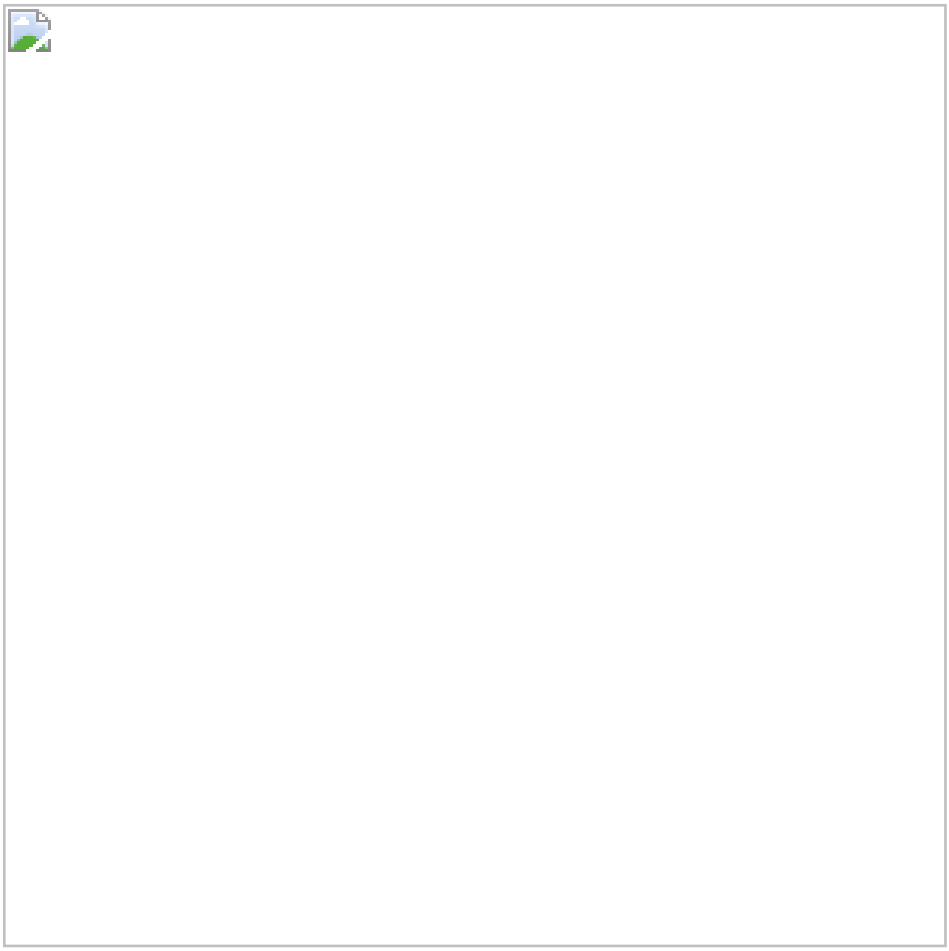

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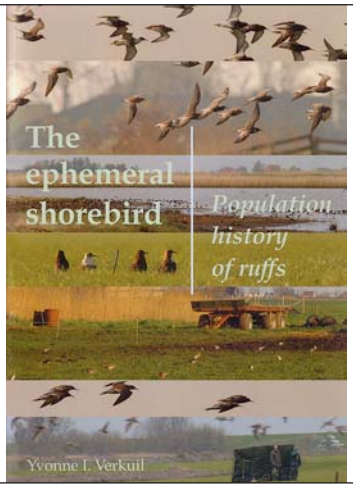
Verkuil Y.I. 2010. The ephemeral shorebird: Population history of ruffs. PhD thesis, University of Groningen, The Netherlands. ISBN: 978-90-367-4456-0, paperback, 192 pp. Available at http://irs.ub.rug.nl/ppn/327704772



The Ruff, *Philomachus pugnax*, is a very special bird, and the University of Groningen has produced three PhD theses on the behaviour of this exceptional species. The first thesis was presented by my wife, Lidy Hogan-Warburg, in 1966. Using standard ethological methods of observation, she described the social behaviour of the birds on their traditional breeding grounds (leks). She discovered that there were two kinds of males, called independents and satellites, which differed in both their behaviour and plumage. Among other conclusions, she argued that these two types of male were an expression of a balanced, genetically-based, behavioural polymorphism, a suggestion that was highly controversial at the time. A few years later, Johan van Rhijn (1973) presented the second thesis. Using both field observations and analysis of film, he looked in quantitative detail at the behavioural dimorphism to examine both its causation and biological significance. His results were also compatible with a genetically-based balanced polymorphism, but it was not until many years later that Dove Lank (Lank *et al.* 1995) was able to show conclusively that the genetic hypothesis was correct.

Yvonne Verkuil was also interested in genetic aspects of the Ruff's behaviour – primarily migratory behaviour and its evolution. Her thesis describes seasonal migration and changes in range occupation of Ruffs, and presents a comparative analysis of the population genetics of Ruffs and related shorebird species. It addresses two hypotheses postulated about shorebird evolution. The first is whether flexible routing or evolutionary constraints better explain migration (*inflexible migration hypothesis* – Sutherland 1998). The second is whether genetic variation in Ruffs and other inland, freshwater-adapted shorebirds is higher than in marine, coastal shorebirds (*habitat dichotomy hypothesis* – Piersma 2003). Her results are largely based on sampling migrant Ruffs en route from West Africa to the breeding grounds in northern Western Europe.

Verkuil's thesis comprises eight manuscripts, published or submitted, plus an introduction and synthesis. The first three papers investigate the molecular ecology of Ruffs using analysis of DNA sequences. The first shows that Ruffs have evolved a novel mitochondrial gene order compared to all other shorebirds that have been studied. This includes a duplication of the control region, a site for initiation and termination of DNA replication, which may act as a repair mechanism to avoid transcription error. Because Ruff populations are genetically variable, though apparently geographically unstructured, such morphometric variation indicates that segregating selective pressures are acting in areas within its vast migratory and breeding range. This fact becomes important in the context of the second paper.

Ruffs, an inland species, are generally considered to be morphologically uniform across their vast range, in contrast to long-distance migrant shorebirds living in coastal habitats. The second paper investigated the correlation between habitat and genetic make-up. Ruffs

were sampled at seven breeding locations in Scandinavia and Russia, two migration routes through Europe and two wintering areas in Northwest Europe and Africa. The genetic markers examined showed that Ruffs, indeed, have no geographically isolated lineages. Nonetheless, analysis of migrants passing through The Netherlands revealed significant size-related differences in timing of migration: shorter-winged birds migrated through later than larger birds, and are more likely to be found in eastern breeding locations. These results suggest that population structuring might be evolving.

The behavioural polymorphism in male Ruffs has raised the question of whether Ruffs are also genetically polymorphic. In the third paper, genetic variation was examined in both the mitochondrial genome (maternally inherited) and the nuclear microsatellites (biparentally inherited). As expected, but never earlier confirmed, genetic variation in the maternal genetic markers was high compared to other sandpipers, but in the biparental genetic markers was relatively low. In Ruffs, low genetic variation in the biparental genome is an effect of the lekking behaviour of males, which produces a skew in lifetime reproductive success of males, but not of females. This skew also explains the strong sexual selection on male Ruffs.

The second part of the thesis examines the migration ecology of Ruffs in four papers. The first paper analyzes a large set of morphometric data collected over many years in different countries and seasons for the occurrence of 'faeder' Ruffs (males that are female look-alikes). On ecological grounds, one would expect their migratory behaviour to track that of females. In fact, they were found to associate with males both during the winter and when migrating. The second paper presents the results of a type of validation study in which resighting data collected from males that had been caught, tagged, and measured were analyzed. The question was the reliability of estimates of staging duration (time spent in The Netherlands between wintering grounds and breeding grounds – generally about three weeks). Happily, most estimates proved to be reliable and there was very little effect of catching the birds. This confirmation was necessary for the interpretation of the results of the next two papers.

In many ways, the results of the third and fourth papers in this part are the most important contribution of the thesis. In the third paper, data were analyzed that had been collected by Verkuil and her many collaborators in the staging areas in The Netherlands (Fryslân) and Belarus (Pripyat river flood plains). These included number of individuals present during the migration period between late March and early May, from 2001 to 2010, body mass increase during the stay in the staging area, and resightings of marked birds. In The Netherlands additional measures of length of stay and moult stage were analyzed when available. The analysis shows that, during the period studied, the number of migrants using the Fryslân staging area declined by more than two-thirds (an estimated loss of 15,000 individuals), length of stay in the staging area was reduced by several days, and the increase in body mass during the stay also declined drastically. In contrast, in Pripyat, the number of migrants increased by about 20,000 individuals, and increase in body mass remained constant. After full consideration of several alternative interpretations, Verkuil concludes that the decline in migrants in The Netherlands has been induced by loss of habitat quality in the staging area due to agricultural intensification. The evidence strongly suggests that the birds are changing their migration route and are now using more easterly staging areas. Analysis of data collected in the high Arctic by Russian workers, and presented in the fourth paper, shows that the redistribution of breeding Ruffs cannot be explained by temperature change on the breeding grounds.

The final chapter is a discussion of the significance and implications of her results. With respect to the *inflexible migration hypothesis*, Verkuil concludes that migration can be highly flexible in shorebirds. Sutherland (1998) had proposed that migration routes would generally be genetically constrained in shorebirds where juveniles migrate independently of their parents. Ruff juveniles do migrate independently of their parents, but the data of many colour-marked individuals using routes 1500 km apart show that Ruffs are not held back by genetic programs from exploring alternative routes. It remains to be discovered how the experience of an individual Ruff leads to taking a different route. If a bird has a bad experience this year in the fields of Fryslân, how will it 'know' next year to follow a conspecific who had a good experience in Pripyat? Verkuil does not discuss this problem. Another interesting point is that although the Ruff migration has flexible aspects, the dimorphism in male sexual behaviour is highly inflexible. This indicates to me that we must be much more careful than is often the case in thinking about genetic control.

With respect to the *habitat dichotomy hypothesis*, Verkuil has a long discussion of whether genetic variation in Ruffs and other inland, freshwater shorebirds is higher than in marine, coastal shorebirds. Although many species follow this general rule, there are several significant exceptions, including golden plovers and Bar-tailed Godwits. After detailed consideration of

many reasons for these exceptions, she proposes an additional hypothesis to explain her results: wintering at northern latitudes would lead to frequent population fluctuations and thus reduce genetic variation.

Finally, the Dutch summary ("De ongrijpbare kemphaan: populatieveranderingen van toen en nu") presents a delightful and easily accessible review of her main results in a general ecological context.

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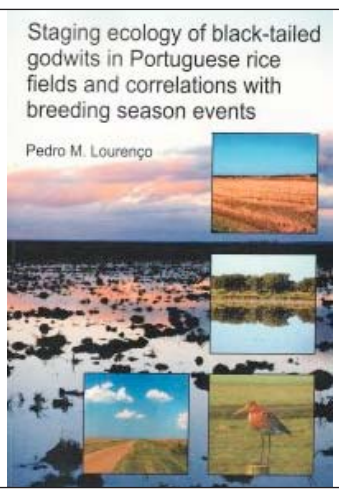
Lourenço P.M. 2010. Staging ecology of black-tailed godwits in Portuguese rice fields and correlations with breeding season events. PhD thesis, University of Groningen, The Netherlands. ISBN: 978-90-367-4289-4, paperback, 188 pp. Available at http://irs.ub.rug.nl/ppn/328429503.



Many migrating birds do not cover the distance between wintering and breeding grounds in one single flight, but stage at stopovers in between. Which stopovers to use and how long to stop are intriguing questions, but these are difficult to address. Even more difficult to study are the consequences of these stopover decisions on subsequent survival and breeding success.

For many bird watchers in The Netherlands spring starts with their first observation of the year of Black-tailed Godwits *Limosa limosa*. Reading this thesis gives you insight into the events that happen in the months before the godwits' arrival at the breeding grounds. In this thesis, Pedro Lourenço demonstrates how much can be learnt when birds can be recognized individually. He cleverly uses the Black-tailed Godwits that were colour-ringed both in the Netherlands and in Iceland in order to study their stopover ecology in Portugal. Through the colour-rings he could distinguish between the two subspecies. This comparison is interesting because of the different population developments. While the nominate population in The Netherlands declined by 50% since the 1960s, the *islandica* population showed a steady increase. Black-tailed Godwits mostly winter in western Africa, but return northward early, staging in Iberia (Spain and Portugal) from December to March. This is especially true for the continental Black-tailed Godwits, nearly all of which stage in Iberia in spring.

Lourenço showed that Icelandic Black-tailed Godwits appear to forage primarily in estuarine habitats, whereas the nominate subspecies mostly uses rice fields. The numbers using rice fields decreased by 40% since 1990, reflecting the changes at the western breeding grounds. Interestingly, in estuarine habitats the godwits ingest animal prey, whereas those in rice fields eat plant material, primarily rice grains. The suggestion is made that this habitat segregation therefore has a physiological basis, an hypothesis well worth exploring further, because in many more cases a switch from animal to plant diets (or *vice versa*) seems problematic.

Nowadays rice fields represent 15% of world's wetlands, and currently form an important habitat for wetland birds. By comparing godwit densities in rice fields under different management regimes, it was borne out that godwits prefer flooded, recently ploughed fields, where rice grain abundance was highest. Presumably, rice grain depletion by other granivorous species is more rapid in drier, unploughed fields. This findings leads to clear management recommendations in order to maintain the function of rice fields (read: these former natural wetlands) to support wetland birds.

While godwits were present in Portugal from December till March, individual staging periods averaged around three weeks. The turnover at the stopover site turned out to be considerable. The estimated number using this staging site was therefore 20–30% higher

than the peak number. That the peak number at a staging site is a poor reflector of the real number stopping over is probably a general phenomenon. In total, 38–44% of the breeding population of western godwits is staging in the lower valleys of the Tejo and Sado rivers in Portugal.

In his study of site selection and resource depletion, Lourenço made two assumptions that in my opinion are questionable. First, he assumed that a patch should be abandoned when the local intake rate falls below the required level to balance the current energy budget. However, Charnov's marginal value theorem actually predicts that a forager should leave a patch as soon as the local intake rate falls below the average that can be obtained in the environment. This could be well above the level at which the costs are balanced. Lourenço states himself that a staging bird is expected to have an energy surplus in order to build up reserves. In fact, the calculated intake rate was 40% higher than the daily energy requirement. Second, he assumes that ideal and free foragers would distribute themselves proportionally to the food abundance in each patch (foragers and prey "match"). This assumption however only holds for continuous input systems as for instance ducks feeding in a stream, but not for standing stock systems like the rice fields. In those latter systems, large deviations from matching are expected depending on the strength of interference competition, variation in competitive ability of foragers, and depletion rate. These factors may all explain Lourenço's finding of a non-proportional distribution of godwits amongst fields of varying food abundance.

Interestingly, Lourenço did not find any evidence for the so-called "domino effect": there was no correlation between the timing of staging in Portugal and the timing of arrival in The Netherlands nor the timing of egg-laying. In other words, birds departing early from Portugal did not breed earlier than late departing birds. Individual schedules were, however, repeatable. This suggests that more than one migration strategy leads to Rome, perhaps because one strategy is better than another in some years but not in other years.

We already knew that western Black-tailed Godwits are dependent on agricultural lands in the breeding as well as at the wintering grounds. This thesis nicely demonstrates they heavily use agricultural lands also at their stopover sites, making this subspecies exceptionally vulnerable for changes in agricultural policy.

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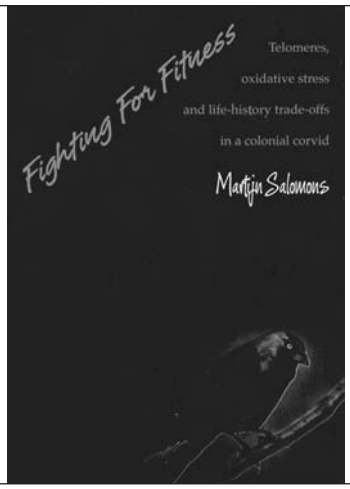
Salomons H.M. 2009. Fighting for fitness. Telomeres, oxidative stress and life-history trade-offs in a colonial corvid. PhD thesis, University of Groningen The Netherlands. ISBN: 978-90-367-3956-6, paperback, 140 pp. Available at http://irs.ub.rug.nl/ppn/321812034.



This thesis revolves around a colony of Jackdaws *Corvus monedula* conveniently situated in nestboxes at the biology department of the University of Groningen. What struck me while browsing through Martijn Salomons' thesis was the wide array of subjects that he has covered. His research stretches from the level of DNA to the social behaviour of the birds, from oxidative damage, energy metabolism and embryonic growth to dominance hierarchy. But all subjects serve one goal, to understand life-history decisions of the adult birds. The thesis contains seven research chapters and a general introduction, divided into two parts: "current versus future reproduction" and "social dominance and reproduction". I may be biased, but the first part to me is the core of the thesis, containing innovative research on the physiology underlying reproductive trade-offs. Life-history predicts that the current reproductive effort will be traded off with future reproduction so that life-time reproduction is maximised. A major component determining future reproduction is survival of the parents, and several studies have shown that adult survival indeed diminishes as reproductive effort increases. Although the mechanisms that are responsible for an earlier death remain elusive, it is generally thought that oxidative stress, i.e. damage to cells and molecules through reactive oxygen species ('free radicals'), plays a pivotal role in mediating effort and senescence. This said, it becomes clear that the animal ecologist needs to do intricate physiological measurements to causally

explain the observed life-history trade-offs. And that is just what Salomons has done, needless to say, with the assistance of several co-workers.

The first research chapter reports on how telomere lengths are affected by reproductive effort. Telomeres are long non-coding stretches of DNA sitting at the end of each chromosome. Telomeres shorten with age and this shortening is correlated with remaining lifespan. Oxidative stress can cause shortening of telomeres while an increase in reproductive effort may increase oxidative stress, thereby linking reproduction with mortality. In some species it has been shown that individuals with long telomeres survived better, but this could be the result of selective disappearance, where individuals with high rates of telomere shortening had higher mortality rates. To study this, Salomons measured telomere lengths in red blood cells of individual birds during three subsequent years and he demonstrates that individuals whose telomeres shorten fast are less likely to survive. Intriguingly, in the last year of their life telomeres show a dramatically accelerated shortening rate. Within an individual not all telomeres are equally long, and it is predicted that short telomeres are better protected against further shortening that long ones. Salomons also tested this and confirmed the prediction. These findings suggest that the shortening rate of long telomeres can potentially be used as biomarkers of 'life stress' and remaining life span. A startling prospect!

The next two chapters study sex-dependent effects of brood size on growth and oxidative stress in nestlings. Chicks in experimentally enlarged broods typically grow less well and do worse as adults than those in reduced broods and here the question is raised whether, apart from growth, oxidative stress is affected by rearing conditions. In four years 90 nests with 325 nestlings were used in the experiment. Apart from the effects of brood size on growth – most pronounced in females – and fledging probability, the antioxidative capacities of blood plasma was lowered in chicks from enlarged broods, suggesting heightened levels of oxidative stress. Surprisingly, measures of oxidative damage indicated more damage in male chicks from reduced brood and no effect of brood size in female chicks. Telomere shortening was twice as fast in male chicks from enlarged compared to reduced broods, while no effect was seen in females. Apparently the trade-off between growth and physiological condition differs between the sexes, prioritising growth in males and health in females.

The next chapter reports on the effects of reproductive effort on the parents. No less than 185 adults were captured at least once and 312 blood samples were collected when chicks were 5 or 20 days of age. Although many physiological parameters of body condition were measured, not one was convincingly affected by brood size. Despite rearing double the mass in chicks, parents with enlarged broods seem not to do worse than parents with much smaller broods. The challenged parents apparently keep themselves cool and are not willing to sacrifice their future reproductive output.

Chapter 6 comes with the surprising finding that dominant males are less successful reproducers than their subdominants. Also survival of the dominant males is not better. This is very counterintuitive, but apparently the males that are dominant at the feeding pit pair up with females that are in lower condition and produce smaller eggs. This finding can not be explained by extra-pair fertilizations since they hardly occur. Salomons discusses the possibility that the circumstances in this particular colony may be responsible for the result. First, food availability is high through which being dominant may not pay off: the dominant males are merely wasting energy and time protecting a feeding pit while food is overabundant. A second reason could lie in the high nest density. This could increase number of interactions and testosterone levels above ordinary levels, leading to more aggressive interactions among partners which would result in less parental care.

In the last two chapters attention shifts to primary sex ratios, thereby deviating from the earlier taken experimental path. It is predicted that sex ratios may be biased in socially structured populations like the Jackdaw's. Male Jackdaws also are 5–10% larger than females making raising male offspring more costly than female offspring, which would also contribute to a sex ratio bias. For six years blood samples of chicks were collected or samples were taken from nonviable eggs. To be sure to include all chicks, eggs were taken to an incubator 1–2 days before hatching and chicks were returned swiftly after they hatched. Close to 500 samples were collected and analysis showed a strong correlation between sex ratio and dominance rank of the males. Interestingly, this relationship varied considerably, from positive to negative, over the years. But no variables could be identified that may explain this finding. In the final chapter a potential mechanism of sex ratio allocation is studied: variation in the embryonic period, which is the time between laying and hatching of an egg. In combination with brood reduction, when a female lays more eggs than usually would fledge, this could result in sex ratio bias. This study was done in the Jackdaws but also in Black-headed Gulls *Larus ridibundus*. No differences were found in embryonic period of female and male embryos.

I am impressed by the broad front strategy employed by Salomons to advance our understanding of life-history processes. Moreover, this thesis raises lots of new interesting questions about the Jackdaws' life-history and, more general, about physiological mechanisms underlying life-history trade-offs. As such it is an excellent starting point for other studies.

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