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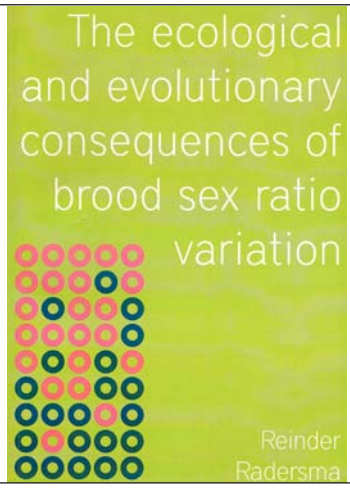
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Radersma R. 2011. The ecological and evolutionary consequences of brood sex ratio variation.
PhD thesis, University of Groningen, The Netherlands.
ISBN: 978-90-367-5239-8. Paperback, 118 pp.



Sex allocation theory is one of the most successful and productive areas of research in evolutionary biology. The decision whether to produce sons, daughters or both under different circumstances can be predicted from theory and is supported by a wealth of empirical evidence. This evidence is however not conclusive for all taxa. Especially in birds and mammals there is a large discrepancy between theoretical models and empirical findings. An important reason for this may be that the complexity of the life history of birds and mammals is not taken into account in sex allocation theory. In this dissertation, Reinder Radersma takes up the challenge to disentangle the complex relationship between sex allocation and fitness in birds. He approaches this problem by experimentally manipulating brood sex ratios in a population of Great Tits *Parus major* in the Lauwersmeer, The Netherlands. Subsequently, he investigated the relation between brood sex ratio (BSR) and parental fitness (Chapter 2) and explored possible underlying mechanisms of this relationship (Chapter 3–6).

The first research chapter (Chapter 2) investigates the relation between BSR and parental fitness using two years of experimental data. Radersma constructed several models taking different selection patterns into account to explain the relation between BSR and fitness. He found that parent Great Tits gained higher long term fitness benefits from producing broods with a sex ratio at parity. A closer examination revealed that this was because offspring raised in broods with equal sex ratios had higher fecundity than broods with biased sex ratios, resulting in stabilizing selection on sex ratio. No effect of BSR was found on offspring recruitment and survival and fecundity of parents. Radersma concludes that these findings therefore demonstrate that parental production of equal BSRs is adaptive.

Chapter 3 marks the start of the exploration of possible mechanisms underlying the relationship between BSR and fitness. Radersma first focuses on fledging behaviour and his expectation was that the timing and the age at fledging would depend on BSR due to existing competitive asymmetries between male and female nestlings. To monitor the fledging process nestlings were implanted with transponders. The results revealed no effect of BSR on brood age or asynchrony at fledging. Brood age at fledging was found to be best explained by average wing length of the brood (negative), average body mass of the brood (positive) and hatching date (negative). Within nests, individuals with larger wings at the age of 14 days fledged earlier, but no sex specific difference in fledging order could be discerned. Females were found to be less heavy than their male nest mates at the age of 14 days, but their wing lengths were the same. This might indicate that females allocate more resources to wing development to keep up with their male nest mates. Radersma hypothesizes that this sex difference in wing growth explains why no effect of BSR or sex on fledging behaviour was detected. Chapter 4 investigates whether wing length and fledging order might positively affect offspring recruitment chances. Surprisingly no effects

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could be discerned. These results thus suggest that wing length has no apparent adaptive value. Intriguingly, the author did find a previously never demonstrated pattern, that young had higher chances of recruitment when they fledged early in the morning.

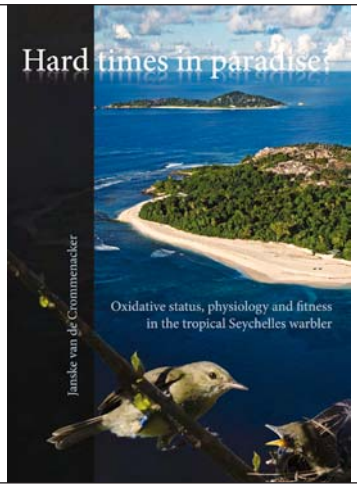
Chapter 5 explores whether social networks of Great Tit fledglings during the winter period can affect their future fecundity. Over a period of three years, nestlings were implanted with transponders and subsequently, visits of fledged individuals to feeding stations were recorded. Social network analysis was used to show which individuals were detected more often together than expected by chance. Unfortunately, there was not enough data for the analysis of females. Analysis of the male individuals showed that males raised in broods with BSR around parity were seen with more different individuals. It is suggested that these individuals may have sampled more individuals before partner choice, which might eventually lead to higher fecundity. There were, however, no significant correlations between sociality and fecundity.

The final research chapter (Chapter 6), explores whether experimentally manipulated BSRs can affect specific offspring traits (tarsus size and body mass as adult) or environment related traits (natal dispersal distance, laying date and local population density) that in turn could affect offspring fecundity. Individuals that were raised as the rare sex were found to have longer tarsi in their adulthood than individuals that were raised as the abundant sex in their brood. Further analysis showed that BSR affected the individual difference in tarsus size after the moment tarsus size was measured in the nestling phase (nestling age of 14 days). Radersma could however not show a correlation between tarsus size and clutch size that could explain his earlier observed effect of BSR on offspring fecundity. The author suspects that other developmental factors associated with tarsus growth were responsible for the BSR effect on offspring clutch size.

In conclusion, in this dissertation Radersma faced the challenge to disentangle the relationship between sex allocation and fitness in a model species with a complex life history. Using an experimental approach, the author succeeded in getting a grasp on this relationship and his work makes a major contribution to our understanding of how sex allocation and fitness are intertwined. As pointed out in the synthesis of the results in Chapter 7, the finding that equal brood sex ratios were under stabilizing selection could have major evolutionary consequences. Stabilizing selection for equal BSRs could play a key role in the preservation of chromosomal sex determination in birds and mammals and oppose the establishment of more flexible sex determination systems. Future investigations are needed to test the generality of the relation between BSR and fitness shown in this thesis. Priority should also be to further investigate the underlying mechanistic pathway, for which Radersma's work provides a solid scientific basis.

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Van de Crommenacker J. 2011. Hard times in paradise? Oxidative status, physiology and fitness in the tropical Seychelles warbler. PhD thesis, University of Groningen, The Netherlands.
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Available at http://irs.ub.rug.nl/ppn/338463518.



The fundamental problems in life history evolution of how, when, and why, we develop, reproduce and die can only be fully resolved with an understanding of the underlying physiological mechanisms. Palm trees, sandy feet, and turquoise waters aside (all of which can be taken in during the refreshing intermezzo), Janske van de Crommenacker's thesis highlights how the analysis of oxidative states can be used to shed new light on traditional life-history questions. Her thesis is wide ranging, for the large part covering correlative and causative relationships between life-history parameters and oxidative stress. This includes (A) comprehensive correlative studies of ecological factors, social status, and fitness in relation to oxidative states in the

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wild-living Seychelles warbler (*Acrocephalus sechellensis*; Chapters 2, 3, 5 & 7), (B) experimental studies of immune function and oxidative status in aviary-reared homing pigeons (*Columba livia*; Chapter 4 & Box C), and (C) a brief flirtation with the reptilian realm in a correlative study showing that aggression, but not testosterone, increases oxidative stress in White's skinks (*Egernia whitii*; Chapter 6). Her thesis also provides enlightening reviews on why defining oxidative balance can be contentious (Box A) and the trials and tribulations of measuring oxidative balance using reactive oxygen metabolites (ROMs) and the antioxidant component OXY (Box B). She even provides pragmatic science-lead conservation evaluations of how best to assess habitats for translocation of endangered endemic birds (Box D).

As implied by the thesis title, the lion's share of her work investigates variation in oxidative states of Seychelles warblers in the wild. From a population of less than 30 booming to nearly 5000 in just 25 years, the Seychelles warbler is a resounding conservation success story. As part of the conservation effort, the population has been monitored and an impressive volume and breadth of life-history data has been collected (in part through her own impressive personal efforts). Some of this data has been combined with her novel data on oxidative stress in this thesis.

Chapter 2 investigates the association between territory quality (i.e. insect availability) and oxidative stress. Seasonal changes in prevailing wind direction and associated salt spray cause dramatic defoliation and reduce insect availability in exposed areas. Van de Crommenacker predicts that food scarcity increases foraging effort and hence oxidant production in affected territories. She predicts that this could create an oxidative imbalance that would be exacerbated by a decline in diet derived antioxidant defences. Results suggest that oxidative stress is higher in poor environments, but the balance is tipped by the increased oxidant generation, and not the loss of diet derived antioxidants. As a by-product of this study, oxidative parameters were shown to exhibit diurnal patterns within and between individuals, suggesting diurnal variations in motility with a lag in the anti-oxidant response; the first such finding in the wild.

In Seychelles warblers ecological constraints can restrict independent breeding and consequently many individuals become subordinates in an established group, often on their natal territory, where they either remain as non-helping subordinates or become helpers. This variation in helping behaviour is interesting as while the benefits of cooperative breeding are measured in terms of inclusive fitness, costs have proven difficult to measure. Chapter 3 explores whether pre-breeding body condition and oxidative status are related to a subordinate's decision whether or not to help – i.e. do subordinates only help when they can afford to, and is there a cost to those that help? Well, it certainly seems that way – if not only for females. Prior to the reproductive events at the territory, non-helping females were more likely to be in bad shape, and had both poor body condition and high levels of pro-oxidants compared to the dominant females and helpers. Yet, over the breeding season the body and oxidative condition of non-helpers improved – while that of birds exhibiting helping behaviour dropped. By the end of the season the overall condition of non-helping birds was equal to or even surpassed that of their helpful counterparts.

When it comes to defining prime suspects in the creation of oxidative stress, pathogens and the immune response are high on the list. The immune system actually purposefully generates pro-oxidants to use as a weapon against the alien pathogen intruders. To separate confounds arising from the uncontrolled nature of ecological variables on the underlying physiological fundamentals of life history trade-offs, the experimental identification of causal relationships alongside observations in natural conditions is necessary. Given the Seychelles warbler is a vulnerable endemic species, laboratory experiments are somewhat difficult to justify. To this end, the pigeon was used to experimentally investigate how birds are physiologically affected by immune-derived oxidative damage in Chapter 4 and Box C. And then this concept was applied to the Seychelles warbler system in the wild in Chapter 5 to identify if a real-life pathogenic threat from avian malaria influences oxidative states.

The controlled pigeon studies investigate 1) how injection of a bacterial endotoxin used to mimic bacterial infection altered oxidative balance, 2) how oral-supplementation of lysozymes that bind these endotoxins as part of the innate immune system altered oxidative balance in both baseline and endotoxin-challenged states, and 3) the affects of the introduction of endotoxin and lysozymes on circulating populations of leucocytes. The mimicked immune threat increased pro-oxidant levels and oxygen consumption and lead to a reduction in body mass. Levels of pro-oxidant and oxygen consumption were higher in birds that had immune lysozyme supplementation. Moreover, birds that had lysozyme supplementation in the absence of the immune threat consumed more oxygen, had higher levels of pro-oxidants, and had lost more body mass

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than controls. As is typical of the acute infection response, the heterophil/lymphocyte ratio increased. Changes in both the heterophil/lymphocyte ratio and monocyte number were related to increases in pro-oxidant levels, suggesting that part of the increase in pro-oxidants may be generated by leucocytes in response to pathogenic threat. In summary, the lysozyme supplementation augmented immune function but exacted an oxidative and metabolic cost.

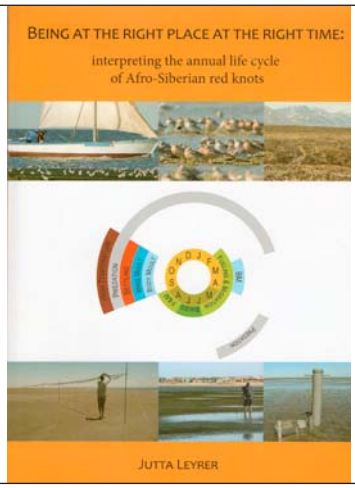
The Cousin Island Seychelles warbler population provides a simplified and tractable system in which to investigate the association between malarial infection and physiological parameters in the wild. Just one single strain of avian malaria is found in the Cousin Island population, with a consistent prevalence of 40%. No other malaria strains are present, in fact no other blood or gastrointestinal parasites have ever been discovered, which neatly cuts down the confounding issues surrounding multiple infections moving through the population. Chapter 5 elegantly represents the first *in vivo* study investigating the relationship between avian malaria and oxidative stress. Malarial infection increased oxidative stress and this link was strongly influenced by breeding stage, such that malaria + chick provisioning = some seriously stressed out birds.

Fitness is the central tenet of evolution, and as such in the investigation of the physiological processes underpinning variation in life-histories, it is also important to examine potential changes in proxies of fitness. Chapter 7 considers this link between oxidative status and fitness, measured as current and future reproductive success and annual survival. This study found no significant relationships. Van de Crommenacker suggests that acute oxidative imbalances measured here may not be as important in determining fitness as the chronic oxidative damage accumulated throughout life on long-term survival and senescence.

To conclude, this thesis makes the first vital steps in understanding the role of oxidative stress over an impressively wide range of internal, abiotic, and social environments in both controlled and natural conditions. Given this field of research is in its infancy, getting to grips with the significant target variables is vital. This compilation of work will be a stimulating read for anyone interested in the proximate mechanisms behind ultimate questions, with even greater appeal to those of us who are inexorably tied to wanting to know how it all works in the real world.

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Leyrer J. 2011. Being at the right place at the right time: interpreting the annual life cycle of Afro-Siberian red knots. PhD thesis, University of Groningen, The Netherlands. ISBN: 978-90-367-5151-3. Paperback, 163 pp. Available at http://irs.ub.rug.nl/ppn/338115749.



The focal animal in this thesis is the Red Knot *Calidris canutus* and in particular the nominate subspecies *C. c. canutus*. These shorebirds are true migrants that can fly thousands of miles non-stop between their Arctic breeding and African wintering habitat with the German Wadden Sea as an important stopover site half way. Leyrer has studied the migration of *C. c. canutus* in relation to timing, survival and carry-over effects between the Wadden Sea of Schleswig-Holstein, Germany, and their main wintering habitat Banc d'Arguin, Mauritania, where 75% of this subpopulation resides during the non-breeding period. Leyrer, together with many co-authors, tries to tease apart potential selection pressures using different methods. Specifically, Leyrer and colleagues have caught knots and marked them with colour rings to make them individually identifiable. In doing this, individual habitat use, timing of migration and survival could be quantified. Also, several knots were equipped with radio tags to increase temporal and spatial resolution for these analyses. Leyrer's thesis consists of seven chapters, which are structured in five parts entitled: 'spacing behaviour on the wintering grounds', 'on migration', 'stopover ecology', 'survival throughout the annual cycle' and 'synthesis'.

In Chapter 2 Leyrer presents a study on daily space use by means of radio-telemetry and resighting data of individual colour-ringed Red Knots in Banc d'Arguin. Leyrer found that knots were very faithful to their

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roosting site, that their daily foraging areas were small with 2–16 km^2 and that knots seemed to return to the same locations in subsequent winters. These results are put in contrast to Red Knots of the *islandica* subspecies wintering in the European Wadden Sea where their foraging range is about 800 km^2 and where they readily switch roosting sites. Similarly small foraging ranges were reported for Red Knots in Patagonia and northwestern Australia, but there space use between day and night differed with Mauritania and Europe. The authors suggest that the combination of food predictability and the absence of day-night differences in predation pressure allow Red Knots wintering at the Banc d'Arguin to have small and predictable home ranges compared to knots wintering in other areas.

Based on over 1600 resightings, in Chapter 3 Leyrer shows sex- and age-related differences in site use by Red Knots between two high tide roosts in Banc d'Arguin using multi-state mark-recapture models. One roosting site had more males (58% vs. 48%) and juveniles (45% vs. 22%) than the other. Contrary to theoretical predictions, adult survival was 3% lower at the 'male/juvenile' site (81%) than at the 'female/adult' site (84%). Leyrer and colleagues explain the survival differences by differences in food quality surrounding each roosting site. Moreover, they hypothesize that even in a gregarious species such as the Red Knot, subtle intraspecific competition may exclude particular classes of individuals from sites where food is most abundant and survival is highest.

In Chapters 4 and 5 Leyrer shows how wind can influence migration from West Africa to the Schleswig-Holstein Wadden Sea. In Chapter 4 a long term monitoring series is presented which confirms that the numbers of Red Knots visiting the French Atlantic coast are highly variable. In Chapter 5 this variation is shown to be positively correlated to modelled wind conditions en route from West Africa to the Arctic via the Schleswig-Holstein Wadden Sea. In combination with the fact that the body mass of the birds stopping in these areas were particularly low, it is concluded that the French Atlantic coast is probably an intermediate emergency staging site in case wind conditions en route are unfavourable.

Turning to the benthic food of Red Knots, Chapter 6 describes the large-scale distribution of macrozoobenthos in the Schleswig-Holstein Wadden Sea. The settlement of bivalve larvae was patchy and variable between years and there seemed to be a north-south gradient in macrozoobenthic community and sediment type. Particularly, in the north the Edible Cockle *Cerastoderma edule* was more abundant and the sediment was sandier, while in the south the Baltic Tellin *Macoma balthica* was more abundant and the sediment was muddier. Distance to the river Elbe was shown to explain most variance in macrozoobenthic communities. However, this distance was also correlated with salinity and sediment type. Leyrer concludes that more sophisticated analyses are needed to tease these factors apart and pinpoints which is most important determining the macrozoobenthic community in the Schleswig-Holstein Wadden Sea.

In Chapter 7 Leyrer reports of an observation in June 2008 that Red Knots in Schleswig-Holstein departed to their Siberian-breeding grounds in the morning instead of at sunset. Long distant migrants, including shorebirds, typically depart at sunset, possibly to gain the advantages of reduced energetic costs, favourable meteorological conditions and easy calibration of their compass for navigation. The author discusses several costs and benefits of the decision when to depart on migration and hypothesize that the observed morning departures could be a potential strategy to avoid another day of predation pressure from Peregrine Falcons *Falco peregrinus*.

Chapter 8 shows a seasonal survival analyses for Red Knots. Data on seasonal survival for migratory animals are scarce and it is assumed that survival is lowest during breeding and migration. Using their 8 year mark–recapture data set on Red Knots, it is shown that survival was lower on the tropical wintering grounds than during breeding and migration combined. Especially the first months after returning on the wintering grounds in Mauretania showed low survival probabilities. With these observations Leyrer showed that tropical marine non-breeding habitats do not necessarily provide easy environments for long distance migrants such as Red Knots. The chapter is concluded hypothesizing that physiological challenges (e.g. moulting, dissipating heat) and social interactions (i.e. exclusion from most profitable areas) might amplify carry-over effects from migration and breeding and ultimately reduce survival on the wintering grounds.

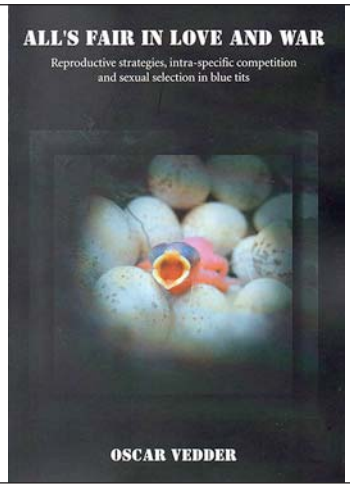
Chapter 9 summarizes the findings reported in this thesis and shows that many unknowns still remain in this relatively well studied species on a well studied flyway. Also potentially important state variables are defined that can be brought together in annual routine models to aid further understanding of long distant migration. Finally, Leyrer calculates that based on current knowledge, the Schleswig-Holstein Wadden Sea should be visited by roughly 300,000 Red Knots. However, the total number of knots counted never reached over 100,000, nor did the fortnight high-tide

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roost counts add up to the expected 300,000 birds. Where these missing knots are, nobody seems to know and no satisfactory hypothesis can be formulated. Here lies a great opportunity for further research perhaps by tracking individuals during migration using novel techniques. The remarkable amount of data gathered in this thesis should provide a good stepping stone for such research into the decisions that individual Red Knots make on their long distance migration.

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Vedder O. 2011. All's fair in love and war. Reproductive strategies, intra-specific competition and sexual selection in blue tits. PhD thesis, University of Groningen, The Netherlands.
ISBN 978-90-367-4812-4. Paperback, 192 pp.



That "all's fair in love and war" is all too apparent after reading Oscar Vedder's doctoral thesis. Female Blue Tits lay eggs in other females' nests (conspecific brood parasitism), males sometimes attract two instead of one female (polygyny) and both sexes frequently mate outside the pair bond (extra-pair copulations). What also becomes apparent when reading this thesis is that Vedder has mastered the art of logical reasoning; the reader is confidently guided through the vast tangle of ideas and arguments used in the fields of extra-pair behaviour and sexual selection. Vedder's thesis, subtitled "reproductive strategies, intra-specific competition and sexual selection in Blue Tits", contains nine chapters and is split in three parts. The nine chapters nicely show Vedder's progression of ideas; hypotheses derived from findings in one study are tested in new studies, exactly the way science should be done. The first part describes and quantifies above mentioned alternative reproductive strategies in the study population of Blue Tits, and discusses whether or not these strategies enhance the opportunity for sexual selection. In Chapter 2 the first formal description of conspecific brood parasitism in Blue Tits is presented. Six incidences are described and it is shown that parasitic and host eggs do not differ in mass or yolk testosterone content, two parameters that could affect a hatchling's competitive abilities. Although the authors conclude that the observation is real (box A refutes a peer's comment on misinterpretation of their findings), conspecific brood parasitism in blue tits does not appear to represent a true alternative reproductive strategy because it occurs only seldom and provides relatively little fitness benefits. Extra-pair copulations, however, occur frequently in Blue Tits. In Chapter 3, using an incredible sample size (n = 1693), Vedder shows that 11% of all fledglings were not sired by the social male. This extra-pair paternity, combined with some 15% of males mating polygynously, resulted in a considerable increase in the variation in reproductive success among males. This increase means that there is a larger potential for sexual selection, and extra-pair paternity and polygyny therefore represent true alternative reproductive strategies in Blue Tits. Because the degree of paternity losses, but not paternity gains, was consistent within individual males across different females and breeding seasons, among male variation in paternity losses will contribute most to sexual selection. Furthermore, lack of covariance between paternity losses and gains coupled with the observation that young polygynous males had greater paternity losses than young monogamous males, contradicts the idea of a general female preference for successful males. Instead Vedder suggests that female Blue Tits may benefit most from extra-pair copulations by insuring their eggs against functional infertility of the social male.

Other hypotheses seeking to explain why females engage in extra-pair copulations differ from the infertility insurance hypothesis in that they revolve around genetic benefits for the extra-pair offspring. Such 'good genes' hypotheses have received some support from studies showing that extra-pair offspring have higher survival to fledgling, are in better condition, or have greater immunocompetence than their half-siblings. In

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the second part of his thesis, Vedder cautions against comparing fitness components between within- and extra-pair offspring, because non-genetic effects could account for superior performance of extra-pair offspring. Vedder shows in Chapter 4 that the position in the laying order, a non-genetic effect, indeed explains differences in fitness components between within- and extra-pair offspring. Extra-pair offspring were over-represented in the earliest eggs of a clutch, and chicks hatching from early eggs had greater nestling survival and fledgling condition than chicks hatching from later laid eggs. However, when controlling for the effect of laying order, differences in survival and condition between within- and extra-pair young disappeared. The next chapter investigates why extra-pair offspring are over-represented among the earliest eggs in the laying order. Addition of model eggs to nests a few days prior to the onset of laying resulted in an earlier onset of incubation in the laying period and a lower proportion of extra-pair offspring in the nest. This led Vedder to suggest that hormonal changes associated with incubation may very well curb female motivation to engage in extra-pair copulations. Chapter six further explores the idea that the decline in extra-pair paternity with laying order is associated with female incubation. In an experiment, in part of the nests up to 10 eggs were removed on the day of laying, whereas in other nests eggs were left untouched. Using all nests, the occurrence of extra-pair offspring in a clutch was indeed negatively correlated with the duration of female incubation, but only in the very early laying phase. However, even though no eggs were present in the nests of manipulated females, incubation duration at this early phase was unaffected by the experimental treatment. This indicates that there is no direct effect of incubation on paternity, but suggests that a female's physiological state associated with extra-pair behaviour just before onset of laying influences her incubation behaviour in the early laying phase. In the last chapter of the second part, Vedder shows that multiple extra-pair offspring sired by the same extra-pair male and located in a single brood will usually be the result of multiple extra-pair copulations. This is important to know, because many studies on the benefits for females of extra-pair paternity have studied the number, and not merely the presence, of extra-pair offspring.

The third part of this thesis investigates the possibility that the Blue Tits' ultraviolet crown patch signals resource holding potential. Previous work has generally shown that experimental reduction of UV reflectance of the crown patch makes male Blue Tits less attractive to females. In Chapter 8 Vedder demonstrates that a similar reduction of UV reflectance has no effect on the probability of winning conflicts over food provided in winter at feeding tables. Therefore the UV reflectance of the Blue Tit's crown does not serve as a signal of status in competition over winter food. More likely, individual recognition and conventions over space use (position of the feeding table in relation to winter territories) determined the outcome of conflicts over food. That individual recognition is of paramount importance in the outcome of conflicts over resources is clear from the result in the final chapter. Unlike their wild counterparts in winter, captive males with experimentally reduced UV reflectance were more likely to lose conflicts over food than control treated males. However, when the same dyads were tested again several weeks later, but with the UV treatment reversed between opponents, the winner was most likely the male that won at their first encounter. These findings stress the need to incorporate the context in which the role of sexual signals in conflict settlement is studied.

Vedder himself concludes that "the research presented in this thesis emphasizes the difficulty in demonstrating unambiguous examples of contemporary sexual selection". I can only agree with this statement. Nevertheless, Vedder's thesis has provided us with a major step forward in thinking about and understanding extra-pair paternity.

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