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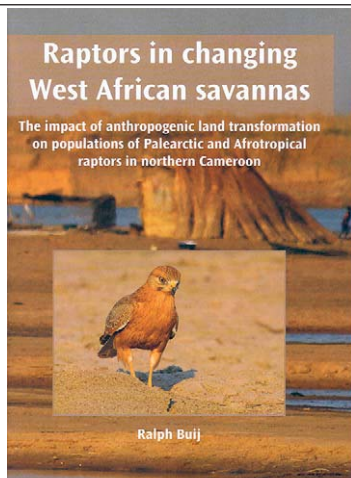
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Buij R. 2013. Raptors in changing West African savannas. The impact of anthropogenic land transformation on populations of Palearctic and Afrotropical raptors in northern Cameroon. PhD thesis, University of Leiden, The Netherlands. ISBN 978-90-6464-626-3. Paperback, 260 pp.
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When Jean-Marc Thiollay planned to repeat his road transects in West Africa in the early 2000s, after a time lapse of some 30 years, he was in for a surprise: numbers of eagles and vultures had dropped by 86–98%. Declines in other species were smaller, or even absent. Whereas declines outside protected areas were much larger than in National Parks, the most likely trigger for these changes seemed to be anthropogenic. Ralph Buij spent four years in semi-arid northern

Cameroon where several National Parks (Bénoué, Boubandjidda, Faro) and the Waza Logone floodplains are surrounded by degraded savannah and cropland. The raptor fortunes in (semi-)protected areas were compared to those in cultivated areas in use as grazing pastures or cropland (mainly dry-season sorghum, millet and rice). The study area also covers a range of savannah ecosystems, from the Sahel in the north (450–700 mm rainfall per annum) to the Sudan belt (700–1100 mm) and the Guinea belt (1100–1600 mm) to the south. Human population density is low but rapidly increasing (at present: 5% per annum). This region is home to a wide variety of sedentary African raptor species and hosts important numbers of Palearctic and Afrotropical migrants. How are the various raptor species coping with changes in the landscape wrought about by man?

Three species of Palearctic harriers, i.e. Northern Marsh *Circus aeruginosus*, Montagu's *C. pygargus* and Pallid *C. macrourus*, showed quite some overlap in habitat use, although Marsh and Montagu's Harriers were recorded significantly less in dry grasslands, the major hunting ground of Pallid. Interspecific competition was largely absent because prey choice was related to body size: Marsh Harriers captured heavier prey than the smaller-sized Montagu's and Pallid Harriers. The latter two showed almost complete overlap in prey type (as evident from pellet analysis), not surprising given their similar sizes, but avoided competition by hunting in different habitat types or targeting abundant prey species like grasshoppers and small mammals. Pallid Harriers were also quite adroit in capturing Red-billed Queleas *Quelea quelea*, especially when using ambush tactics near waterholes and overt attacks with rapid acceleration (18.8% of 149 capture attempts successful). Within-species habitat segregation was most noticeable in Pallid Harrier, where size dimorphism between male and female is greatest. Some evidence accumulated that juvenile harriers on average exploited different habitats than adults, but how this came about and why this should be so remained unclear. The present suite of habitats, though heavily fragmented and degraded, still harbours – and perhaps facilitates – massive and diverse prey populations, enabling coexistence of large numbers of harriers. This will most likely be a temporary respite from the anticipated large-scale losses of floodplain habitat, conversion of savannah into cultivated fields and intensification of existing farmland.

It is rather surprising to note that basic life history traits of typical Sahelian raptor species are still a mystery except some anecdotes published in the ornithological literature, and that not much has changed since Leslie Brown produced his *African birds of prey* in 1970. Two of these, i.e. Grasshopper Buzzard *Butaster rufipennis* and African Swallow-tailed Kite *Chelictinia riocourii*, are demystified in the present thesis. The third, Fox Kestrel *Falco alopex*, remains an enigma. The Grasshopper Buzzard is a small migratory raptor species that follows the rains northwards to exploit the grasshopper boom as soon as grazing and dry season fires have reduced the grass cover. Onset of laying was synchronous and succeeded the first seasonal rains. Siblicide and starvation often reduced brood size from two to one, or from three to two/one. Prey items delivered to the nest were small and easily monopolized by the oldest chick (which was already larger at hatching than its nest mates). Incubation time was short, growth rates of chicks rapid and postfledging dependence period short, suggestive of the rapid seasonal change in food availability determined by rainfall and subsequent desiccation. The high starvation rate and large difference in growth of first- and second-born chicks also indicate that breeding in the Sahel is a balancing act between extremes. Chicks growing up in transformed habitats performed less well than those in nests in natural habitat, also when corrected for potentially confounding variables like hatch order, sex, hatch date, rainfall and presence of siblings. Higher precipitation during the nestling stage was associated with higher nestling growth rates. Although still numerous as a breeding bird, Grasshopper Buzzards are in for a hard ride given the ongoing transformation of natural into cultivated habitats, higher nest losses in transformed habitats, smaller food supplies in cultivated areas and future scenarios suggesting less rainfall. The study of African Swallow-tailed Kites in northern Cameroon and Senegal (together with Simon Cavallè and Wim Mullié) may hint at what the future has in store for other still thriving Sahelian raptor species: reduction of quality and availability of roosts and nest sites, resulting in a very low nest success (using Mayfield: 17% in Cameroon and 4% in Senegal).

Habitat transformation should have an even greater impact on sedentary raptor species, like Dark Chanting Goshawk *Melierax metabates*. Still common, its decline was reported by Thiollay to exceed 50% between 1969 and 2004. Twelve adult males were radio-tracked, six each for three days in respectively transformed and natural habitats in Cameroon. Chanting Goshawks

hunting in natural habitats made fewer successful strikes per hunting hour than those hunting in degraded habitat, but captured larger prey. Energy intake per hour (in kJ) was similar in both habitats, but does not warrant the conclusion that the greater prey catching rates in transformed habitat is offset by a lower energy content of prey. In fact, this study shows that energy content of the various prey types (reptiles, rodents, passerines, grasshoppers) is similar in terms of kJ ash free dry weight (g). Evidently, Chanting Goshawks in natural habitats capture fewer but larger prey, which sets the proposed conservation management in a different light.

The last three chapters focus on species richness and habitat associations of the raptor fauna at different spatial and temporal scales. One of the methods employed were roadside surveys, a rather risky enterprise because the placement of the roads may not be representative of the habitat or the species to be sampled (not tested in this study). In the three biogeographical savannah zones 55 raptor species were recorded during wet and dry seasons in four years. Palearctic species were more or less indifferent to land use. Species richness of Afrotropical raptors was negatively related to habitat modification in the inundation zone and Sudan zone, and peaked at moderate levels of woodland clearance in Guinea savannahs. Large raptor species were apparently more sensitive to habitat modification than smaller species, and Afrotropical sedentary raptors more so than migratory ones. In the floodplains, a habitat that has undergone rapid cultivation in favour of rice cropping, Afrotropical raptors were more numerous in the remaining natural floodplain vegetation (excluding Yellow-billed Kites *Milvus migrans parasitus* and Hooded Vulture *Necrosyrtes monachus*), whereas Palearctic migrants were recorded more often in rice fields (which is not to say that they preferred this habitat, as stated in this study). Between biogeographical zones, the raptor assemblages showed various richness and density, depending on season, human exploitation and presence/absence of protected areas. The latter two seemed to override the dominance of biogeography in shaping raptor faunas, a conclusion in line with the tentative findings of Thiollay.

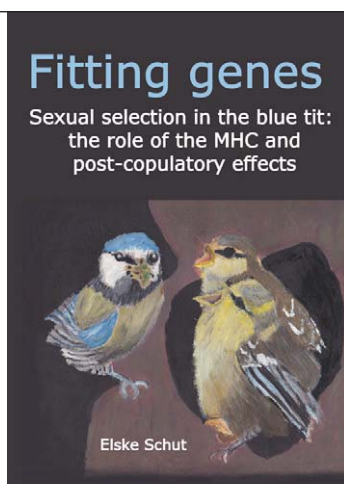
The study of Buij in northern Cameroon is a welcome addition to our knowledge of raptors in Africa, especially because he used hardcore fieldwork and included Afrotropical species. Forty years ago, a similar study was done by Chris Smeenk and his wife in Kenya (Ardea 62: 1–97, 63: 93–115) and in Nigeria (65: 148–164). A comparison of the propositions made in the respective theses showed that only 1 out of 27 in

Smeenk's related to conservation (pesticide usage in Africa), whereas 9 out of 10 in Buij's are focused on conservation issues. We have lost our innocence in the intervening years.

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Schut E. 2012. Fitting genes. Sexual selection in the blue tit: the role of the MHC and post-copulatory effects. PhD thesis, University of Groningen, The Netherlands. ISBN: 978-90-367-5391-3. Paperback, 168 pp.

Available at <http://irs.ub.rug.nl/ppn/34051888X>



Sexual selection can take many forms. In some species females choose the brightest plumage or most elaborate song, whereas in others sperm mobility or the size of the ejaculate matters most. Hence, sexual selection can operate both before and after copulation and can include both a female and a male component. The Blue Tit *Cyanistes caeruleus* is an ideal species for investigating sexual selection as it displays sexual dimorphism in size, crown UV coloration and vocalization, and a high rate of extra pair fertilizations; a situation that enhances the opportunity for post-copulatory sexual selection. Examining pre-copulatory sexual selection processes, based on female choice for male characteristics in wild animals, is relatively straightforward and consequently, has been well studied in numerous clades. However, examining sexual selection processes occurring after sperm insemination in the wild is chal-

lenging. Consequently, the literature is dominated by studies that have used invasive methods mostly in captive or semi-wild settings, which have limited value in a wider context, for instance for conservation research. In her thesis, Schut takes up this challenge and investigates the processes leading to pre- and post-copulatory selection in a nest box population of Blue Tits in De Vosbergen estate, near Groningen, The Netherlands. More specifically, she investigates the number of sperm that female have available for fertilization to gain insights on their probability of infertility, and subsequently explores the role of major histocompatibility complex (MHC) genes in mate choice to understand whether genetic characteristics play a role in the mating decisions of Blue Tits.

Schut's thesis contains six research chapters. The first research chapter (Chapter 2) describes a novel method to distinguish between the two main causes of hatching failure in passerine eggs, infertility and early embryo mortality (EEM), using the Zebra Finch *Taeniopygia guttata* as a model species. As hatching success is one of the main determinants of reproductive performance it is important to understand the causes of hatching failure, especially for species of conservation concern. The methodology involved counting the number of sperm on the layers surrounding the egg yolk, and determining whether the number was sufficient to achieve fertilization. Moreover, the method was successfully applied to the unhatched eggs of wild Tree Sparrows *Passer montanus* that were incubated to full term; revealing that sperm counts could be obtained even several weeks after egg laying. Hence, this method can be used to discriminate between infertility and EEM in unhatched eggs from wild species.

In Chapter 3, Schut explores whether Blue Tits suffer from sperm depletion, a likely cause of egg infertility, by counting the sperm trapped between the layers surrounding the egg yolk. Blue Tits have the largest average clutch size of all passerines, and are expected to cease or decrease copulation early during the laying sequence (as in other passerine species). Hence, Schut predicted that the likelihood of hatching failure might increase over the laying sequence. However, she found no association between the likelihood of egg infertility and laying order, no change in sperm counts between the 2nd and the 10th eggs, and no difference in sperm counts between clutches of different size. Moreover, she failed to find an association between sperm count and the proportion of fertile eggs in a clutch. She concluded that copulation appears to continue throughout the laying period of Blue Tits and, therefore, they are not subject to sperm depletion.

Chapter 4 examines the link between characteristics of the females' social partner and the number of sperm available for fertilization. Using the 'sperm counting' method described above, Schut showed that the number of sperm is repeatable in eggs of the same clutch and that females paired with larger males have higher numbers of sperm. Based on this relationship, she suggested that between-individual differences in the number of sperm stem from copulation behaviour or from post-copulatory tactics, rather than from differences in the sperm storage capacities of females. Unfortunately, as it was not possible to attribute sperm to individual males, the exact relationship could not be identified. Nevertheless, this is the first study to demonstrate an association between male characteristics and female sperm count in a wild bird species; a finding that awaits further exploration.

Genes of the MHC are the central component of the vertebrate adaptive immune system. They play an important role in parasite resistance, and hence can have direct effects on the survival of their bearers. MHC genes are commonly linked to the evolution of mating preferences due to the potential genetic benefits that may be conferred to offspring through MHC-based mate choice. Chapter 5 marks the start of the exploration of Blue Tit MHC class I exon 3 variation with the aim of understanding the role of MHC genes in mating decisions. As no data was available on Blue Tit MHC genes, Schut initially characterized the genetic region and developed a screening method for MHC genotyping. In Chapter 5, she investigates the MHC variation among 17 Blue Tits originating from three locations across Europe: Spain, The Netherlands and Sweden; and compares Blue Tit MHC variation with the diversity observed in other passerine studies. The phylogeny of the alleles revealed the presence of a single cluster with low nucleotide diversity, while the remaining alleles were diverse and subject to balancing selection at the peptide-binding region. Samples from geographically disparate regions were not genetically distinct, and there were no differences in diversity among migratory and non-migratory bird species. Overall, the Blue Tit exhibited low MHC diversity compared to other passerine species.

In Chapter 6, Schut describes how the MHC screening method, reference strand mediated conformation analysis (RSCA), was applied to separate MHC alleles. The method uses fluorescently labelled reference strands that are hybridized to the PCR products to be screened. These hybrids are separated according to their specific mobility in a non-denaturing environment. This technique provides an advantage over other

indirect typing methods as it enables the differentiation of highly similar alleles. However the application of next generation sequencing methods for MHC genotyping is replacing the use of indirect typing methods, especially in species necessitating multilocus typing. Nevertheless, Schut showed that individuals have between 2-8 MHC class I alleles, and estimated that the Blue Tit has at least four functional MHC loci.

In Chapter 7, Schut then applies the RSCA method to screen 14 known Blue Tit pairs to investigate MHC based mate choice. She shows that MHC class I heterozygosity was positively correlated between the female and her social partner. However there was no indication that MHC heterozygosity or similarity between mates had an effect on the likelihood that the social male was cuckolded. In conclusion, Schut revealed evidence for MHC-based assortative mating in terms of MHC heterozygosity in the Blue Tit.

Elske Schut's thesis successfully confronts two significant methodological challenges: investigating post-copulatory mechanisms of sexual selection in a wild species and examining the molecular basis of mate choice decisions in a non-model wild bird species using a previously undescribed, complex genetic region. Her findings suggest that sexual selection occur both pre-copulatory and post-copulatory in the Blue Tit, and provide a solid first step towards understanding both the factors determining the number of sperm in the female reproductive tract, and the mechanisms by which selection can operate on MHC class I genes. Furthermore, the thesis is very well written, hypotheses are clearly stated, and methods are nicely presented, all of which made reading this thesis particularly enjoyable.

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