



## PhD-Dissertation Reviews

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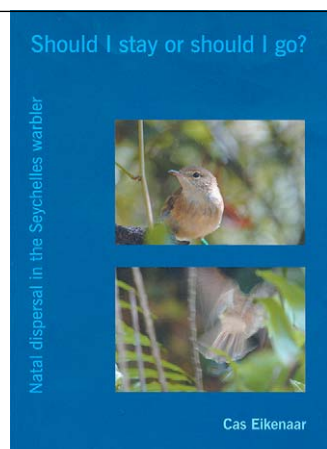
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**Eikenaar C.** 2008. Should I stay or should I go? – Natal dispersal in the Seychelles warbler. PhD-thesis University of Groningen, The Netherlands. ISBN 978-90-367-3338-0. Paperback, 144 pp. Available at: [http://dissertations.ub.rug.nl/FILES/faculties/science/2008/c.eikenaar/01\\_c1.pdf](http://dissertations.ub.rug.nl/FILES/faculties/science/2008/c.eikenaar/01_c1.pdf).



If a bird is to reproduce, it has to find a place to breed. Often, an individual cannot breed in the

place it was born, so it has to move. This makes natal dispersal, the movement from the place of birth to the place of first breeding, an extremely important life history parameter. Unfortunately, the study of natal dispersal is fraught with difficulty. The most important problem is that birds may move out of one's study area. Because we don't know where such birds go, we cannot obtain a reliable estimate of dispersal distance. Ideally, one would like to study a population where one could be sure that the birds do not leave the study area. It would be even better if one would be able to individually mark every individual in the population and follow its movements over the course of its life. Better still, it would be great if one could create breeding vacancies artificially, preferably without harming the individuals that you take away. Obviously, few study species combine all these properties. Enter the Seychelles warbler. Confined to several small islands in the Indian Ocean, with the entire population on one island individually colour-banded, they make an ideal system in which to study natal dispersal. The whole island is saturated with breeding territories (and has been for many years), severely limiting the dispersal options for young birds. Helping-at-the-nest occurs frequently as an alternative to independent breeding. In his thesis, Cas Eikenaar examines many aspects of dispersal in this system. The backbone of the thesis is formed by a translocation experiment, in which birds are removed from their territories and transported to another island. This experiment was part of ongoing conservation efforts for this species. Similar experiments have been spectacularly successful in the past (Komdeur *et al.* 1995). By watching what happens in the vacancies created in this way, Eikenaar was able to test some of the hypotheses experimentally.

The thesis starts by describing some basic patterns of dispersal in the Seychelles warbler (chapter 2). Given that the study site, Cousin Island, measures only 29 ha, it could well be that all birds

can in principle move to any vacancy anywhere on the island. If so, one would not expect to see the female-biased natal dispersal common to most birds. Perhaps surprisingly, a sex-bias was apparent in the data. Males usually moved to fill breeding vacancies in nearby territories, especially when there were many other territories close to their natal territory. Females tended to move further away (four territory-widths on average) and their dispersal distance was not influenced by local breeding density.

So Seychelles warblers are like other birds; females breed further from their place of birth than males. But why? A popular idea is that by moving different distances, brothers and sisters end up in different places, which should help to avoid inbreeding. Chapter 3 examines whether dispersal patterns help to avoid inbreeding in the Seychelles warbler. Using the extensive data on microsatellite genotypes that is available for this population, Eikenaar calculates a "relatedness landscape"; the pairwise relatedness between focal individuals. For example, one can estimate the relatedness of a newly dispersed female to her new mate and compare that to her relatedness to all candidate males in the population. No evidence for inbreeding avoidance was found. Chosen mates actually appeared to be more related to the dispersing individual than the average candidate males. Individuals did not disperse further when there were many closely related individuals in adjacent territories. Territory inheritance (either in naturally occurring vacancies or those created in the removal experiment) was not more likely with a stepparent than with a parent. Last, there was no clustering of related males around the natal territories of dispersing females and vice versa. Thus, by dispersing further, females did not avoid concentrations of related males. The apparent lack of inbreeding avoidance in the Seychelles warbler is puzzling. Eikenaar suggests a combination of low cost to inbreeding and an advantage of short-distance dispersal. Inbreeding may not be very costly in the Seychelles warbler because recessive deleterious alleles that are harmful when homozygous would have been purged from the population dur-

ing the early part of the twentieth century when the entire population was reduced to c. 30 birds. On the other hand, individuals of both sexes have an advantage when competing for breeding vacancies in nearby territories over birds from further away. While these considerations may explain the lack of inbreeding avoidance mechanisms, it leaves us without a satisfying explanation for the sex-bias in dispersal distance. Eikenaar finds little merit in alternative explanations for sex-biased dispersal that have been proposed. In the end Eikenaar muses that sex-biased dispersal in the Seychelles warbler may not be adaptive at all, but just a genetic hang-over from the selective forces that shaped its ancestors.

Dispersing off the natal territory is of course only the start of an individual's quest for fitness. In order to reproduce, it has to obtain a breeding position. In a cooperatively breeding species like the Seychelles warbler this is not completely true, since an individual can gain some fitness through kin selection by helping his or her parents raising younger siblings. In fact it is even less true for females than for male. Many subordinate females lay eggs in the same nest as the dominant female. The father of all the eggs in the nest, however, is always the dominant male and never subordinate males. Thus, one might expect males to be more eager to obtain a breeding position than females. Chapter 4 examines this prediction and other aspects of territory acquisition. Here, the translocation experiment comes into its own. By removing birds permanently from their territory Eikenaar and his colleagues artificially created breeding vacancies and were able to monitor closely how these were filled. The 37 vacancies that were created in this way were filled in various ways. Six were annexed by expansive neighbours, two were still not filled after three months, but the majority of vacancies were taken up by birds that were previously subordinate on another territory (more rarely on the same territory). Perhaps surprisingly, this appeared to be a fairly peaceful affair that was usually settled in a few days and without major battles. However, more subtle competition must have gone on, at least among males, because

older males were more likely to obtain the position than younger ones. Data from naturally occurring territory acquisitions suggested that age was more of an issue for males than for females. Females that acquired a breeding position did so at an earlier age than males.

The finding that older candidates are more likely to fill a breeding vacancy than younger ones, means that Seychelles warblers are forced to wait until they are old enough to compete successfully for a breeding position. Given that all the available habitat is taken up by territories, the most obvious place to wait is on the natal territory. Selection should favour parents that tolerate mature offspring on their territory if this enhances their chance of becoming a successful breeder later in life. Parents may gain some additional benefit when loitering offspring help raise the new brood of their parents, as in the Seychelles warbler. Chapter 5 examines what happens when the dominant birds on your natal territory are not your parents. This sometimes happens naturally when one or both of the dominant birds are replaced by unrelated adults at a time when the subordinates present are still too young to take over the territory. Furthermore, this situation was created artificially in the translocation experiment. The results of both datasets show the same pattern: when one or both of the parents is replaced by an unrelated individual, many of the young (<1 year old) subordinates leave the territory. Presumably, the step-parents do not tolerate the offspring of the previous territory owner. It turns out that having to disperse at an early age is a bad thing for these birds. Of 27 individuals that dispersed within their first year of life off a territory with both parents, 18 did so to fill a breeding vacancy. By contrast, only 4 out of 16 first-year individuals that dispersed when one of their parents was replaced obtained a breeding position.

In chapter 6, Eikenaar leaves the topic of dispersal distance and considers the timing of dispersal. In his recent data he finds no sex-bias in the likelihood of dispersing during the first year of life. This must come as a bit of a surprise to those familiar with older work on the Seychelles warbler

(it did to me at least). We were always taught that in the Seychelles warbler, the males dispersed and floated in search of a new vacancy, while females stayed in the natal territory. Well aware of this, Eikenaar compares his data to that collected between 1985 and 1994. There turns out to be a significant difference, mainly due to the females tending to disperse earlier in life in recent years. Explaining such a pattern necessarily involves a bit of arm-waving, but intimate knowledge of the study system allows Eikenaar to come up with a plausible hypothesis. Measurements of territory quality (including factors such as vegetation cover and insect availability) have changed drastically over these years. During the period 1985–1994, territory quality varied considerably, with some territories of very low and some of very high quality. Due to vegetation succession, this variation has disappeared in recent years, with all territories now being of fairly low quality. As a consequence there are no longer very good territories with enough resources to accommodate many female helpers.

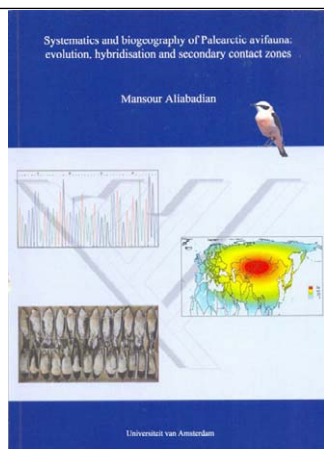
Chapter 7 is the odd one out and deals with the timing of extra-pair fertilizations in relation to mate guarding.

All in all, Eikenaar's thesis is a very nice piece of work that shows that a lot can be learned about dispersal from a species in which the maximum dispersal distance is about 500 meters. Eikenaar highlights several pitfalls that others should keep in mind when studying this topic. The challenge now is to integrate these findings in a coherent framework, involving genetic constraints in sex-biased dispersal distance as well as plasticity in the timing of dispersal.

Komdeur J., Huffstadt A., Prast W., Castle G., Mileto R. & Wattel J. 1995. Transfer experiments of Seychelles warblers to new islands: changes in dispersal and helping behaviour. *Anim. Behav.* 49: 695–708.

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**Aliabadian, M.** 2007. Systematics and biogeography of Palearctic avifauna: evolution, hybridisation and secondary contact zones. PhD-thesis University of Amsterdam. ISBN 978-90-76894-80-5. Paperback, 142 pp.



It is an exciting experience to watch the instrumental development of a scientific discipline in one person's work as is the case in this thesis. Here themes like hybridisation, the character of hybrid zones, relatedness between species, phylogenetics and geographic species richness patterns are studied with morphometric, statistical and genetic data. The first six chapters of Aliabadian's thesis concern modified versions of earlier publications (chapter 1 and 2) and unmodified versions of earlier publications with some minor additions (chapters 3 to 6). The final three chapters present brand new results.

Aliabadian appears to have two aims with this thesis. The first is "to explore the biogeography and systematics status of Palearctic avifauna with emphasis on those species that hybridise and/or that occur in secondary contact zones". The second aim is "to reveal new information on the date, origin, and correlation of the geographic distribution of parapatric species in the Palearctic region". The efforts of Aliabadian and his co-workers concentrate in the first three chapters on species richness patterns and hybridisation processes in Palearctic species occurring in secondary contact zones. These

being the zones where closely related species came into secondary contact after a process of speciation from a common ancestor due to separation during one or several of the (inter)glacials. Information on the distribution of all closely related parapatric species of the Palearctic avifauna, that hybridise or make secondary contact zones, was brought together and analysed. Parapatric species are species having contiguous geographical ranges, which are not overlapping. Analysis was possible after constructing a large database of digitized distribution maps of Palearctic birds.

The first introductory chapter is a modified version of an earlier publication and concentrates on the incidence of avian hybrids and the geographic distribution of hybridisation in the Palearctic region. This zone contains important areas of secondary contact between the East and West Palearctic and along the southern regions of the Palearctic bordering the Saharo – Sindian desert to Turkmenistan. In this chapter the borders of the Palearctic region are defined and the zones of secondary contact are recognized in relation to the climatic conditions having occurred since the Ice Age. Aliabadian distinguishes between hybridisation parapatry and ecological parapatry. In the first situation there is a narrow hybrid zone between a parapatric species pair and in the second situation a small zone of overlap without hybridisation. Attention is then paid to the incidence of hybridisation in 23 orders of birds. Up to 19% of the species hybridise and in 86% of these cases the ranges of interbreeding populations overlap and in only 10% the ranges contact but do not overlap.

In order to study the hybridisation patterns in more detail a database was constructed with distribution maps of 3036 phylogenetic species of Palearctic songbirds corresponding with 537–662 biological species. This database is introduced in the second chapter and is used to analyse range sizes and patterns of diversity and distribution of Palearctic songbirds. About 25% of the taxa appear to have range sizes smaller than 110 000 km<sup>2</sup>, while 25% of the species have ranges larger than 1 040 000 km<sup>2</sup>. So-called 'hotspots' are introduced being defined by a large species richness

and a large degree of endemism. Areas with a high diversity of songbirds mainly concern mountainous regions and areas with a high degree of endemism were often recognized on islands (as could be expected), and along the southern borders of the Palearctic.

In the third chapter the 'mid-domain effect' is introduced. I was not familiar with this effect, so I learned about authors, who claimed that geometric constraints alone were enough to explain diversity gradients and species richness patterns: no biological mechanisms were needed! The so-called MDE-effect models generate purely by chance a mid-domain peak in species richness in the centre of the domain. These models can be both one-dimensional (latitude) and two-dimensional (also longitude). Given the results from the preceding chapter 1 would also expect 3-dimensional models (mountainous regions being rich in species), but these do not seem to be developed as yet. However, the predictive power of these bi-dimensional MDE-models generally appears to be less than 25%, whereas models including environmental factors generally have predictive power larger than 75%. The distribution data were used to assess the predictive power of such a 2-dimensional MDE-model, and the predictive power appeared to be low, since hotspots were not only located in the central parts of the Palearctic. Oppositely, coldspots could also be located there. MDE-models thus failed to explain a significant proportion of the observed variation, which also seemed logical to me as an ecologist. But it always nice to have it shown.

The fourth chapter focused on the identification of contact zone hotspots in Palearctic passerines using the dataset of the second and third chapter. Hypotheses to explain the causation of contact zone patterns are summarized by Aliabadian and include both historical (e.g. refuge) and geometrical ones (e.g. MDE from earlier chapter). In total, 52 phylogenetic species pairs appear to contact in the Palearctic and nearly all are found along a series of mountain chains in the Middle East, central N Asia, SW Asia, S Europe and NW Africa. Again the MDE-models had a low

predictive power.

The chapters 5 to 7 deal with some specific cases: the phylogeny of Palearctic wheatears, hybridisation in divers and hybridisation between the Lesser and Greater White-fronted Geese. Molecular and morphometric data were used to unravel the phylogenetic relationships in wheatears. Three clades were recognizable in both the molecular and morphometric data. However, the results differed from earlier published ones, due to the variable recognition in the past of taxa as species, subspecies, hybrids or colour-morphs. Aliabadian and his colleagues also warn against a too exclusive attention for the chromatic characters, when studying colour morphs. The divers are a small order with few species and the incidence of hybridisation in these orders is thought to be generally small. One specimen collected at Schellingwoude (The Netherlands) in 1890 appears to be such a hybrid between a White-billed and a Great Northern Diver. Morphometric and plumage characters nearly always fitted with either of both parents and in one character it was intermediate. Aliabadian and colleagues present information that hybridisation in the group of divers is quite common and thus not in agreement with the general ideas. Thirdly, two hybrids of the Lesser and Greater White-fronted Geese were identified in the museum collections of Amsterdam and Leiden. Hybridisation between both species is interesting due to the recent debate raised by the Swedish captive breeding project, where hybridisation was evident and declared unwanted. It even resulted in the Netherlands in not to consider these Lesser Whitefronts formally to represent a natural population when wintering in the Netherlands. Hybridisation between Greater and Lesser Whitefronts is shown in this thesis to have occurred in the past under natural circumstances with at least 2 hybrids against 47 Lesser Whitefronts. These results must be used to strengthen the efforts for safeguarding the Fennoscandian population of Lesser White-fronted Geese and to protect their recent but regular wintering grounds in The Netherlands.

The 8th chapter returns to the avian hybrid zones in the Palearctic and the mid-domain effect

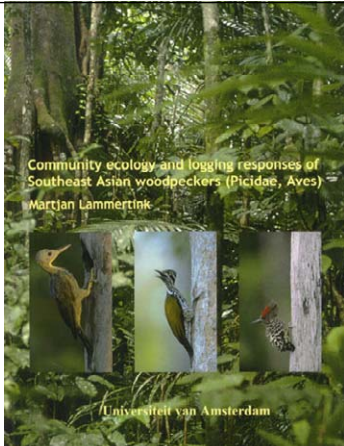
(MDE). The data set of the birds is restricted to the hybridising parapatric species pairs. These species pairs are presented. The maps are now digitized in ArcGIS. The MDE is included again in the analyses even though it performed so bad in two earlier chapters. Also four environmental predictors (net primary production, elevation, elevation heterogeneity and vegetation heterogeneity) are included in order to predict the occurrence of hybridisation cold- and hotspots. In the second part of this chapter cytochrome b sequences are used to estimate the divergence times of 22 of the 61 species pairs analysed. The abstract of this chapter also promised results with respect to the relationship between climatic and environmental variations, but they were lacking (or 'elevation' had to function as such). The rich areas of hybridisation appear to be rather the same ones as presented in chapter 4 and the MDE-effect has low predictive power again. The environmental predictors did somewhat better, but they also explain only 8 percent of the variance with elevation and elevation height scoring best. And why should they do better? To me, it appears strange to include the distribution of a species pair like *Larus argentatus* and *cachinnans* in an analysis with variables like elevation and net primary productivity without the inclusion of factors like water availability or salinity. It is against all logics. Nevertheless, hybridisation needs species-pairs having diverged for whatever reason in earlier times. Therefore genetic distances were measured and divergence times calculated with  $2 \pm 0.5\%$  divergence per million years. It is a pity, that the calculated divergence times with their 95% confidence intervals are not presented properly per species pair and being reflected against the background of the geological timescale of (inter)glacials. I admit, it is due to my forgetfulness with respect to the timing of the (inter)glacials, but for the reader's convenience... It should also have increased our understanding, since then the divergence times could have been combined per hybridisation hotspot and simultaneous processes of divergence in different species pairs could then have been allocated. However, it can still be done.

The final chapter continues with analysing the sequence diversity in mitochondrial DNA of 2719 phylogenetic bird species. In this chapter the effectiveness of cytochrome c oxidase subunit 1 (*cox 1*) for species recognition on a global scale is studied. I learned from this chapter, that generally *cox 1* has been successful in species recognition, but not in distinguishing between closely allied allopatric taxa or between hybridising sister taxa. Expecting better differentiation, DNA-sequences of cytochrome b (*cob*) and 16S (two other mitochondrial genes) were gathered and analysed with the attention focused on the hybridising parapatric species pairs of the Palearctic. The calculated genetic distances between both members in hybridising parapatric species-pairs appeared to be small for all three genes, but they nearly doubled for *cox 1* and *cob* in non-hybridising species-pairs. The mean genetic distances of non-hybridising and hybridising species-pairs were rather the same for 16S. The study showed, that more than 50% of the parapatric species-pairs (both hybridising and non-hybridising) cannot be distinguished based on the genetic distances for these three genes. These results thus enforce the ones of the earlier studies. The authors reach over two explanations. One is, that some individuals in one species are closer to the ones of another species than to conspecifics. The other is, that the start of speciation was too recent to result in large enough genetic divergences. Which one is true, remains to be sorted out for the future.

This thesis includes the great changes in bio-systematics, since all the genetic techniques and statistical tools became available in recent times. This thesis shows how the somewhat dreary science of systematics has changed in a very short time period in a very modern science providing many new results. Mansour Aliabadian is thanked for sharing his efforts and results with us. He learned me a lot! Nevertheless I should have skipped that so-called 'MDE-effect' from the front cover, since it is nothing more than an UFO!

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**Lammertink J.M.** 2007. Community ecology and logging responses of Southeast Asian woodpeckers (Picidae, Aves). PhD-thesis University of Amsterdam. Paperback, 139 pp.



Woodpeckers are an intriguing group of bird species that attract both naturalists and layman. Who hasn't come across an enthusiastic neighbour telling you he saw a 'spotted' woodpecker. Most birdwatchers however, leave it at that and don't make a study of these forest-dwelling birds. And indeed, is not easy to study forest birds and especially a species group that always tends to be on the other side of the tree. Martjan Lammertink is one of the rare birdwatchers that spend almost all their time in forests chasing woodpeckers. In the nineties he spent a lot of time looking for Black Woodpeckers and chasing the ghosts of the near-extinct Ivory-billed Woodpecker on Cuba (which was most likely recovered in 2004 in Arkansas (Fitzpatrick *et al.* 2005; Fitzpatrick *et al.* 2007)). After his MSc-work on forest birds in Mexico he envisaged himself working on the spectacular woodpeckers of southern America. But it turned out to be very different. On a hint of Jan Wattel he found himself in Indonesia studying the very large but drab, thin-necked Great Slaty Woodpecker and 13 other sympatric woodpecker-species. Research in tropical rain forests cannot be compared with research in temperate forests. Martjan had to cope with mosquitoes, malaria, hostile native people,

transportation problems, permit problems and many other challenges before and during his research. Fortunately he also met a lot of nice and cooperative people and married even with one of them.

His research aimed at describing the possibilities of using woodpeckers as indicators for forest disturbance in Indonesia. The Sundaic region (Borneo, Sumatra, Java and Peninsular Malaysia) are amongst the most species-rich ecosystems in the world. The lowland-forests in this region host the most diverse woodpecker community in the world. This would therefore be ideal to study the effects of selective logging on the forest community. Moreover, within the region numerous small islands can be found that became isolated from the mainland since the last Ice-age (<10 000 years ago). This would be ideal to compare the expected niche-shifts from logging, and therefore isolation of undisturbed forest, with the long-term isolation effects on the islands. Martjan conducted most of his research in Gunung-Palung National in Kalimantan (the Indonesian part of Borneo). This park hosts the last large remaining (near-)undisturbed track of primary lowland-forest on the island. Here an estimated 7000 ha of truly undisturbed forest was left in 2000, a far cry from the large areas of this forest type that once covered the region. Up till now almost all preservation attention has been focused on hill forests. However, Martjan discovered that hill forests can by no means be a substitute for the protection of the biodiversity of lowland forests.

After the introduction the first topical chapter, published in Conservation Biology, Martjan describes the influences of selective logging on the composition of the woodpecker community. The quantity of timber removed (cut basal area) proved to be a better predictor for woodpecker density than the proportion of the area that remained unlogged. The time since logging, which varied from 3 to 22 years, had little predictive value. Even in heavily logged lowland forests he found the woodpecker density, biomass and diversity to be lower than in undisturbed hill forests. One species, that drab Great Slaty Woodpecker



that he became to love during his studies, proved to be the best indicator for forest disturbance and was totally absent from hill forests. The world population of this woodpecker is therefore greatly dependent on undisturbed lowland forests.

The next chapter describes the foraging differentiation between the 14 studied woodpecker species. An interesting behavioural aspect of Sundaic woodpeckers is that they often forage in mixed groups with other woodpecker species. Separations in foraging strategies were primarily observed in height strata and microhabitats and secondarily in substrate manipulation and search behaviour. However, species with comparable body masses mainly differed in behavioural aspects. Body mass proved to be a good predictor for foraging strategy in most species. The largest species however, the Great Slaty Woodpecker, showed a very different foraging strategy with much more relatively small habitat elements compared to its body mass. This may indicate that for very large woodpeckers good foraging substrate (large diameter and rough-barked trees) is rare, even in undisturbed forests.

Chapter four describes the evolution of niche differentiation resulting from the long-term isolation of woodpecker habitats. As a result from the rise of the sea level since the last ice many forests have become isolated on islands. The same process is happening nowadays due to clear cuts or logging of forests. Both processes result in fragmented patches of forest. Martjan compared the occupied niches on the islands with the niches on the mainland. Most islands have lost one to many of their woodpecker species in the last 10 000 years. He found that niche-shifting towards vacant niches is common phenomena on these islands. The most striking example was found on the island of Simeuleu, that became separated from the mainland more than 10 000 years ago. Here only one woodpecker species survived, but decreased 39% in body mass as compared the individuals on the mainland. However, the total body mass density of these woodpeckers was three as time as high as total woodpecker body mass on the mainland. This suggests, that evolutionary adaption occurs only a time-scale of >10 000 years.

The next two chapters focus on the largest woodpecker species of the region, the Great Slaty Woodpecker. This is the second or third largest woodpecker species in the world, depending on the current survival of the Ivory-billed Woodpecker. Its body weight is around 430 grams, which is large compared to the more commonly known Eurasian Black Woodpecker (300 grams) and American Pileated Woodpecker (250–350 grams). A striking feature of the ecology of Great Slaty's is that the majority of the birds live in groups. Out of 36 independent units, 81% involved groups of three to six birds. Also the care of nests is not restricted to the traditional male-female relationships. In one of the two nest that he found, two males and one female took care of the nest. The fact that only two nests were found, shows also why the nesting ecology is so poorly known: is it simply very difficult to find nest of this species. In 18% of the groups, the Great Slaty's were joined by White-bellied Woodpeckers. This is the second largest woodpecker species of the region (250 grams). The social status of the Great Slaty has probably evolved from the difficulty in finding food resources for such a large woodpecker: flocking behaviour might benefit the chances of finding suitable food resources.

In 2007 the IUCN has listed the Great Slaty Woodpecker as a Red list species of least concern: the world population is bigger than 10 000 mature individuals and the decline was thought to be less than 30% in three generations. Martjan debates this choice in chapter 6 where he evaluates the population decline and Red list status of the species. Since no trend data exist for the Great Slaty, he used another way to estimate the trend of the species. The density of the species was estimated in 21 transects throughout the core range of the species in southeast-Asia: west-Borneo, Indonesia and Myanmar. Logging intensities varied from no logging to intensive logging in the transects. The hard field work resulted in a range of densities for varying degrees of logging in the region. Next he estimated the amount of primary, old growth and disturbed forest within the region. Combining the two information sources he estimates

that world population of the Great Slaty Woodpecker has declined by approx. 60% over the last three generations (18–24 years). The species should therefore be categorized as IUCN Vulnerable or Endangered.

Martjan finishes his thesis with the conclusion that the woodpecker community of the lowland forests of the Sundaic region (SE Asia) is in severe peril. Logging, even selective logging, has severe effects on the woodpecker community. Although he discovered that most woodpecker species are able to invade vacant niches as a result of the local extinction of species, it is likely that evolutionary adaption takes a time span longer than 10 000 years. A question still left to be answered is the rate of niche-shifts in logged forests. Only a small fraction of primary lowland forests remains and is still under heavy pressure of logging or clear-cutting. Forest reserves in the hills are not enough to maintain the woodpecker diversity on the long run. Especially the Great Slaty Woodpecker is dependent on large tracks of undisturbed old growth lowland forest. Without huge conservation efforts it is very likely that the species will suffer the same fate as the Ivory-billed Woodpecker. This thesis should provide ample evidence for nature conservation organisations in the region to take the protection of lowland primary forest at hand and convince governments to install large nature reserves for the protection of their unique biodiversity.

- Fitzpatrick J.W., Lammertink M., Luneau M.D., Gallagher T.W., Harrison B.R., Sparling G.M., Rosenberg K.V., Rohrbaugh R.W., Swarthout E.C.H., Wrege P.H., Swarthout S.B., Dantzker M.S., Charif R.A., Barksdale T.R., Remsen J.V., Simon S.D. & Zollner D. 2005. Ivory-billed woodpecker (*Campephilus principalis*) persists in continental North America. *Science* 308: 1460–1462
- Fitzpatrick J.W., Lammertink M., Luneau M.D., Rosenberg K.V., Gallagher T.W. & Rohrbaugh R.W. 2007. Ivory-billed or pileated woodpecker? Response. *Science* 315: 1495–1496.

#### Publications from this dissertation

- Lammertink M. 2004. Grouping and cooperative breeding in the Great Slaty Woodpecker. *Condor* 106: 309–319.
- Lammertink M. 2004. A multiple-site comparison of woodpecker communities in Bornean lowland and hill forests. *Cons. Biol.* 18: 746–757.

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- Veen T.** 2008. Mating decision in a hybrid zone. PhD-thesis University of Groningen.  
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As also reiterated as the first ‘statement’ in this thesis, hybridisation ‘*may be the grossest blunder in sexual preference which we can conceive of an animal making*’ (Fisher 1930). While this may often be true, this thesis explores some of the circumstances and reasons when it may not, by studying the context and costs as well as possible benefits of hybridisation between the Collared Flycatcher *Ficedula albicollis* and the Pied Flycatcher *F. hypoleuca*. These two species are quite different in

plumage and vocalisations, yet frequently hybridise (about 2–5% of all pairs) despite the fact that hybrid offspring have a low fitness.

This thesis is comprised of eight chapters, of which several have already been published in peer-reviewed international journals. Chapter 1 gives an overview of the topics covered and the structure of the thesis. Various aspects of the reproductive process are treated sequentially and it is reviewed for birds in general why hybridisation may occur, and what its negative or positive consequences can be. From this treatment it becomes clear that there are surprisingly many potential benefits to hybridisation, especially when the social aspects of forming a heterospecific pair bond are included, such as reduced searching costs for (rare) conspecifics, a better territory, more parental investment, reduced overlap of resource use, increased genetic or ecological hybrid vigour, and increased hybrid attractiveness. The various costs and benefits of hybridisation across the stages of an organism's life cycle are summarised in a useful table. Since these costs and benefits will be quite specific to certain combinations of hybridising species, we need these to be estimated in different study systems, and this thesis contributes to this effort for the flycatchers. Next comes a presentation of the details of flycatcher biology and hybrid zones. Included are 19 attractive colour photos of flycatchers and habitats. It becomes clear that while some hybrid males may be easily identified, this is not the case for others and especially not so for females. It is thus reassuring to read that hybrids were generally identified by the co-occurrence of species-specific genetic markers in the same individual. Also noteworthy is the comment that so far all flycatcher hybridisation studies have been conducted in areas where Collared Flycatchers predominate: would similar studies in areas where Pied Flycatchers predominate give identical or symmetric results, or show some surprises?

In chapter 2 the results of an important earlier study are revisited (Veen *et al.* 2001). There it was found that female Collareds mating with male Pies have lower costs of hybridisation than

expected. Hybrid females are sterile, but males are not, and hybridising females were found to have a larger than normal proportion of males in their nests, reducing the cost of hybridisation. It was also found that a larger than normal proportion of chicks was not fathered by the social mate (the Pied male), but in all cases they were actually fathered by a Collared male. So to some extent the females appeared to us to be hybridising, but actually were reproducing with a conspecific. Finally, later in the breeding season hybridising females fledged more chicks than non-hybridising females, and this advantage was even large enough to overcome the remaining negative aspects of still having a few hybrids in the nest. However, it was not clear what underlying mechanisms caused these patterns: did female Collared Flycatchers adaptively manipulate their offspring sex ratio and seek conspecific extra-pair fertilisations, or is there some sort of unselected conspecific sperm precedence and early mortality of female hybrids? In order to distinguish between these explanations, male Collared Flycatchers were caught and painted to look like Pied Flycatchers before they obtained a mate. If female Collared Flycatchers mating to such individuals would change their sex ratios and mate more often with other males, then this would support the adaptive female behaviour scenario. But in fact no such effects were found, which favours the explanation that not active behavioural but more passive genetic interactions are responsible for the earlier reported patterns.

Chapter 3 tries to elucidate why hybridising females had a higher fledging success than non-hybridising females later in the season. Using infrared cameras installed in the nest boxes, it was determined that Collared and Pied Flycatchers are not using different food resources, and that male Pies are not better fathers than male Collareds. However, by comparing the average reproductive output (brood mass) of pure Collared Flycatcher pairs using nest boxes only ever used by Collared Flycatchers to those using boxes sometimes also used by Pied Flycatchers, it was demonstrated that hybridising females breed in territories that do not suffer the same seasonal decline in habitat quality

that is experienced by females breeding with conspecifics. Thus a female Collared Flycatcher benefits from mating with a male Pied (or choosing his territory?) later in the season because on average he has a better territory for raising offspring. In the next chapter (4) it is shown that this can be explained by a difference in the timing when most food is available in these territories (as measured by the amount of caterpillar droppings), which is probably related to a difference in the vegetation structure around the nest box (as measured by tree species and size composition).

There are many potential reasons why hybrids may be less fit, but they are not all equally easy to study. One mostly untested suggestion has been that in migratory species hybrids suffer because they might use suboptimal intermediate migration routes and wintering sites. Chapter 5 is a nice example of how to test for such effects when the individuals actually cannot be followed directly. First, there did not seem to be a reduced annual survival of hybrids relative to pure individuals, which suggest that perhaps hybrids do not migrate and winter in suboptimal habitats. Second, analysis of the stable isotopes of feathers moulted on the wintering grounds indicated that isotope signatures differed between Collared and Pied Flycatchers, but hybrids strongly resembled Pieds. Hence, the authors conclude that migration route and wintering areas may have a dominant genetic determination, which in this case 'saved' hybrids from following a suboptimal annual migratory routine.

Given the fact that the flycatchers hybridise at a non-zero rate, that male hybrids are fertile and do not suffer from reduced survival, and that the two species have largely overlapping distributions, one might wonder if perhaps these two species are in the process of fusing completely in the future. This fusing would be promoted if the genetic linkage between the male traits that females prefer and the preferences for these traits that currently exists in the two species is dissolved by hybridisation. Therefore the location of genes for traits and preferences was investigated in chapter 6 by cleverly comparing the mating status of hybrids and

cross-fostered females and males. This chapter stands out from the others in that the focus is not on the costs and benefits of hybridisation in the context of individual variation, but on species-traits that limit hybridisation *per se*. Nevertheless, the results are very interesting and relevant to understanding hybridisation and mating patterns in this system. Since female hybrids strongly biased their matings towards the species of their genetic father, there does not seem to be a role for the autosomal chromosomes to influence mate choice. Next, pure females growing up in a nest with a heterospecific foster-father (either due to extra-pair fertilisations or experimental cross-fostering) mated the same as pure females that were not cross-fostered: this indicates that females did not imprint on their foster-fathers in order to find a suitable mate. This leaves the Z sex-chromosome as the location for genes for mate choice. Since plumage traits were earlier shown to be located on this same chromosome, and sex chromosomes do not seem to recombine between the species, the genetic linkage between sexual traits and preferences is to a large degree protected from disruption by hybridisation. One could wonder if possibly there is (species) selection on sexual traits to reside on sex chromosomes, and thus whether this pattern may be expected to be quite general.

This thesis is surprisingly empirical for having been performed in a theoretical biology group, but chapter 7 explores an interesting and underdeveloped aspect of sexual selection theory: what happens to the evolution of a sexual trait if it functions in both intra- and intersexual selection (such as the flycatcher forehead patch)? Through simplified yet still complex modelling it is found that the evolutionary equilibrium values attained by dual function traits can differ from those of single function traits, and that the use of a trait in one context (say female choice) can facilitate its use in another context (say male-male competition). The authors are very careful in pointing out the many assumptions made and problems yet to solve, so the insights are perhaps best interpreted as being preliminary. Yet the study does confirm that single versus dual function can make a difference to a

sexual trait, and there are many examples of traits that do function in both contexts in nature, so it seems imperative that more theoretical attention is devoted to this topic.

In the final chapter the various aspects treated in the first chapter are reviewed again, but then specifically for the flycatcher system. Here the author lists results obtained from other studies together with the results from his thesis, and how these contribute to our understanding of costs and benefits of hybridisation for this system, with an especially useful overview provided by the same table as used in chapter 1. Overall, it appears that female Pied Flycatchers do not normally benefit from hybridisation, and neither do male Pied or Collared Flycatchers. However, under some circumstances (late in the season), female Collareds may benefit, which can partly explain why these species do hybridise at times.

In general, this thesis is well-written and mostly easy to read. Perhaps as a function of having been published in high-impact journals, the main text of several chapters is concise and streamlined. It also becomes clear that in a system with so many contributing investigators over so many years, insight becomes more detailed, effects can be estimated with more precision, and some fundamental or novel research questions can finally be addressed. As such, this thesis is not only a testament to the author's accomplishments, but also to the value of long-term collaborative projects.

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