PhD-Dissertation Reviews

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PhD-dissertation reviews

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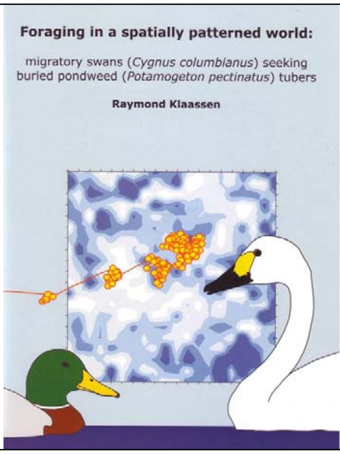
Klaassen R.H.G. 2006. Foraging in a spatially patterned world: migratory swans (*Cygnus columbianus*) seeking buried pondweed (*Potamogeton pectinatus*) tubers. PhD thesis, University of Groningen, The Netherlands. ISBN 90-367-2665-4, paperback, 192 pp. Available at http://irs.ub.rug.nl/ppn/296163988.



Optimal foraging theory deals with the choices animals make with regards to foraging decisions. A relatively new paradigm that has appeared in ecology is that the animal's foraging arena is spatially heterogeneous. How spatial pattern influences foraging decisions is the core theme of this thesis. Klaassen efficiently attacks the spatial foraging problems from a theoretical, observational and experimental approach.

Chapter 2 generates theoretical expectations for three foraging strategies in habitats that differ in spatial pattern. The gain rate of omniscient, ignorant and Baysian foragers are compared for habitats that differ in density and spatial heterogeneity. The habitat is a one dimensional world where each unit is either empty or filled. The structure of the world is generated by a Markov process having discrete time, i.e. the probability of a unit containing food depends only on the state of its predecessor. This way of modelling the environment allows the spatial pattern and density to be function of only the transition rates. When the foragers are compared in terms of food items harvested per unit time it turns out that when there is spatial pattern (either clumped or regular) the Baysian assessors achieve higher long-term intake rates than ignorant foragers. But as one could expect, it is found that Baysian foragers do not perform better than ignorant foragers when the environments are relatively poor or rich in food.

Probably the most interesting part of the thesis is chapter 3 where the theoretical expectations are put to the test. The hypothesis that movement decisions of animals depend on the encountered food density is evaluated. In order to address this problem the researchers performed observations on Bewick's Swans foraging on the edge of the shallow fresh water lake Lauwersmeer in The Netherlands. During a short period in October the swans forage on pondweed tubers that are buried in the mud of the lake. This system with cryptic resource is extremely suitable for the purpose because the tuber density can only be assessed by the swans through sampling. Furthermore, it was possible to generate the necessary spatial heterogeneity by removing aboveground biomass at different moments during the growing season. Before the foraging of the swans started the density of tubers was measured at a fine spatial resolution. These measurements allowed the researchers to calculate the probability that swans would find food as a function of distance travelled. In combination with the functional response and energetic costs of travelling between patches and exploiting food, the optimal distance to move was calculated. The positions through time of the foraging swans were determined by triangulation. Due to the positive spatial autocorrelation it was expected that swans that encountered many tubers in a patch would move short distance and show sinuous movement. In accordance with the predictions swans moved long distances from poor patches and short from rich patches. Based on a combination of parameters from the current and earlier studies on tundra swans it was calculated that the long-term intake rate increased by 38% compared to ignorant foraging. Furthermore it was shown that the rich patches were the most intensively exploited ones. Consequently, the spatial auto-correlation should decrease through the season and therefore the optimal travel distance was not expected to be constant. This exciting chapter shows very interesting results and leaves the reader eager to learn about follow-up investigations.

A crucial assumption of the third chapter is that movement decisions do not depend on interactions with conspecifics. The freedom of movement was assured by only analyzing the movements that were unaffected by interactions. Chapter 4 shows that it certainly was necessary to account for social interaction because interactions have profound effects on the movement decision. The effect of interactions depended on the dominance ranking of the interacting individuals, which in its turn was dependent on the group size in which the swans reside.

Charnov's patch leaving rule predicted that a forager should leave a patch when the current intake rate in the patch drops to the average intake rate for the habitat, i.e. they use a fixed patch leaving threshold. The consequence for the environment is homogenization of resources. More recent optimal foraging models that incorporate exploitative competition for depletable resources predict that animals benefit from using a flexible patch-leaving threshold. In order to test whether this was the case for the specific situation of foraging swans in the Lauwersmeer, simulations of the different rules were performed based on parameters from previous work. The simulations predicted that highest gain was to be expected for swans decreasing the residence time per foraging patch and that a flexible patch leaving threshold rule should be applied. Secondly, a flexible patch leaving threshold should decrease the variance in tuber density. Both predictions of flexible patch leaving threshold and its consequence of decreased variance in resource density could not be confirmed. On the contrary, variance in resource density increased. The authors end the story by discussing several options responsible for the discrepancy. The most important reason they note is that (the avoidance of) social interactions may be responsible for this.

As shown, swans enhance their foraging efficiency by making use of the information of the spatial structure of their habitat. The question arises whether and how such spatial structure may be maintained. Chapter 6 examines variance and spatial autocorrelation of Fennel Pondweed tubers through a yearly cycle of growth, grazing and winter mortality. This descriptive study shows that growth and winter mortality increase the level of spatial heterogeneity whereas grazing by swans has an opposite effect. The study raises interesting points about process and pattern in the light of long-term interactions between exploitation and growth of the pondweed year after year.

Since behaviour of a forager relates to the abundance of food it is important to describe the environment through the eyes of the forager. The so-called foraging scale is very playfully investigated with an indoor experiment using Mallards. The ducks were offered millet in a chessboard configuration where the cell size differed between 1.0 and 6.5 cm. A magnet was attached to the ducks lower mandible so that the underlain tray with magnet sensors could record the duck's exact position. The ducks responded to spatial pattern by restricting their searching area to the patch where they had been successful. The study successfully determined the foraging scale of ducks. Only when the cell sizes were smaller than 2 cm the ducks were no longer able allocate more time in rich patches and therefore to benefit a higher intake rate from the spatial pattern.

A logical follow up of this experiment is performed in the last chapter of the thesis where ducks were "taught" a spatial pattern for five days. On the sixth day the patch assessment and movement as a function of state of previous patch were evaluated. For spatially heterogeneous environments it was predicted and verified that ducks would spend less time in an empty patch when the previous neighbouring patch had been empty than when it had been full. Movements between patches unexpectedly did not appear to be affected by spatial pattern.

Due to the notion of spatial heterogeneity optimal foraging theory is gaining realism that is also testable. The strength of Klaassen's clearly written thesis is that it tests new hypotheses both theoretically and empirically. The hypotheses are logically consistent and intuitive to grasp and tested in a straightforward manner. But, throughout the thesis one starts to wonder what the effects of the social forces in the gregarious swans and ducks could be since the decision making is regarded to be influenced only by the acquired information on the level of the individual. Just as all scientific work should, Klaassen's work both answers and raises questions.

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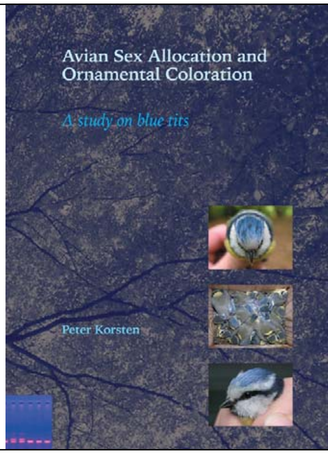
Korsten P. 2006. Avian sex allocation and ornamental coloration. PhD thesis, University of Groningen, The Netherlands. ISBN 90-367-2841-X, paperback, 171 pp. Available at http://irs.ub.rug.nl/ppn/298509423.



For humans the most conspicuous morphological characters of the blue tit *Cyanistes caeruleus*, especially when comparing it to any other species of the Paridae family, are the beautiful blue crown, tail and wing parts. But, beauty is in the eye of the beholder. After detecting ultraviolet (UV) vision in birds, we recognised that blue tits among other birds have a different perception of the world than we do. Our blue tit turned out to be an ultraviolet tit. Moreover, although males are hardly distinguishable from females in their "blueness" (Cramp & Perrins 1993), males differ in their UV reflectance from females (Andersson *et al.* 1998), which made the already popular species for answering questions related to mate choice and sexual selection, even more interesting. Initial studies in the late 1990s investigated mate choice (Andersson *et al.* 1998) and sex allocation (Sheldon *et al.* 1999) in relation to male UV coloration, and the work presented in this thesis is based on the knowledge collected from these first studies and nicely elaborates on that.

In his thesis, Peter Korsten addresses three issues related to the evolution of UV plumage coloration, particularly concerning sexual selection and sex allocation. First, whether plumage coloration is a heritable trait, a requirement when this trait plays the expected role in sexual selection. Second, whether and how females are able to influence reproductive outcome related to the (experimentally changed) UV coloration of their mates. And the third part of the thesis tries to answer questions on the role of UV coloration in intra-sexual conflict. Thereby the role of variation in ultraviolet plumage coloration in male-male competition and whether is used by males to signal their status to other males was studied. Peter Korsten's project was imbedded in an NWO funded research program in which both proximate and ultimate questions were addressed on avian sex allocation both with experimental and modelling approaches.

A general characteristic feature of the research presented in this thesis is thoroughness. Results and methods of former studies are not simply taken for granted, but Peter Korsten first validates these studies, before generalising former outcomes or questioning generalities. The thesis is built around the theme of sexual selection, where selection acts as a consequence of variation in mating success. The existence of a heritable component of variation of these sexually selected characters is an essential assumption underlying predictions on sexual selection. Rather than relying on the scarce information that is available on this topic, Korsten investigated whether variation in UV coloration contains a heritable component in his population in chapter 2. He found that between 20 and 40% of the variation in crown coloration is heritable. This was in contrast to findings in a British study, which combined animal models with a cross-foster experiment to estimate the additive genetic component (Hadfield *et al.* 2006). In that study a weak non-significant heritable component (11%) was detected. Korsten concluded that both population and methodological differences could underlie the dissimilar results, showing that components of variance might be population specific, but more study is needed to explain and verify these differences. Another example of the thoroughness is presented in chapter 3, in which Korsten validates the most-used method to experimentally alter (i.e. block) the UV crown coloration of individuals: applying a mixture of UV blocking chemicals and duck preen fat. Korsten shows that UV chroma (a measure of UV reflectance) drops below the natural range just after treatment in either captive or wild birds. However, in captive birds no significant effect of the treatment could be detected after only six days, while in wild birds the treatment effect lasted up to 14 days after application. These results are the basis of the experimental work of the thesis and validate the conclusions made by others in past studies. Moreover, they will help many future studies on experimental change of UV plumage coloration in planning their experiments and formulating the right hypotheses.

In the remaining chapters, Korsten studies the consequences of variation in UV crown coloration by applying the experimental treatment validated in chapter 3. This seems very logical, but in fact is quite remarkable. The importance to experimentally changing the traits of interest to find causal relationships and measure the adaptive consequences is greatly accepted, but nevertheless much less applied. Korsten's plea for an experimental approach in studies on the adaptive value of sex ratio differences (stelling 5) is therefore completely valid and confirms the care with which his hypotheses have been tested. Chapter 4 thereby launches the second part of the thesis. In this part Peter Korsten describes some of the possible consequences for the reproductive decisions of a female in relation to the crown coloration of her mate. In chapter 4 the trait of interest was the sex ratio of the brood. Korsten thereby repeated a study by Sheldon *et al.* (1999) and tried to replicate their results that showed that pre-manipulation and experimental crown coloration interacted in their relation to sex ratio. Studies on primary sex ratio adjustment in birds have been controversial and the generality of the phenomenon has been questioned. Again questioning and testing the generality of outcomes was the drive to do this experiment. Interestingly, comparable results were found: an interaction between pre-manipulation and experimental treatment had an effect on sex ratio. Sheldon *et al.* (1999) suggested that this might be explained by the substantial reduction in variation in crown coloration caused by the experiment. Korsten, however, correctly concludes that carefully designed experiments and behavioural observations are needed to test alternative explanations. Chapter 5 describes how levels of hormones deposited in eggs by the female, are influenced by an experimental decrease in crown UV reflectance. Depending on the egg sequence, females of UV reduced males had lower yolk testosterone levels early in the laying sequence. However, unexpectedly, the second egg, which was collected to show a baseline difference, had similar hormone levels in both treatments. Although Korsten found significant effects of the UV treatment in both studies, he also warns us to treat these results with some caution. Since the experiment caused a substantial (i.e. beyond the natural range) reduction in crown coloration, the females could percept this as a sudden illness of the males instead of a reaction to natural variation.

Chapter 6 and 7 give a very clear answer to the question whether, apart from being a signal to the female, variation in male crown coloration could also function as a signal to other males. Thereby experiments on both territorial intrusions in breeding males and winter dominance showed that males do not change their behaviour towards males with reduced crow UV coloration.

In conclusion, the thesis presents a very comprehensive and well carried-out study. Rather than trying to take big steps when attempting to assess the importance and measure the consequences of this relatively recently discovered trait, Peter Korsten has produced a firm basis for future directions. He thereby validated the choice for the blue tit as a model species and crown UV coloration as a valuable and interesting trait, playing an important role as signal for females decisions during the reproductive process, like in mate choice and egg production. His final conclusion is therefore completely valid; future studies can now fully focus on the inheritance, as well as the functional significance of variation in UV crown coloration, preferably tested in several populations, since the basic patterns are now well-described.

Andersson S., Örnborg J. & Andersson M. 1998. Ultraviolet sexual dimorphism and assortative mating in blue tits. Proc. Roy. Soc. London B 265: 445–450.
Cramp S. & Perrins C.M. 1993. Blue tit. In: Cramp S. & Perrins C.M. (eds) The birds of the Western Palearctic: 225–248. Oxford University Press, Oxford.
Hadfield J.D., Burgess M.D., Lord A., Phillimore A.B., Clegg S.M. & Owens I.P.F. 2006. Direct versus indirect sexual selection: genetic basis of colour, size and recruitment in a wild bird. Proc. Roy. Soc. London B 273: 1347–1353.
Sheldon B., Andersson S., Griffith S.C., Örnborg J. & Sendecka J. 1999. Ultraviolet colour variation influences blue tit sex ratios. Nature 402: 874–877.

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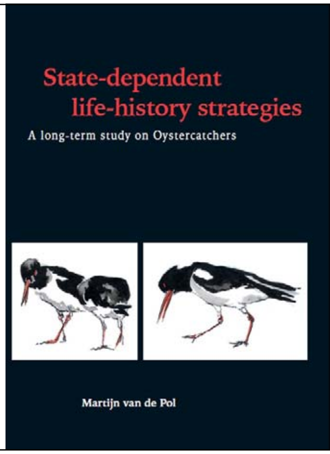
Van de Pol M. 2006. State-dependent life-history strategies: A long-term study on Oystercatchers. PhD thesis, University of Groningen, The Netherlands. ISBN: 90 367 2678 6, paperback, 213 pp. Available at http://irs.ub.rug.nl/ppn/296208205.



The striking amount of variation in life-histories among species, populations and individuals continues to fascinate. To understand where this variation comes from and how it is maintained, we need to know how different life-history traits relate to each other, but also how they depend on environmental conditions, i.e. their state-dependency. To do this, biologists have typically relied on elegant short-term experiments to test whether there is a causal relationship between, for example, reproductive success and clutch size. Over the last couple of years however, new statistical methods applied to datasets that are often spanning several decades have provided us with a powerful alternative approach, providing exciting new insights into the evolution of life-histories. As both approaches have there own inherent strengths and weaknesses, it is their combination that is particularly fruitful.

Martijn van de Pol's thesis on state-dependent life-history strategies in Oystercatchers *Haematopus ostralegus* provides a prime example of this, exploiting the possibilities offered by both. Analysing data from over twenty years of research on a breeding population of Oystercatchers on the Dutch Wadden Sea island of Schiermonnikoog, in combination with a number of elegant experiments, Van de Pol, together with 14 co-authors, does not only address a range of fundamental questions in evolution and ecology, but also offers a detailed investigation of the possible causes of the rapid decline of this population.

The nine chapters (and 3 boxes) that make up his thesis have been structured into four parts. The first introductory part consists of two chapters. The first chapter is relatively brief and introduces the reader to the most important aspects of life-history strategies and their state dependency, as well as of the study system. However, in chapter 2, Van de Pol does not only provide a far more detailed description of the study system, he also tries to answer the question why the number of Oystercatchers has declined so steeply in this population over the last two decades. He explores long-term trends in the different life-history parameters that may be responsible for this decline, and relates these changes to changes in food availability (all of which is illustrated with not less than fifty figures!). From this overwhelming amount of data he deduces that it must have been a decline in reproductive output, rather than reduced juvenile or adult survival that is resulting in the declining numbers, and that this decline may in its turn be driven by changes in food availability.

The first of the two main sections deals with age-dependent life-history decisions. As the analysis of age-dependent traits is far from straightforward, especially if there is a lot of variation in the age at which individuals start reproducing, Van de Pol first sets out to develop a new statistical method that allows for the separation of within and between-individual effects, and thereby the effects of e.g. age and selection. Having described the technical details of the model, he applies it to egg size, the timing of breeding, and to data on extra-pair copulations, analyses that are all interesting by themselves.

Van de Pol subsequently moves on to tackle the question whether there is an association between the number of years a male and a female Oystercatcher are together and how successful they are. He shows that there is indeed a positive correlation between the two. Although this has been shown before in this population, as well as in many other populations and species, the question remains whether there is a causal relationship between the two, or that it is driven by the effects of age or experience. An unequivocal answer to this question however requires the experimental manipulation of pair-bond duration. During the breeding season he thus removed one of the two partners, forcing them to remate, and looked at the effect this had on their reproductive success in the following years. Although during the subsequent years the salt marshes flooded during breeding season, making it impossible to measure many aspects of their reproductive success, birds that were forced to remate started laying significantly later, only to improve during the subsequent breeding seasons. At first sight these results seem to provide the first experimental evidence for a causal relationship between pair-bond duration and reproductive success. Unfortunately however, this experimental setup does not allow for the separation of the effects of the manipulated pair-bond itself, and the fact that the bird that lost its partner had to invest in finding a new partner, which may well have been of lower quality.

A second box on the question whether delayed maturity is favoured in declining populations (in theory: yes; in practice: probably not) concludes this section on age-dependent life-history strategies, and Van de Pol moves on to discuss condition-dependent life-history strategies. This section starts of with an in-depth investigation of the different sources of variation and covariation underlying a number of reproductive traits, something which is essential if we want to understand the evolution of life-history traits. Using state-of-the-art statistical techniques it is possible to estimate these (co)variances across years, territories and individual birds. Some of the main results from this exercise were that, not unsurprisingly, most of the variation had an environmental basis, and, more surprisingly, that some combinations of males and females performed better than other pairs, independent of the individual quality of the male and the female. This implies that at least in Oystercatchers many life-history traits are a function of the pair, rather than of the individuals that make up the pair, making their evolutionary dynamics far more complex than is usually assumed.

From there Van de Pol moves on to another experimental chapter, in which he tests whether higher quality of offspring born in good habitats can be explained by females investing more resources in their eggs. This is a question that can easily be answered by exchanging eggs between females breeding in different habitats, and that is exactly what he did. Although eggs laid in high-quality environments were larger, this surprisingly did not result in a higher fledging success, and females in high-quality habitats had a higher fledging success, irrespective of where their eggs came from. Chapter 7 continues to investigate the effects of the habitat where you grow up in more detail. Although it is typically thought that early environmental conditions mainly have short-term effects, a careful analysis of data collected on birds born between 1985 and 1996 showed that there were large long-term effects as well, with birds born in good territories having a higher survival rate and being more likely to breed in a good territory themselves.

Chapter 8 subsequently brings us back to the question when and where to start breeding. In this chapter, Van de Pol builds on from an earlier model predicting optimal queuing decisions by making the decision where to breed condition-dependent. This new model is remarkably good at predicting Oystercatcher settlement decisions, providing an elegant illustration of the importance of the state-dependency of many life-history traits in this system.

In the concluding chapter, Van de Pol synthesises the findings from the earlier chapters. He discusses many of the potential sources of environmental variation, and throughout he emphasises the importance of understanding how environmental factors affect life-history decisions, and how these in turn affect population dynamics. He also briefly goes into the potential role of genetic variation, or rather why he chose to ignore it in his research. While the amount of data may as yet indeed be too limited for a meaningful quantitative genetic analysis, provided that more data being collected during the coming years (and breeding success increases), this may become feasible in the not too distant future, opening up a whole range of exciting new questions.

Overall, Van de Pol's thesis underlines the value of long-term datasets. Although they are costly in terms of time, energy and money, it provides a prime example of how such data sets continue to shed light on the dynamics of natural populations in an age of unprecedented environmental change.

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