species that are hunted by large falcons. Contrary to what one may expect, shorebirds were not hunted relative to their abundance at the site. Falcons preferentially attacked both small flocks and those species that foraged close to shore, as they take advantage of the low dunes bordering the mudflats to launch surprise attacks on unsuspecting individuals. There was also an effect of age on the risk of being hunted: juvenile Red Knots *Calidris canutus* were killed ten times more frequently than adults, presumably because the juveniles use riskier habitats. Chapter 5 introduces the trade-off between food and safety. Animals with low energy reserves are predicted to accept higher predation risk in return for higher energy gains. Hence, an individual that forages in an area that is both more dangerous and offers less food appears to behave maladaptively. However, van den Hout shows that this is not necessarily the case. In Red Knots, the trade-off between food and safety appears to be mediated by individual foraging skills and by the ability to compete with others. Individuals that are less skilled in foraging in seagrass habitat and that are outcompeted by dominant conspecifics will thus achieve higher feeding success in the nutritionally poor and dangerous nearshore areas than in the richer and safer offshore seagrass habitat.

Not only do Red Knots take predation risk into account when deciding where to forage, but in Chapter 6 we also learn that they have 'safety careers'. Young animals must learn to efficiently allocate time and energy to various activities and still maintain a balance between the risks of predation and starvation. Juveniles are often found segregated from the main flocks in areas with a high occurrence of predator attacks. By monitoring habitat use of individually marked birds in age classes of up to 11 years old, van den Hout was able to show that Red Knots increased the use of safe foraging areas as a function of age. This interesting finding was not an effect of age-differential survival, but a result of increased movement to safer habitat with age, which suggests a learning process. Thus, throughout their life, individual Red Knots gain increased safety from predators, i.e. they have 'safety careers'.

In Chapters 7–9 we learn about adaptive flexible phenotypic responses to predation risk. To cope with changes in the environment, organisms not only show behavioural but also phenotypic adjustments, e.g. in the digestive tract. Chapter 7 presents the first evidence of birds adjusting their flight machinery in response to predation risk. In an indoor experiment, Ruddy Turnstones *Arenaria interpres* were subjected to an unpredictable daily appearance of a model of either a flying raptor or a small gull, which served as a control. Ruddy Turnstones experiencing the simulated threat of a raptor refrained from feeding after the disturbance for longer than when exposed to the gull model. Pectoral muscle mass increased within a few days to changes in the perceived threat of predation, while lean mean remained constant. As a result, pectoral muscle mass was 3.6% higher than aerodynamically predicted for constant flight performance, demonstrating that perceived risk factors may directly affect organ size.

Chapter 8 introduces the threat-sensitive predator avoidance hypothesis, which states that prey should match the intensity of their anti-predation response to the degree of threat posed by a predator. The predictions were tested on Red Knots, which indeed adjusted the level of both vigilance and escape flight according to the perceived risk. Escape flight, which is the most important means of escape from predators for most birds, is also the main topic of Chapter 9. Fat stores protect birds against starvation, but they may also decrease their escape performance due to increased wing loading. To compensate for an increase in wing loading, birds can independently decrease body mass or increase pectoral muscle mass. In Chapter 9, shorebird species foraging close to shore and far away from shore are compared. It is hypothesized that nearshore foragers should respond to increased predation by increasing their pectoral muscle mass to promote rapid escape. Farshore foragers, on the other hand, should decrease body mass to improve agility for manoeuvring escape. The outcomes of their experiments with Red Knots and Ruddy Turnstones were consistent with these predictions.

In conclusion, this very nicely written thesis makes an important contribution to our understanding of how shorebirds cope with predation risk, a hitherto somewhat neglected piece of their life-history puzzle. While raptor-fans may not agree with the author's description of them as 'boring, elusive creatures lurking behind the scenes for a chance to get a meal', every reader of this thesis would surely concur that they have 'tremendous influence on the structure and dynamics of shorebird populations and communities'. The author has convincingly demonstrated that shorebirds are able to mitigate predation risk by making behavioural and physiological adjustments, and that the decisions regarding food and safety trade-offs are dependent on individual abilities. Predator-prey interactions have usually been studied on the population level, but his work has shown that instead we might have to focus on the level of the individual to fully understand these interactions. Finally, I should add that reading this thesis is made particularly enjoyable by its truly beautiful photographs of falcons and their shorebird prey.

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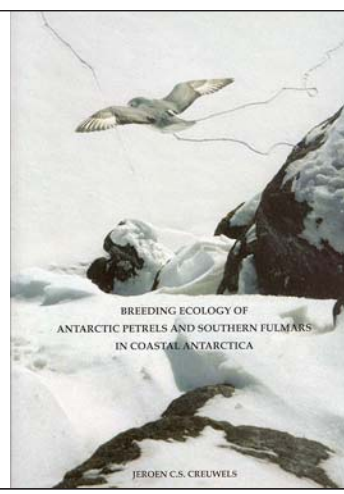
Creuwels J.C.S. 2010. Breeding ecology of Antarctic Petrels and Southern Fulmars in Coastal Antarctica. PhD thesis, University of Groningen, The Netherlands. ISBN 978-90-367-4705-9. Paperback, 208 pp. Available at http://irs.ub.rug.nl/ppn/330728350.



In 1982 the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR) came into force to conserve marine life of the Southern Ocean by regulating krill harvesting to make it sustainable. One of the tools for monitoring effects of fishery activities was the CCAMLR Ecosystem Monitoring Program (CEMP). In this program data is collected on harvestable resources and on the dependant predator species. In addition to several species of penguins, fur seals and albatross, the Antarctic Petrel *Thalassoica antarctica* is designated as indicator species within the CEMP. Many seabirds, particularly food generalists with a large foraging radius such as the fulmarine petrels (Procellariidae), are ideal indicators of a variety of aspects of ecosystem dynamics. Thorough understanding of the breeding and feeding ecology of these species is a prerequisite for a successful monitoring program and this is what the thesis of Jeroen Creuwels aims to provide. It contains eight chapters (five of which were published as articles in peer-reviewed journals) and two boxes investigating two fulmarine petrel species, the Antarctic Petrel and the Southern Fulmar *Fulmarus glacialis*. Step by step he describes many fundamental aspects of the breeding ecology of these species and some unexpected phenomena and consequences.

Chapter 1 introduces the Antarctic ecosystem, the group of fulmarine petrels and a paragraph is dedicated to the two studied species. Creuwels aimed to describe and quantify the breeding biology of Antarctic Petrels as background for the CEMP. For comparison with Antarctic Petrels, similar data was collected from a sympatric species, the Southern Fulmar. A second aim of the study was to explain a decline in breeding success of the Antarctic Petrels at the same location. The results shown in the thesis are from field data collected during three breeding seasons on Ardery Island in the Australian sector of Antarctica.

The breeding phenology of both species is examined in Chapter 2. Here, two species-specific breeding strategies are unravelled by studying a large proportion of individually recognizable birds within the study colony. The length of the breeding period was similar for both species, however, Antarctic Petrels started almost three weeks earlier than the Fulmars. Furthermore, Antarctic Petrels bred more synchronized, made longer foraging trips and spent less time guarding their chicks than Southern Fulmar. This implies that, if breeding failed, it would occur much earlier in the season for Antarctic Petrels (egg-phase and just after hatching) than for Southern Fulmars (chick phase). In the discussion Creuwels poses that differential flight behaviour might be causing these different breeding strategies with fulmars having more difficulties to cross large sea-ice areas than the Antarctic Petrels.

Box 1 gives an insight in the timing of moult within the annual cycle of the two species. Southern Fulmars started moulting substantially earlier than Antarctic Petrels. This delay in moult enables the 'high-wing-load' Antarctic Petrel to bring heavier meals from long provisioning flights to their demanding chicks. Due to their size and later breeding season, Southern Fulmars could not avoid overlap between moult and breeding, which resulted in prolonged colony attendance at the end of the season.

Chapter 3 describes the investment of petrel parents through the eyes of their chicks. Creuwels investigated how provisioning of the chicks influenced growth in both species. This was done with a self-developed automatic weighing system to study chick growth, meal size and feeding behaviour. Fulmars delivered meals to their chicks twice as often (every 14 h) compared to Antarctic Petrels and more so during the day, whereas Antarctic Petrels delivered more in the morning and evenings. Meals of Antarctic Petrels were not larger but had a higher energy density than those of the fulmars.

Chapter 4 looks into the consequences of weather conditions, in particular snow cover, on the breeding success of Antarctic Petrels. In prior seasons remarkable reductions in breeding success and survival were found. In Creuwels' first field season a possible reason for these reductions was discovered. Unlike earlier seasons, the island, including the rock ledges where the Antarctic Petrels breed, was covered under a thick layer of snow. Under these circumstances Southern Giant Petrels *Macronectus giganteus* were able to crash-land in the snow and walk towards their smaller cousins, making them an easy kill. The subsequent panic in the colonies made the eggs available for predation by South Polar Skuas *Catharacta maccormicki*, causing a further reduction of breeding success. Predation stopped after snow melt. In the discussion Creuwels suggests that this unexpected chain of events might have site-dependent implications of the locally expected increase in precipitation due to global climate change.

In Chapter 5 Creuwels makes a nice side-step from the smaller fulmarines towards the largest species within the fulmarines. Following the results of Chapter 4, a more in-depth study of the main predators of Antarctic Petrels was made: the Southern Giant Petrels breeding on nearby islands. A notable search into grey literature, unpublished field notes and station logs, combined with inventive analysis techniques revealed that many of the previously found population trends of the species on the Frazier Islands were mainly due to inconsistent survey methods. The results show a recent increase of the breeding population of 35%, although this figure falls within the range of periodic fluctuations seen in a long-term stable population. In the discussion a proposal for standardized census methods for this disturbance-sensitive species, is introduced.

Chapter 6 illustrates a remarkable and slightly macabre aspect of breeding in a hostile environment like the Antarctic. Three banded Southern Giant Petrels were found to have died while incubating. Generally it is assumed that long-lived species prefer abandoning their clutch to endangering their own life. The reason behind this is, according to Creuwels, that the Southern Giant Petrels on the Frazier Islands breed at the southernmost limit of their breeding range. In these colonies the breeding period is strongly constrained by environmental conditions and thus birds have to deal with less favourable conditions than individuals in more northern colonies. In the case described here, birds were trapped in a blizzard and covered in heavy snow. Breeding birds covered in snow is a common sight in the Antarctic but when the snow extent is too heavy or lasts too long, birds get trapped and will freeze or starve to death.

Chapter 7 deals with a fundamental aspect of Southern Fulmars' ecology, giving a review of published and unpublished information on the breeding distribution and population size around the Antarctic continent. Creuwels estimated a minimum global population of 400,000 breeding pairs on 73 locations. Due to survey methodology this certainly is an underestimation of the global population. Moreover, because a relatively small area of the Antarctic is (regularly) surveyed, several undiscovered colonies are expected to be found in the future. Extrapolating these numbers for the whole Antarctic, a global population of 1,000,000 breeding pairs is expected of which 72% is nesting on islands in the Scotia Sea and south Atlantic.

Box 2 gives results of a pilot study on the location of foraging grounds of both Antarctic Petrels and Southern Fulmars. Nowadays, numerous studies using GPS-loggers and other positioning devises dominate the seabird literature. However, in the season 1996, when this study was done, the technique was still new for use on these relatively small bird species. Compared to devices available now, 'huge' data-loggers were fitted on both species tracking their movements during foraging. Clear separation of foraging areas of both species was found, with Antarctic Petrels travelling much further away from the colony. Despite the small sample size this box gives a nice insight into the movements at sea of the study species.

In the final chapter the results of all studies are summarized, discussed and conclusions are drawn. It is indeed, as Creuwels states, remarkable that despite the many differences in their strategies, the two closely–related petrel species achieve a similar reproductive output. Differences in breeding success, time constraints in the breeding season, adult survival, contrasting provision strategies, breeding distribution and foraging areas of both species are discussed. Consequences of changes in climate on sea-ice and food-availability remain difficult to predict, but Creuwels' thesis shows that local weather changes already have substantial implications for the locally breeding petrels. Therefore, to assess the consequences of human activities taking place in the foraging areas on the basis of breeding data is difficult, since many parameters of the breeding ecology seemed to be heavily influenced by natural factors. Creuwels suggests that more detailed research on foraging strategies and breeding ecology is needed to get a better grasp on these processes.

Jeroen Creuwels' thesis is a comprehensive document on wide-ranging aspects of the breeding ecology of two Antarctic fulmarine petrels. It also shows how the different breeding strategies of these two species have very different ecological implications. It gives in-depth background knowledge, useful for better interpretation of population monitoring and breeding success censuses of birds in the Antarctic. It is clear that with dedication and persistence, Creuwels managed to compile impressive results for two fascinating bird species living in a fascinating environment. Last but not least, the beautiful pictures throughout the thesis need to be mentioned as well. They add visual delight to a pleasant read.

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Van Turnhout C.A.M. 2011. Birding for science and conservation. Explaining temporal changes in breeding bird diversity in The Netherlands. PhD thesis, Radboud University Nijmegen, The Netherlands. ISBN 978-90-9025945-1. Paperback, 219 pp. Available at http://www.ru.nl/publish/pages/607962/2011vanturnhout_phdthesis_110315.pdf.

Bird watchers, ecologists, conservationists, nature lovers and laymen – there are many who want to know how our bird populations are doing. Therefore, most European countries have a Common Bird Monitoring Scheme (CBMS), where hundreds (or thousands) of volunteers count birds according to strictly standardised routines. From that we learn which species are increasing or decreasing in numbers. The CBMS often have sister projects, Breeding Birds Atlases, which describe where in a country the birds are breeding. When an atlas is repeated, with a decade or two in between, additional information is gained regarding patterns of population changes. Until recently, these activities have been carried out mainly outside the academic world, or at least with only a low academic status. The PhD thesis of Chris van Turnhout is a beautiful example of how this now is changing. Combining advanced statistics with solid knowledge about the ecology of Dutch birds, van Turnhout "describes, quantifies and explains changes in breeding bird diversity in The Netherlands the last decades". The thesis is also a tribute to all the volunteers working within monitoring and atlas programmes who are birding for science and conservation.

In the Introduction we are told about the general history of bird monitoring and how birds have been used as monitors of environmental change. We are also made aware of the key importance of volunteers. Around the world, thousands of birdwatchers take part each year in systematic bird counts, coordinated by professional biologists that also take care of the often complex analyses – a very successful symbiosis known as "citizen science". More specifically, this chapter gives a thorough and insightful description of the history of Dutch monitoring, as well as the historic changes of Dutch landscapes and bird communities. For example, we are presented with the surprising and counter-intuitive fact that, despite the enormous anthropogenic effects on the Dutch landscape over the last hundred years, fourty-seven species have entered the breeding bird fauna since 1900, whereas only five have been lost!

When the Dutch CBMS started in 1984, it was strictly standardized *how* volunteers should count the birds, but they were allowed themselves to decide *where* to count. The latter is a potential weakness that the Dutch CBMS shares with several first-generation monitoring schemes of Europe. Therefore, new schemes have been started around Europe, where the surveyors are told also where to count. The methodological weakness of the first schemes is that the population trend of a species may differ between different habitats and areas. For example, if many counts are carried out in a small area where the birds are doing well, and only few counts in a much larger but poorer area, the national trend may look too favourable. In Chapter 2, van Turnhout and his co-workers try to correct for this by refining the statistical analysis. They found that the new, more representative, trends are often slightly more positive or negative than the uncorrected trends, but that differences are small and can be dealt with. The conclusion is that the scheme from 1984 should be continued.

In Chapter 3, van Turnhout and co-workers dive into the population development of 23 typical marshland birds since the 1950s, combining data from several different bird surveys. Despite the dramatic changes that have taken place in the past few centuries, where wetlands have contracted and deteriorated in many ways, about half of the typical marshland bird species have increased in number, and only slightly less than half have decreased in number. Species typical of reedbeds over standing water have declined most strongly. The effects of various changes in land-use are discussed, such as changes in water table management, falling water tables and eutrophication.

The following two chapters deal with changes at the bird community level, that is, large-scale patterns of diversity. Based on the first (1973–1977) and second (1998–2000) Dutch atlases, Chapter 4 reveals some striking patterns in the Dutch avifauna. Overall, species richness and biodiversity increased between the two atlases, and more species were increasing than decreasing in range and abundance. However, these changes were not evenly distributed over the country: species richness increased in the previously poorer western parts, and decreased in the previously richer eastern parts. Overall this has led to a homogenization of the fauna, that is, bird communities look more and more the same in different regions.

Do species that are doing poorly have some common characteristics of their ecology? This is investigated in Chapter 5. Van Turnhout and his co-workers investigated the population trends of 170 species, and looked at whether they could be grouped according to 25 different life-history, ecological and behavioural traits, including factors such as body mass, clutch size, timing of spring arrival, migration behaviour, main diet and nest location. They found that ground nesting and late spring arrival characterizes declining species, which suggests that agricultural intensification, eutrophication and climate change are the driving factors. In contrast, herbivores, residents, short-distance migrants and large species are often increasing. The authors suggest that for conservation to be successful, it should be targeted on the traits identified as responsible for a species' population change.

Chapter 6 focuses more specifically on the effect of climate change on bird numbers. The analysis was confined to insect-eating birds living in forest and/or marshes. The pattern found was that long-distance migrants in the forest declined strongly, but they did not decline in marshes. The explanation is the following. The food peak during breeding, crucial for the successful rearing of young, has only a short duration in forest and a much longer duration in marshes. Long-distance migrants have problems adjusting their arrival to the ever earlier peak in food abundance in forest, whereas the marshes are more forgiving for a late arriving bird. The fact that residents and short-distance migrants in both habitats were doing relatively well suggests that the habitat effect among long-distance migrants was not solely due to forest having become a poorer habitat.

Whereas the papers so far dealt with overall patterns in species abundance and population trends, Chapter 7 adds another dimension to the use of monitoring data. It is a type of analysis that is carried out much too seldom, but crucial to conservation ecology. Large amounts of money are spent on habitat management and nature restoration around Europe without being properly assessed. Did the measures taken have the effect we wanted? In this case, data from around 200 Dutch CBMS sites are used to evaluate the long-term effects of flood plain restoration along the great rivers in the south. The sites were distributed in rehabilitated and non-rehabilitated areas. Among the 93 bird species investigated, 35 species did better in rehabilitated sites, and only 8 did worse. However, it should be noted that species of high conservation concern did on average not benefit more than non-protected species on average. The authors conclude that artificial rejuvenation of Dutch floodplains will be necessary also in the future, to secure the conservation of characteristic river birds.

Van Turnhout ends his thesis by describing the efforts taken to run a sustainable bird monitoring scheme in The Netherlands. Whereas schemes and analysis methods must now and then be developed and refined, to fulfil new demands and information needs, it must also be comparable backwards in time. And of course, it must fulfil the needs and wishes of the most important part of the scheme, the volunteers. From a Swedish perspective, Dutch bird monitoring seems to have full and perfect coverage already. We often refer to the Dutch situation as: "– In The Netherlands, each bird is counted once a month". Sweden has a population density only one twentieth of that in The Netherlands and in the most northern part, twice the size of The Netherlands, there are only about 20 bird watchers. Nevertheless, the basic problems seem to be the same, and it is reassuring to know that Dutch monitoring is ever improving, and that a sound and solid understanding of the mechanisms driving the bird populations are emerging.

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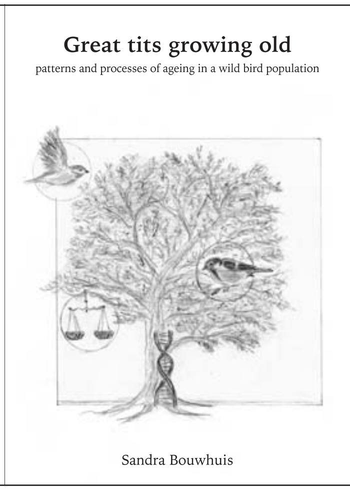
Bouwhuis S. 2011. Great tits growing old: patterns and processes of ageing in a wild bird population. PhD thesis, University of Groningen, The Netherlands. ISBN: 978-90-367-4812-1. Paperback, 164 pp.



To us humans, ageing is evident. With age we gain more wrinkles, lose physical strength and mortality chances increase. For a long time ageing was recognised only in our own species and in large animals in captivity. Especially in the wild and in short-lived species ageing was presumed to be absent. In her thesis, Sandra Bouwhuis adequately falsifies this notion studying a wild population of Great Tits *Parus major* in Wytham Woods, Oxfordshire, UK. In Chapter 6 she shows, using capture–recapture histories, that annual survival chances decline from 50% at ages 1 to 3 to almost 0% at age 9. Also, reproductive performance declines steeply after 3 years of age in female Great Tits (Chapter 2). The scale of the data analysed in this thesis, gathered in Wytham during half a century, makes these findings robust and valuable. Moreover, in Chapter 3 Bouwhuis shows that the decline in reproductive performance of Great Tits is not unique to Wytham, but also occurs on the Dutch island of Vlieland. Interestingly, the patterns of senescence found in Wytham and on Vlieland are indistinguishable even though the populations differ in a large number of aspects, such as immigration rate, occurrence of multiple breeding, breeding density and clutch size. Bouwhuis suggests that the demographies of the two populations, with highly similar average breeding age and reproductive lifespan, underlie the selection pressure shaping reproductive senescence patterns.

Starting from this strong basis of evidence substantiating senescence in the wild, Bouwhuis shows intriguing relationships explaining individual differences in reproductive senescence. In Chapter 2, Bouwhuis shows that females with longer reproductive lifespans outperform other females at all ages in terms of number of recruits produced. This indicates an effect of female quality which interestingly only becomes apparent at the level of recruits. Clutch size, brood size and number of fledglings produced did not differ significantly between females with different reproductive lifespans. This suggests differences in quality of fledglings or in post-fledging care and/or differences in emigration rates from the study area. Indeed, Bouwhuis shows that natal dispersal distance is shorter in recruits from females with longer reproductive lifespans. Possibly complementary to this finding, females that were born within the study area outperformed immigrants but also only with regard to recruits.

In Chapter 4, variation in reproductive performance of recruits is linked to the age of their mothers when they were born. Intriguingly, daughters from young mothers perform slightly worse during early life but live on to slightly outperform daughters from older mothers at older ages (>3 years). These different patterns of reproductive performance with age did not result in differences in lifetime reproductive success, possibly suggesting a stable equilibrium of different strategies. In laboratory animals there is evidence that offspring from older mothers have a shortened lifespan, coined the Lansing-effect. In the natural population of Great Tits that Bouwhuis studied there is however no such effect; reproductive lifespan was not affected by maternal age. Future study of natural populations may confirm that this is due to a laboratory artefact or has other unknown causes.

The associations of reproductive senescence with natal conditions (hatching date, sibling number, natal year quality, natal density, natal beech mast, and maternal age) are the subject of Chapter 5. Bouwhuis shows that there are no significant associations between these parameters and the number of recruits produced at ages 3–9, nor with the decline with age in the number of recruits produced. In this chapter Bouwhuis also tests the disposable soma theory by examining effects of early reproduction. The disposable soma theory states that investment in reproduction is at the expense of somatic maintenance, thereby accelerating ageing. In support of this theory, females that produced more fledglings early in life showed an accelerated decline in fledgling reproduction at older ages. Lifetime reproductive success increased with increasing early life fledgling production, suggesting that the return on investment in early life outweighs its accelerating effect on reproductive senescence.

Another theory of ageing is the rate of living theory, which states that high metabolism is at the expense of lifespan. This is also in accordance with the free radical theory of ageing, which assigns free radicals, that are inevitably produced during aerobic metabolism, as the main agent causing ageing. Higher rates of metabolism are thus predicted to accelerate senescence. In winter, Bouwhuis measured basal metabolic rates (BMR) of nearly 700 male and female Great Tits. Using the parameters she earlier showed to be associated with reproductive senescence (maternal age, immigrant status and reproduction in early life) as proxies for rates of reproductive senescence, she tested this hypothesis in Chapter 7. BMR rate was repeatable and declined with age, but was not associated with these proxies. Measurements taken on the same birds in winter and in the breeding season, measured in a smaller subset of tits, were however not repeatable. It therefore remains possible that BMR in the breeding season is associated with reproductive senescence.

Although senescence is detectable and substantial in the natural populations of Great Tits that Bouwhuis studied, she also reports that the summed fitness costs of reproductive and survival senescence are a mere 4%. Compared to other species, with fitness costs ranging from 5% in the Sparrowhawk to 25% in Red Squirrels, this is relatively low. The proportion of these costs caused by survival versus reproductive senescence is relatively constant across species, ranging between 0.44 and 0.66. Explaining this similarity and differences between species in fitness costs of senescence is a promising venture to reveal possible universal mechanisms of senescence. The similarity between Vlieland and Wytham in reproductive senescence and the lack of associations with natal conditions might actually be a consequence of the dominant importance of reproduction in early life over reproductive senescence. Theoretically it is actually an open question whether senescence is expected to cause considerable fitness costs, given that intrinsic mortality is selected to match expected extrinsic mortality chances.

The thesis of Bouwhuis is great in showing how carefully maintained long-term databases together with high quality analysis can produce great progress. Bouwhuis has built a firm basis of knowledge concerning reproductive senescence in Great Tits. She has also unravelled intriguing new insights into detailed mechanisms of senescence. The effects of female quality, early reproduction, maternal age and lack of an association with BMR, all warrant additional research. By calculating fitness costs of senescence and taking this to a between species level, Bouwhuis has broadened the impact of her thesis on the study of senescence even further.

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