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l'habilitation à diriger des recherches**

**CAUSES, MECANISMES ET CONSEQUENCES
DE LA DISPERSION: UNE APPROCHE COMPORTEMENTALE**

*ETUDES EMPIRIQUES DANS UNE POPULATION FRAGMENTEE
NATURELLE*

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CAUSES, MECHANISMS AND CONSEQUENCES OF DISPERSAL: A BEHAVIOURAL APPROACH

EMPIRICAL STUDIES IN A FRAGMENTED NATURAL POPULATION

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FOREWORD: GENERAL PRESENTATION OF THE RESEARCH WORK

Context, general presentation and organisation of the work

Global changes due to human activities lead to a major challenge in terms of biodiversity conservation. Natural populations indeed face large and brutal environmental variations induced by these activities. Behavioural flexibility is one of the most efficient ways for individuals to face such variations (Duckworth & Badyaev 2007). In particular, dispersal (Clobert *et al.* 2001; Clobert, Ims & Rousset 2004; Bowler & Benton 2005; Ronce 2007) to new habitats is a solution to escape the degradation of local environmental conditions. Dispersal is defined as the movement of an individual from its natal site (natal dispersal) or its previous breeding site (breeding dispersal) to its subsequent breeding site (Greenwood & Harvey 1982; Clobert *et al.* 2001). Dispersal has long been considered as a key life-history trait for evolutionary and ecological processes in the wild because of its influence on the structure and dynamics of populations and communities (Clobert *et al.* 2001; Bullock, Kenward & Hails 2002; Clobert *et al.* 2004; Ronce 2007) and on gene flow between populations (e.g. Postma & van Noordwijk 2005). The role of dispersal in shaping changes in spatial distribution of species, either natural or human-induced, has however only recently been emphasized, although successful colonisation of a new habitat is the first crucial step in population dynamics and speciation processes (Kokko & López-Sepulcre 2006; Duckworth & Badyaev 2007). Dispersal can also be a key process in the dynamics of biodiversity because of its potential to accelerate population differentiation, which, again, has only recently been emphasized. Indeed, dispersing individuals are rarely a random sample of populations with respect to many potential traits (Garant *et al.* 2005; Postma & van Noordwijk 2005; Duckworth & Badyaev 2007) and dispersal movements themselves are not random (Edelaar, Siepielski & Clobert 2008). Dispersal could therefore favour oriented gene flow and local adaptation processes, challenging the classical view of dispersal as a population homogenising factor. As a consequence, in order to understand the influence of dispersal on the adaptive potential of populations and predict expected changes in spatial distribution of populations, thus variations in local biodiversity, a topical issue, it is necessary to understand the mechanisms and consequences of dispersal.

Because of its manifold and crucial effects, dispersal has been the subject of many theoretical and empirical studies over the past decades, and still remains a very active field of research nowadays (Clobert *et al.* 2001; Clobert, de Fraipont & Danchin 2008). Theoretical studies have mostly helped identifying the ultimate causes of dispersal, linked to environmental variation (Clobert *et al.* 2008). Dispersal is expected to evolve because of variation in (i) the non social environment (habitat quality *sensu lato*), (ii) the social environment (e.g. presence of competitors or breeding partners) and (iii) the genetic environment (competition between relatives, inbreeding avoidance, delayed dispersal and helping; Clobert *et al.* 2008). Dispersal is therefore a single individual response to multiple selective pressures. Recently, theoretical approaches have specifically investigated the relative influence of different causes on dispersal evolution as well as feedback effects of dispersal on these selective pressures (e.g. Gandon & Michalakis 2001). Overall, models have provided extremely useful tools to understand the selective pressures acting upon dispersal evolution.

On the empirical side, studies focused either on (i) the proximate causes of dispersal (e.g. the role of internal state or energetic reserves on the timing of dispersal; Clobert *et al.* 2001; Dufty, Clobert & Møller 2002) or (ii) habitat selection processes, which consider dispersal only as the by-product of individual habitat selection decisions (emigration from, and immigration into, a breeding patch) in spatio-temporally varying environments (Cody 1985a). Surprisingly, these two empirical fields remained relatively separated until recently. The importance of accounting for individual decision-making processes in the study of dispersal evolution was only recently emphasized (Stamps 2001; Edelaar *et al.* 2008; Clobert *et al.* 2009). For instance, dispersal and breeding habitat selection can be linked *via* the information extracted by individuals from conspecifics according to their dispersal status (Cote & Clobert 2007) or individual breeding habitat selection decisions leading to biased dispersal events (Edelaar *et al.* 2008) and dispersing individuals being a biased sample of the population (Clobert *et al.* 2009).

Most of my own research work has been dedicated to the understanding of complex dispersal and habitat selection processes in natural populations, based on empirical approaches in a study population of two small passerine birds, the collared flycatcher, a migratory species, and its main competitor on the site, the great tit, a sedentary species. Dispersal is by essence a difficult trait to study empirically due to multiple methodological constraints (Pärt 1991; Koenig, van Vuren & Hooge 1996; Doligez & Pärt 2008): for instance, spatially limited study areas lead to potential disappearance of individuals dispersing outside the study area and thus biases (e.g. Winkler *et al.* 2005); temporal delays are long before responses in individual dispersal behaviour can be observed. Therefore, spatially and temporally large-scale empirical studies are still limited (due to high risk and required investment) but nevertheless strongly needed for a better understanding of the complex mechanisms involved in dispersal. In the past five years, i.e. nearly since my arrival in the Department of Biometry and Evolutionary Biology in Lyon, I took the opportunity to undertake such large-scale experiments in the field, and I aim at continuing in the future. Because of my high investment in field work in the past years, which required 6-7 months of work per year for preparation and organisation (working teams included 10 to 15 persons in the past few years), field work and data management afterwards, and also because of the overlap between the timing of field seasons (late April to early July in most cases) and the timing of competition for PhD grants, it has been impossible for me before this year to get PhD students to take over part of the projects. My working organisation in the past few years has therefore been a clear illustration of trade-offs - time being the limiting resource...

My main study system is a patchy population of two passerine species located on the island of Gotland (Figure 1). In this system, I have mainly worked on dispersal processes using between-patch dispersal events, i.e. defining dispersal as a change of patch by individuals between breeding events (binary variable). Over time, this scale of analysis (patch) and this dispersal definition have proved to be relevant with respect to fitness components, social information use, etc. (Pärt 1994; Doligez, Danchin & Clobert 2002b) and seem less constrained on the methodological point of view than e.g. dispersal distances (Doligez & Pärt 2008; Doligez, Gustafsson & Pärt 2009). The two study species are small, secondary hole-nesting, passerine species (Cramp & Perrins 1993). They readily breed in artificial nest boxes (and compete for the access to these breeding sites; Gustafsson 1986a; Merilä & Wiggins 1995), thus providing both an easy access to precise breeding data (clutch size, laying and hatching dates, identity of parents, etc.) and exceptional opportunities to conduct large-scale experiments using large sample sizes. All individuals caught are marked with numbered rings and their fate can therefore be monitored throughout their lives. The study site was settled in 1980, with continuous research projects going on and addressing different topics since then, mostly on the flycatcher population. A long-term, yearly updated, data base is available for this species that comprises all breeding and morphological data collected on the site. The great tit population has been regularly monitored for a shorter period of time (1996-2000 and 2004-present). The two species have been intensively studied in this and other European populations, providing high quality background knowledge with respect to many research questions.

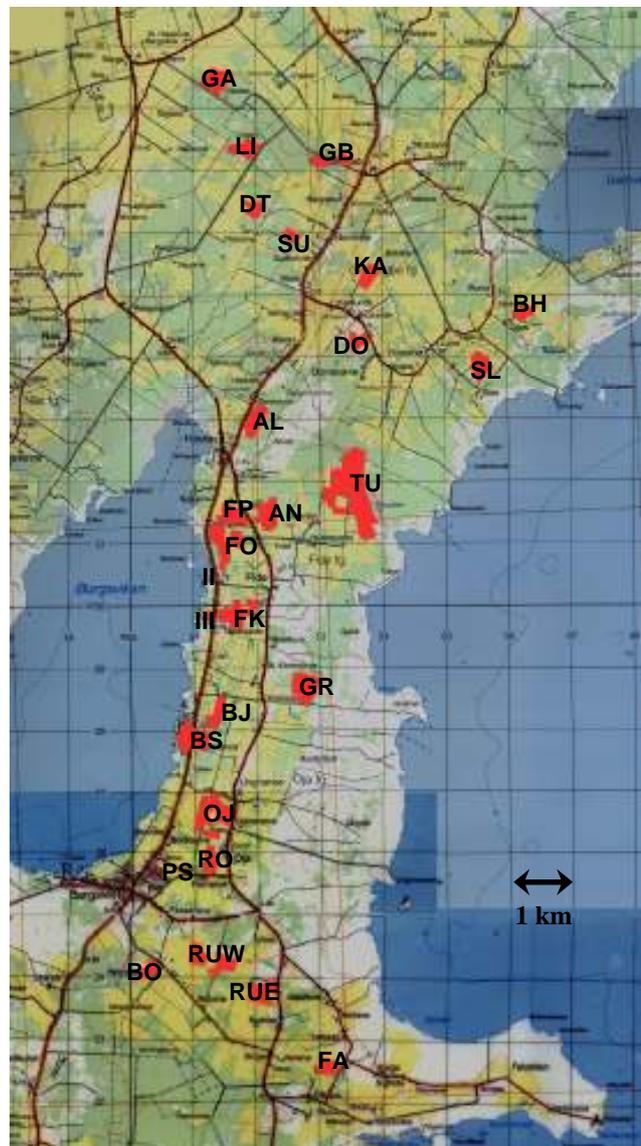
In this thesis, I did not aim at providing full state-of-the-art descriptions or exhaustive reviews of the research topics I have worked on, but rather presenting an overview of the research work I have been conducting in the past few years in collaboration with master and PhD students, post-doctoral and tenured researchers. I have chosen to focus here on the work that is currently under progress, pointing out the role of the students I supervised or collaborated with whenever relevant, and only very briefly present already published research since it is accessible elsewhere. In particular, I did not detail here the studies that constituted the core of my PhD on the use of public information for breeding habitat selection decisions. Manuscripts currently submitted or in advanced stage of preparation are presented at the end of this thesis, and are therefore only briefly discussed in order to place them back into the general context of my work. I have chosen to detail in the thesis the large-scale experiments I have been conducting in the past few years because they are the logical follow-up of my previous research but have not yet been published (for some of them, data collection will end in 2011 only).

During the course of my work over the past 12 years, I have supervised the work of more than 40 undergraduate students; since 2003, I have supervised the work of 7 graduate (DEA / M2) students,

of which 4 have continued (or will continue) with a PhD and 2 did not wish to continue in academic science. Since 2006, I co-supervise one PhD project (ending this autumn). Two students will start their PhD in the autumn 2010 under my supervision and in co-direction with other researchers (see below). Unfortunately, I have not been successful in obtaining funding for post-doc associates so far.

The directions for my future work are detailed in the last section of the thesis. I aim at continuing investigating dispersal mechanisms and consequences at different levels (genetic, behavioural, cognitive) and also integrating dispersal decisions into the set of decisions an individual has to make along its life, in relation to life-history strategies and trade-offs within- and between-breeding events. My work should therefore continue contributing to the understanding of complex dispersal processes and their evolution using empirical approaches.

Figure 1: Map of the main study area, showing the discrete study patches (in red, with their name code) separated by habitat unsuitable for breeding for the study species (fields, houses). The long-term population monitoring has been conducted in breeding patches from FA (South) up to TU (North). Additional patches have been installed North and South of this zone over the years.



Collaborations

The research work that I conducted in the past ten years (i.e. after the end of my PhD) has involved many collaborations, mostly abroad, with tenured researchers, post-doctoral researchers and PhD students. The list of my main current collaborators is given below.

PhD students

Janne-Tuomas Seppanen (2004-2007)

Department of Ecology and Evolutionary Biology, University of Jyväskylä, Finland
(*now a post-doctoral researcher in the same university*)

Mélissa Lemoine (2006-2010) – *co-supervision of her PhD with H. Richner*

Department of Evolutionary Ecology, University of Bern, Switzerland

Suvi Ruuskanen (2007-2010)

Department of Biology, Ecology Section, University of Turku, Finland

Christoph Meier (2007-2010)

Department of Ecological and Evolutionary Dynamics, University of Helsinki, Finland

Laure Cauchard (2010-2013)

Department of Biological Sciences, University of Montréal, Canada

Post-doctoral researchers

Barbara Tschirren

Department of Molecular Population Biology, University of Lund, Sweden
(*will start a SNF professorship from January 2011 at the university of Zurich*)

Pierre Bize (*now associate professor*)

Division of Environmental and Evolutionary Biology, University of Glasgow, United-Kingdom
Department of Ecology and Evolution, University of Lausanne, Switzerland

Jukka Forsman

Department of Animal Ecology, University of Uppsala, Sweden
Department of Biology, University of Oulu, Finland

Julie Morand-Ferron

Department of Biological Sciences, Université du Québec à Montréal (UQAM), Canada
(*now post-doctorate researcher at the Edward Gray Institute, Oxford, United Kingdom*)

Joanna Sendeck

Department of Animal Ecology and Department of University of Uppsala, Sweden

Kate Oddie

Centre for Evolutionary and Functional Ecology (CEFE), CNRS, Montpellier, France
(*has now quitted academic science*)

Tenured researchers

Tomas Pärt

Department of Ecology, University of Agricultural Sciences (SLU), Uppsala, Sweden

Lars Gustafsson

Department of Animal Ecology, Evolutionary Biology Centre, University of Uppsala, Sweden

Toni Laaksonen

Department of Biology, University of Turku, Finland
Finnish Museum of Natural History, Helsinki, Finland

Thierry Boulinier

Department of Population Spatial Ecology, CEFE, Montpellier

Heinz Richner

Department of Evolutionary Ecology, University of Bern, Switzerland

List of manuscripts submitted, in revision and in preparation

The following manuscripts, currently submitted, in revision or in an advanced preparation stage, are included at the end of this thesis to give a more precise overview of the work I have been involved in in the past few years. The studies they describe will be referred to as MS(x) in the thesis (where x is the number of the manuscript in the list).

- (1) A comparison of methods based on capture-recapture data to estimate heritability of dispersal propensity: the collared flycatcher as a case study.
B. Doligez, G. Daniel, P. Warin, T. Pärt, L. Gustafsson and D. Réale
In revision for *Journal of Ornithology*, special issue (Proceedings of the Euring 2009 Technical meeting)
- (2) Territory-specific prospecting is linked to subsequent breeding site choice: effects of multiple cues and adult return rate
T. Pärt, D. Arlt, **B. Doligez**, M. Low and A. Qvarnström
Submitted to *Ecology*
- (3) Influence of host profitability and microenvironmental conditions on parasite specialisation in main and alternative hosts
M. Lemoine, **B. Doligez**, M. Passerault and H. Richner
Submitted to *Journal of Animal Ecology*
- (4) Long-term fitness consequences of high yolk androgen levels: sons pay the costs
S. Ruuskanen, **B. Doligez**, N. Pitala, L. Gustafsson and T. Laaksonen
In preparation
- (5) Does parasite local maladaptation equals host local adaptation? An experimental test in the great tit - hen flea system
M. Lemoine, **B. Doligez** and H. Richner
In preparation
- (6) Intra- and interspecific neighbourhood effects on nest-site choice of collared flycatcher
J.-T. Seppänen, J. T. Forsman, M. Mönkkönen, **B. Doligez** and L. Gustafsson
In preparation
- (7) Public information as a selective force for breeding synchrony
B. Doligez
In preparation
- (8) Effect of female body condition on egg sex ratio in a desert breeding Mongolian passerine *Passer ammodendri*
K. R. Oddie, **B. Doligez** and E. Davaadorj
In preparation

PART A – RESEARCH TOPICS

RESEARCH AXIS 1: Information and individual decision making in the dispersal and breeding context

Individuals of most species live in spatially and temporally varying environments. In most cases, this variation leads to uncertainty, with crucial consequences since individuals' fitness will strongly depend on the local conditions and thus on the alternative chosen (Dall & Johnstone 2002; Dall *et al.* 2005). To adjust decisions to changing environmental conditions (*sensu lato*), i.e. to make optimal choices, individuals should attempt to reduce environmental uncertainty by accurately estimating relevant parameters allowing them to anticipate environmental changes and predict fitness prospects for each alternative. To do so, individuals have to gather, integrate and use information about their environment (Giraldeau 1997; Dall *et al.* 2005; Valone 2006). Information use is a key feature of adaptive behaviour, and as such, is central to evolutionary biology (Dall *et al.* 2005), and all kinds of individual decisions are concerned (e.g. foraging and breeding habitat choice, mate choice, reproductive investment, etc.).

The relevance of information use in individual decision-making and adaptation processes already appeared in classical models of habitat selection, which considered omniscient individuals with both a perfect and instantaneous knowledge of environmental conditions (Ideal Free Distribution and related models (Fretwell & Lucas 1970; Fretwell 1972). However, individuals are likely to deviate from such ideal expectations because of (i) constraints acting on individual spatial and temporal knowledge and (ii) limited reliability of cues used in assessing habitat quality (Pärt & Doligez 2003). More recently, theoretical models and empirical studies have started to accumulate on the issue of the nature of information used by individuals to make optimal decisions (e.g. Giraldeau & Caraco 2000; Dall & Johnstone 2002; Dall *et al.* 2005). These studies have led to conceptual advances in the study of the consequences of information use for evolutionary processes, e.g. fitness consequences of information use (Giraldeau & Beauchamp 1999; Dall & Johnstone 2002); frequency- and density-dependent processes and population consequences of information use (Boulinier & Danchin 1997; Giraldeau, Valone & Templeton 2002; Doligez *et al.* 2003); information and cultural transmission as an alternative to genetic inheritance (Danchin *et al.* 2004).

Information can be derived from the individual's direct experience, history or interactions with the environment ('personal information') or from the environment itself ('external information'). A particular source of external information are interactions of other individuals with the environment ('socially acquired information'; Templeton 1998; Dall *et al.* 2005). Moreover, individuals can gather information either passively (e.g. at the same time as performing other actions or via parental effects; Mousseau & Fox 1998; Danchin, Heg & Doligez 2001), or actively (e.g. via sampling or prospecting behaviour; Shettleworth *et al.* 1988; Reed *et al.* 1999). The first axis of my research work has aimed at addressing several of these issues, by investigating (a) the use of a specific source of information ('public information'), (b) the nature and consequences of information gathering behaviours used to acquire information (prospecting), (c and d) how information is used to adjust different decisions in the context of breeding. Most of this work has focused on decisions linked with breeding habitat selection, but other breeding decisions were also considered.

A – The use of 'public information' for breeding habitat selection

Intraspecific public information

A first part of my research work has addressed the role of public information in breeding habitat selection and its consequences. Public information has historically been defined as the average reproductive success of conspecifics on a habitat patch (Valone 1989) and is a source of socially acquired information (Danchin *et al.* 2004). Public information has been considered as a potentially important source of information about breeding habitat patch quality, because it directly integrates into

one single parameter and with no time delay the effects of all factors locally affecting reproductive success, i.e. the main variable of interest for individuals in the context of breeding habitat selection (Danchin *et al.* 2001; Doligez *et al.* 2002b; Valone 2007; Boulinier *et al.* 2008). In most species, individuals should not be able to easily hide their reproductive success or alter it to provide false information to their conspecifics without paying costs. Conspecific reproductive success can therefore be expected to directly reflect local habitat quality, i.e. the reproductive success that individuals can expect if they breed in the same patch. The value and reliability of this source of information, however, may strongly depend on several factors, among which:

- (1) spatio-temporal patterns of environmental variation in habitat quality; in particular, there should be a sufficiently high degree of temporal autocorrelation in habitat quality between information gathering and use (Boulinier & Danchin 1997; Doligez *et al.* 2003);
- (2) information gathering costs, which depend in particular on the spatio-temporal distribution of breeding events in the population (Danchin *et al.* 2001) and which affects the number of conspecifics upon which public information can be obtained;
- (3) phenotype (and/or genotype) x environment interactions, i.e. the extent to which local reproductive success of conspecifics is indeed a predictor of the individual expected reproductive success; processes such as local adaptation may decrease this predictive power.

I conducted several studies to test whether, how and in which conditions individuals could optimize their breeding habitat selection decisions (emigration from their current breeding patch and immigration into a new breeding patch) by cueing on conspecific reproductive success. Most of this work was based on empirical (correlative and experimental) studies in the study population of collared flycatchers except for one theoretical ESS approach. More specifically, I investigated the first two points above by testing the influence of temporal autocorrelation on the use of public information in a species where information is gathered at the end of a breeding season for choices in the next breeding season (Doligez *et al.* 1999; Doligez *et al.* 2003). Second, I tested (correlatively and experimentally) the use of public information in a species where information gathering costs may be expected to be high due to its breeding ecology, i.e. a non colonial and cavity-nesting species (Doligez *et al.* 1999; Doligez *et al.* 2002b; Doligez *et al.* 2004b). Finally, I investigated information gathering processes in this context (see below - Pärt & Doligez 2003; Doligez, Pärt & Danchin 2004a). All this work has now been published and is therefore not detailed here again. One important point of these studies however is that they clearly emphasized the multiplicity of information sources used by individuals in breeding habitat selection decisions, and the extent to which the use of these information sources is context-dependent.

Interspecific public information

Recently, the use of public information for decision-making (in the context of breeding habitat selection and other contexts; Valone & Templeton 2002) has received an increased interest and several authors proposed that this process may not be restrained to intraspecific social information, but could encompass interspecific social information (Parejo, Danchin & Aviles 2005; Seppanen *et al.* 2007). Heterospecifics comprise individuals of species with which the focal species never or hardly interacts, interacts positively (e.g. symbionts, preys) or negatively (e.g. parasites, predators, competitors). Depending on the degree of similarity between the ecological requirements of individuals of the focal species and the other species under concern, the reproductive success of heterospecifics (i.e. heterospecific public information) may also provide information about habitat quality (Seppanen *et al.* 2007). Along the continuum from non interacting species up to conspecifics, the higher the degree of similarity, the more relevant social information may be expected to be. However, compared to conspecifics, heterospecifics may also provide information on habitat characteristics that would otherwise not be available. For instance, migratory birds have been shown to cue on the presence of resident birds for deciding where to settle (Forsman *et al.* 1998; Mönkkönen *et al.* 1999) or even adjust breeding decisions (Forsman *et al.* 2008): resident birds may have access to different types of information about habitat quality during the non-breeding season that migratory birds cannot obtain directly. Furthermore, heterospecifics may differ in some characteristics from which individuals may directly benefit. By cueing on the presence of resident birds, migratory birds were shown to increase

their reproductive success (Forsman, Seppänen & Mönkkönen 2002; Forsman, Thomson & Seppänen 2007). This may be explained by individuals of the resident species being better skilled at finding food and/or deterring predators, from which individuals of the migratory species settling near resident individuals may benefit. Because this increase of migratory individuals' fitness was made at the expense of residents' fitness (Forsman *et al.* 2007), this process of heterospecific information use is approaching parasitism.

The use of heterospecific social information, and more specifically heterospecific public information, has been investigated in breeding habitat selection decisions in several studies on bird species, but so far their results did not clearly or unambiguously demonstrate this process (e.g. Parejo *et al.* 2005; Fletcher 2007; Parejo *et al.* 2008). In collaboration with J. Forsman, we therefore experimentally tested the use of heterospecific public information in a well-known system of a migratory and a resident cavity-nesting passerine species that have been shown to strongly and negatively interact during the breeding season (Gustafsson 1987; Merilä & Wiggins 1995). The experiment is described in box 1. This large-scale experiment should constitute a powerful test of the use of heterospecific public information use in a system where interactions between the study species have been well described and analysed, providing the necessary background for interpreting the results.

BOX 1: Interspecific public information use for breeding decisions

In order to test whether individuals use the local success of heterospecifics, we conducted an experiment in a sympatric population of two competing passerine birds. This study system is composed of a migratory species, the collared flycatcher, and a resident species, the great tit. Both species are cavity-nesters and use the same nest boxes provided in the study area. They breed during the same period, with a 10 to 15 days delay between the start of breeding of great tits and collared flycatchers, thus they potentially compete for both nest sites and food resources. Despite a high risk of getting killed by great tits, flycatchers are observed visiting tit nest boxes at the beginning of the season. Furthermore, flycatchers have been experimentally shown to use the presence of great tits in nest site selection, and preferentially settle where tit density is high. Thus they use interspecific information in the form of tit presence. To check whether flycatchers also use interspecific public information, i.e. local reproductive success of great tits, in breeding decisions, we experimentally manipulated the mean reproductive success of great tits at the scale of habitat patches. We recorded subsequent responses of flycatchers in terms of (i) reproductive investment in the same year and (ii) patch choice in the next year(s). We predicted that if flycatchers cue on great tit local reproductive success to assess local habitat quality, they should (i) invest more in breeding where tit success is high and (ii) decide to stay (and/or immigrate) preferentially on high great tit success patches and leave low great tit success patches. Because the manipulation was performed when most flycatchers have finished laying, we measured breeding investment by recording feeding rates. Patch choice was recorded by catching and identifying all breeding adults in experimental patches (as well as surrounding non experimental patches). We also recorded great tit feeding rates in order to check whether flycatchers can use it as a source of information about success and record any interspecific prospecting events by flycatchers at great tit nests.

To manipulate great tit local success, we transferred nestlings between nests matched for hatching date (i.e. for nestling age) at a local scale, in order to create (i) patches where most great tit nests receive additional nestlings, thereby increasing mean number of nestlings in the patch ('increased' patches), (ii) patches where nestlings were removed from most nests, thereby decreasing mean number of nestlings in the patch ('decreased' patches) and (iii) control patches where nestlings were transferred between nests within the patch, thereby leaving mean number of nestlings in the patch unchanged while controlling for nestling transfers. The experiment was conducted in years 2006 to 2008, and responses were recorded until spring 2010 (a large proportion of flycatchers being uncaught each year). The number of experimental plots varied between years: 12 in 2006, 14 in 2007 and 9 in 2008, thus a total of 35 plots were manipulated over the three years, with 12 increased patches, 12 decreased

patches and 11 control patches. When a patch was used during several years, the same experimental treatment was applied in the different years, to mimic the natural temporal autocorrelation of habitat features observed in this population. Overall, 6 patches were manipulated during 3 years, 7 patches were manipulated during 2 years and 3 patches were manipulated only once. All experimental patches were of similar size (50 to 80 nest boxes) and breeding density. In experimental patches, 80 to 100% of active great tit nests (i.e. with nestlings) were manipulated so that experimental manipulations would be as strong as possible.

Nestlings were transferred between nests when aged 3 to 5 days (hatching day = 0; great tit young fledge when 19-20 days old). A minimum of 3 nestlings was always left in experimentally decreased nests in order to allow parents to be caught and identified. In order to alleviate the potential negative impact of increasing brood size, supplementary food was provided daily to increased nests from the day of adding nestlings until day 17, in the form of maggots and protein- and vitamin-enriched food for captive insect-eating birds (25g of food provided per day). Food was provided inside the nest box and was therefore not obviously observable from a distance; supplementary feeding should thus not confound the effect of increasing mean number of nestlings. Final brood sizes after nestling transfer were 8 to 10 nestlings in increased nests and 3 to 5 nestlings in decreased nests, and were achieved by transferring 2 to 4 nestlings between experimental nests. Adjustments were planned whenever possible when the final brood sizes did not match these expectations, or changed after within-brood mortality. Prior to transfers, nestlings were individually marked so that their origin could be identified at ringing (on day 9). Marking is done by removing tuft feathers at specific locations (or combinations of locations) on the head, back and wings.

On average, 8 to 20 great tit nests were manipulated per patch per year, and 18 to 25 flycatcher pairs were present on the same patches. Over the three experimental years, feeding rates have been recorded at 290 great tit nests and 380 flycatcher nests approximately.

Breeding site choice: social information and the use of artificial signals

The work presented so far addressed the use of intra- and interspecific social information for breeding habitat choice at the patch scale. However, habitat quality also varies within patches (see Pärt 1994 for this population) and selective pressures acting on breeding habitat choice processes may differ depending on the spatial scale considered (Orians & Wittenberger 1991; Mitchell, Lancia & Gerwin 2001; Doligez *et al.* 2008). Therefore, selection at the nest site, i.e. here box, scale is expected to occur but the role of social information in this process needed further investigation.

A first study addressed the relative role of the presence of hetero- and conspecifics in nest site choice at the box scale (Seppänen *et al.* in prep, MS(6)). Using the long-term population monitoring data set, we show that flycatchers were more likely to settle in a box with tits neighbours but less likely to settle in a box with flycatcher neighbours, i.e. heterospecific attraction but conspecific avoidance. These results are in line with previous results found in this system showing intraspecific competition (Gustafsson 1986a) but a fitness gain for flycatchers when settling near tits (Forsman *et al.* 2002). Migratory individuals benefit from settling near sedentary individuals by accessing information on food resources and nest predation risk (Forsman *et al.* 2002), while sedentary individuals pay a cost due to increased competitive interactions (Forsman *et al.* 2007).

A second study investigated more specifically the ability of individuals to use environmental cues associated with nest box occupancy by a given species to make nest site selection decisions. To address this question, we conducted an experiment using an original approach recently proposed to investigate social learning in the wild (Seppänen & Forsman 2007). Using artificial abstract symbols of various shapes attached to nest sites, migratory passerine birds have been shown to blindly copy manipulated apparent breeding site preference of sedentary species in their own nest site selection at small spatial and temporal scales, i.e. in the same breeding season when selecting between close-by sites (Seppänen & Forsman 2007). We used this method to experimentally explore the ability of individuals to associate an artificial environmental cue to a biological feature potentially influencing fitness rewards and adjust accordingly their future nest site selection. Using artificial symbols as

environmental cues allows us to fully break down the link between true environmental quality and nest site selection. The experiment is described in box 2. It was conducted on the flycatcher and tit study population, which has already proved to be a valid system for the experimental set-up (Seppänen & Forsman 2007). The use of artificial environmental cues by migratory flycatchers has been shown on a short-term, i.e. within-year (Seppänen & Forsman 2007), but is unknown on a longer-term; it is also unknown for the sedentary tit species, which could update information on local quality during the non-breeding season, and may be less prone to store information if it is costly (see below). This experiment therefore tested whether individuals can retain the association between an artificial environmental cue and nest box occupancy by a given species (or emptiness) during the non breeding season and use it for nest site choice in the next year. Because flycatchers benefit from settling near tits, they may be expected to be attracted by boxes bearing the symbol associated with tit presence in the previous year, while tits may avoid boxes bearing the symbol associated with flycatcher presence or show no preference if they can update information during the non-breeding season. Because most individuals in the system are ringed and thus of known origin, the influence of dispersal status on the use of these artificial cues will be tested, to explore whether dispersers have access to restrained local information, for each sex and age class (see e.g. Doligez & Clobert 2003).

If this experiment reveals that individuals can use artificial environmental cues for nest site selection after a time delay of a year, it will open up perspectives regarding the long-term associative memory processes involved. Important issues would in particular be (i) to what extent individual cognitive abilities can constrain these processes and (ii) whether individuals can use these cues in association with more refined information on local habitat quality, such as reproductive success rather than the simple presence of a given species.

BOX 2: Artificial symbol use for nest site choice

The aim of the experiment was to test whether flycatchers and tits remember and use artificial environmental cues (symbols) observed in year t in their nest site selection decisions in year $t+1$. At the time when most nests contained eggs or young (i.e. during the first week of June), active breeding great tits and collared flycatchers, and empty boxes each received a different symbol on each experimental area (with different species-symbol association in the different areas - nest boxes occupied by blue tits received no symbol). Individuals were thus given information in the form of an artificial environmental cue relating to the contents of the nest box. The symbols used were white shapes (square, triangle and rectangle) attached around the entrance hole of nest boxes and nest boxes were manipulated in three experimental areas (Table B1). The three experimental areas used were situated relatively far from each other (approx. 4 km of distance min).

Table B1: symbols used in the experiment testing for the use of artificial symbol in nest site choice.

Nest box contents	Area		
	Öja	Faludden	Fide Odvalds
Great tit nest	□	△	▭
Collared flycatcher nest	△	▭	□
Empty	▭	□	△

In the next year, tit and flycatcher nest box selection according to the presence of each symbol was recorded in the following way.

1. Before the start of the breeding season (in March), an equal proportion of the three symbols randomly distributed in space was attached to nest boxes in each of the experimental areas.
2. From the end of April until the beginning of June, experimental areas were visited every second day. Each time a new great tit (or blue tit) nest was found at an advanced building stage, (i) the symbol present on the box was recorded and (ii) the symbol was removed from the box. Removing symbols prevents subsequent birds to obtain information on the current year's choices made by

conspecifics or heterospecifics according to symbols. Thus any symbol preference detected should be in relation to previous year's symbols. Symbols were counted on each area visit, and whenever one symbol category was under- or overrepresented, a sufficient number of symbols present on randomly chosen boxes were changed to the underrepresented symbol(s) so as to keep the proportion of nest boxes available for each symbol even (c. 1/3) in the area. Because tits may start building nests in several boxes and abandon some of them later on, if a tit nest at an advanced stage did not proceed further in the next six days, nest material was removed and the original symbol or an underrepresented symbol was attached again on the box. Early failed breeding attempts (in particular deserted nests) were treated in the same way. This procedure was repeated until the first collared flycatcher nests were found (early to mid-May).

3. When the first flycatcher nests were detected, the proportions of symbols on empty boxes on each area were checked once more for evenness and random spatial distribution, and the potential adjustments made. The symbol choices of collared flycatchers followed the general same procedure as for tits. Boxes were checked every second day and each time flycatcher nest material was found in a nest box, the symbol chosen was recorded and the symbol was removed from the box. In the flycatcher, however, symbols were removed as soon as nest building started because unlike tits, flycatchers usually do not shift box after starting building their nest. Again, the final number of each symbol category present on empty nest boxes was checked and adjustments were done by changing symbols to the underrepresented category(ies) whenever necessary, so as to keep the proportion of nest boxes available for each symbol even (c. 1/3) in the area (while keeping spatial distribution of available symbols random). If a flycatcher nest did not proceed further from an early stage in the next four days, nest material was removed and the original symbol or an underrepresented symbol was attached again on the box. This procedure was again repeated until most flycatchers had selected their boxes and initiated nest building (late May). The tits starting breeding at the same time were treated in the same way.
4. After most flycatchers had settled by the end of May - beginning of June, symbols were attached again on nest boxes according to their contents (occupied or not, and by which species). Indeed, the experiment was repeated over three years, attaching symbols from 2006 to 2009 included, and symbol choices were recorded from 2007 to 2010 included. The contents-symbol association was kept constant for each experimental area over the years, to mimic natural temporal autocorrelation of habitat features observed in this population. One last visit was made each year during the first week of June and adjustments were made by changing symbols whenever necessary. At the end of the breeding season, all nest boxes were checked to record final fledging success and late nests. Old nests were not removed as in other areas and the correct symbols were attached to nest boxes of late nests whenever necessary. Thus in the end of the season, each area had different numbers of symbols reflecting the different number of pairs of each species and empty boxes.

In 2008, three additional areas were used as controls for the experiment. The same symbols were attached to nest boxes in these control areas where no contents-symbol association had been provided to the birds in the previous year. Symbols were proposed in equal proportions as in the experimental areas. The symbol choices of birds in the three control areas were recorded following the same procedure as described above, and will allow us to control for any innate preference of birds for a given symbol shape.

The total number of nest boxes involved in this symbol experiment was 158 (43 in Faludden, 57 in Fide Odvalds and 58 in Öja) in 2006 and 2007; in 2008 we decided to increase the experimental zone in all three areas, and 275 nest boxes were therefore concerned until 2010 (65 in Faludden, 117 in Fide Odvalds and 93 in Öja). The total number of pairs used for creating the contents-symbol association in years 2006 to 2009 was 172 great tit and 246 collared flycatcher pairs, and 362 empty boxes; symbol choice has been determined for 176 great tit, 89 blue tit and 239 collared flycatcher pairs over the 2007-2010 period. For the three control areas used in 2008, the corresponding figures were 172 boxes used in total, and symbol choice was determined for 38 great tit, 16 blue tit and 84 flycatcher pairs. The data is currently under analysis. Symbol choices will be analysed according to the association

between symbols and the contents of nest boxes, accounting for the dispersal history of individuals, since dispersal may affect the information individuals have acquired on local patch quality.

The context-dependent use of multiple information sources

Individuals can use different sources of information to adjust decisions. The availability, cost, reliability and usefulness of information will greatly differ depending on types of information and information gathering processes. Understanding when a given type of information should be used depending on the context, the individual history, in particular its previous experience with this particular information type (learning), and the other sources of information available at the same time, remains poorly investigated (see e.g. Coolen, Dangles & Casas 2005a). So far, indeed, most empirical studies, including my own, have tested the use of a unique source of information at a time for a single decision, and therefore only provide a simplistic picture, rarely accounting for individual variation in information use or environmental complexity, and providing little insight into the relative influence and/or the context-dependent use of several sources of information. In nature, however, individuals usually face complex situations in which (i) many different sources of information are available and can be gathered by individuals at different expenses and with varying degree of reliability; these sources of information are likely to interact with each other to produce either redundant or conflicting information, (ii) the information available may vary according to spatial and temporal scales, may be used with some delay, and may thus have to be regularly updated, (iii) different decisions often have to be made simultaneously that may require the use of the same of different potentially conflicting information, and (iv) the meaning and usefulness of information may depend upon both an individual's present and past situation, in particular its previous history of information acquisition and use.

These situations lead to trade-offs both in information gathering and information use processes. In the few empirical cases when several sources of information were considered, individuals were often found to make use of one information type depending on circumstances or information acquisition costs (Templeton & Giraldeau 1996; Giraldeau *et al.* 2002; Coolen *et al.* 2005b). Within the framework of dispersal evolution, theoretical models have shown that, whenever the influence of several factors is taken into account, dispersal was likely to evolve according to multiple factors in a conditional way, i.e. with dispersal rates varying according to environmental conditions (Clobert *et al.* 2001; Clobert *et al.* 2004). Thus, individuals should adjust decisions according to different local habitat characteristics simultaneously. Furthermore, the context experienced by an individual will influence the interpretation of a given type of information; for instance, social information may have very different meanings depending on whether an individual faces strong intraspecific competition. To summarize, the nature of information used, the information gathering and integrating processes, and the influence of the context on information use, thus appear crucial to understand the evolution of decision-making processes in complex situations.

In the past few years, I have developed several empirical studies aimed at addressing some of these issues within the context of a project funded by the French National Research Agency (ANR, 2007-2009), and run together with E. Desouhant (LBBE, Lyon 1). The project aimed at investigating two major features of information gathering and use by individuals: (i) the use of multiple information sources, and (ii) the context-dependent use of information. More specifically, the project focused on the following questions:

- when several sources of information are simultaneously available, how do individuals set priorities among the different information sources? Do these priorities depend upon the type of decision that is to be made, in particular when a set of decisions has to be made simultaneously? How do individuals integrate and use redundant and conflicting information?
- how do individuals integrate and combine past and present information for decision-making? In particular, how does personal history (including parental history) modulate the use of current cues? Finally, how do learning processes influence present information use?
- how does the context in which an individual makes a choice affects the use of information for this choice? In particular, how do social status, internal state or other specific constraints, and the previous use of the same or other types of information, affect the probability that an individual will use a given information source compared to others?

The short project duration and technical difficulties in the field (including the large spatio-temporal scales required for conducting such experiments on birds) prevented me to fully address these issues. Nevertheless, it was possible, within the context of the different experiments performed (described in this thesis), to manipulate several sources of information simultaneously (in particular parental dispersal history and con- or heterospecific public information; personal and public information), and I also started to investigate the relative influence of different information sources on dispersal decisions (see below). The next step is therefore to analyse the responses of individuals when accounting for the different information sources to test how they are integrated, prioritized and used for optimizing dispersal decisions. In the long-term, one perspective is to conduct experiments simultaneously manipulating several sources of information in a contradictory way to test how individuals deal with conflicting information.

B – Information acquisition: prospecting behaviours

Prospecting at breeding patches / sites and public information

To use information for optimising breeding habitat selection decisions, individuals first need to gather it. Individuals can collect information about potential breeding patches / sites through a direct, active behaviour called prospecting (Reed *et al.* 1999). Due to the crucial implications of information acquisition in breeding habitat selection, the issue of prospecting and gathering of information about the environment by individuals has received a high interest in behavioural studies (e.g. Slagsvold & Lifjeld 1990; Reed & Oring 1992; Boulinier *et al.* 1996; Ottosson, Backman & Smith 2001; Pärt & Doligez 2003; Bruinzeel & van de Pol 2004; Dittmann, Zinsmeister & Becker 2005). Most empirical data have been acquired via direct behavioural observations of individuals exploring, visiting or ‘squatting’ sites where they do not currently breed (Reed *et al.* 1999). Individuals identified as prospectors are mostly failed or non-breeders, and prospecting activity often peaks late in the season (Boulinier *et al.* 1996; Reed *et al.* 1999). In many cases, however, the nature of information gathered by prospectors and the link between information gathered via prospecting and subsequent breeding habitat selection behaviour are unknown. A major question also concerns the time and energy constraints acting on prospecting, which have rarely been fully considered although they are likely to restrain the access to information by individuals, and thus restrain the dispersal strategies that can actually evolve in nature (Reed *et al.* 1999; Pärt & Doligez 2003). Thus, although prospecting plays a crucial role in breeding habitat selection by shaping individual access to information, the behavioural processes involved are still poorly understood in most cases (Reed *et al.* 1999).

Among the issues that require further investigation in general are the motivations of prospectors. Prospecting behaviour has been defined by its aim (i.e. gathering information for future breeding habitat selection), but in the field, prospectors are mostly defined by their short-term behaviour (i.e. individuals seen exploring, visiting, etc.; Reed *et al.* 1999). So-called prospectors may therefore have other motivations than information gathering. In particular, individuals may aim at getting familiar with a habitat patch or site or its occupants. Familiarity has been shown to enable individuals to choose the best sites, obtain mates with a higher probability, be competitively dominant over non-familiar individuals (Koivula *et al.* 1993; Pärt 1994). Identifying the nature of the information prospectors gather, in particular through experimental manipulations of information, is therefore crucial in order to link prospecting with future breeding habitat selection. We have described prospecting activity at nests during the breeding season and analysed the factors influencing this activity in the collared flycatcher and the northern wheatear. In both species, prospectors are mainly failed or non-breeding yearling males. In the collared flycatcher, we found that (i) more successful nests were more likely to be visited by prospectors and (ii) the timing of prospecting activity is linked with breeding activity (Pärt & Doligez 2003; Doligez *et al.* 2004a). In the northern wheatear, prospectors settled preferentially at successful sites and most of them bred at their prospected site in the next year if it was vacant (Pärt *et al.* submitted, MS(2)). Prospectors seemed to maximise their chances to obtain a high quality territory and thus breed successfully in the next year by favouring sites with breeding aggregations (where vacancies are more likely to occur) and using multiple

information (Pärt *et al.* submitted, MS(2)). These results are in line both with previous results about prospecting in other species and with the use of public information for breeding habitat selection. In particular, we experimentally showed that prospecting individuals cue on parental activity as a measure of nest success (Pärt & Doligez 2003).

However, many questions regarding prospecting activity in these as in many other species remain open. In particular, because prospecting data has long been restricted to easy direct but incomplete observations in species breeding in open habitats such as seabirds on cliffs (Reed *et al.* 1999), both the variation in prospecting behaviour between individuals depending on the specific constraints they face and the timing of prospecting activity usually remain poorly described. To address these issues, we conducted two experiments in the study system.

Individual variation in prospecting activity and post-fledging prospecting

The variation of prospecting behaviour between individuals has been neglected so far because studies usually investigate a single type of prospecting behaviour at a given time (Reed *et al.* 1999), e.g. visits of active nests by individuals not currently breeding there (Slagsvold & Lifjeld 1990; Boulinier *et al.* 1996; Ottosson *et al.* 2001; Pärt & Doligez 2003; Doligez *et al.* 2004a) or random post-fledging movements of individuals using fixed capture sites (Lawn 1994). Although only some categories of individuals are observed prospecting, other categories may use the same information for future breeding habitat selection, and thus also have to gather it. This mismatch has been observed in the collared flycatcher: most of the observed prospectors were failed or non-breeding yearling males (Pärt & Doligez 2003; Doligez *et al.* 2004a) while successful breeders, females and juveniles used the same information as these males (Doligez *et al.* 1999; Doligez *et al.* 2002b; Doligez *et al.* 2004b). Because different categories of individuals may face different time, energy, or social constraints due e.g. to their age and breeding status, they may use different prospecting behaviours to gather information. In particular, they may prospect at different periods of the breeding cycle (e.g. during the nestling *vs.* post-fledging phase), at different spatial scales (e.g. a breeding site or a patch scale), or to gather different components of the same information, which are correlated in natural situations (e.g. offspring number and condition; Doligez *et al.* 2002b). When individuals do not have direct access to information, they may simply rely on others and copy their choices, in particular yearlings with no previous personal information may copy older adults' choices, which start breeding earlier in many species. However, using different prospecting behaviours, or copying other individuals rather than directly gathering information, can have very different implications in terms of constraints and expected benefits. So far, observations of prospectors have mostly identified a single type of prospecting behaviour by a single category of individuals, namely non-breeders (or failed breeders). Detecting and describing prospecting activity by different categories of individuals may require more refined techniques to track precise individual movements. For instance, prospecting visits of successful breeders to neighbouring nests were also detected using transponders (Ottosson *et al.* 2001). Their spatial range of prospecting, however, was much smaller than non-breeding individuals.

Regarding the timing of prospecting, information gathering must precede decision-making. Thus, the periods from departure of the natal site to the first breeding attempt, and subsequently between consecutive breeding attempts, are crucial phases for prospecting (Reed *et al.* 1999). In many species, especially those living in closed environments (e.g. forests), the period following leaving the natal burrow or nest is a very poorly known period of life (Naef-Daenzer, Widmer & Nuber 2001a). Similarly, individuals not engaged in breeding activities (non breeders, or outside the breeding season) are often ignored. These individuals are indeed more difficult to observe because of the higher tendency to hide due to high vulnerability (e.g. just fledged young, or moulting adults, with reduced manoeuvrability), the absence of conspicuous sexual behaviours such as songs, courtships and displays, or higher mobility since individuals are not constrained to return regularly to a fixed breeding site. However, because individuals are likely to be able to devote more time and energy to prospecting activities during the non-breeding and post-breeding phases of their life, these phases probably represent critical periods for information gathering for future decisions during the post-breeding period or the following year. This is especially the case if individuals are under strong time constraints for breeding because of strong seasonal decline in breeding success, and thus cannot prospect at the beginning of the season, e.g. in migratory species (Slagsvold 1987).

My previous work on prospecting activity in the collared flycatcher focused on directly observable prospecting behaviour by individuals at the nests of their conspecifics. By monitoring movements of individuals using radio-tracking devices, I aimed at addressing the issues of individual variation in prospecting activity during the post-fledging phase and how it relates to future breeding habitat choice of individuals. The experiment is described in box 3. We experimentally manipulated information about habitat quality and subsequently monitored prospecting movements of different categories of individuals within and between experimental patches, in the year of the manipulation, and future breeding habitat selection behaviour (emigration and immigration decisions), in the following year(s). This work will help understanding the crucial but still poorly investigated issues of why, when and how individuals prospect, and the consequences of prospecting behaviour (Reed *et al.* 1999).

BOX 3: Post-fledging prospecting behaviour in a forest passerine bird

In order to investigate post-fledging prospecting behaviour in a species where the post-fledging period is not directly observable, we used an experimental approach. Using the collared flycatcher as a model species, we aimed at (i) describing the between-individual variation in prospecting behaviour, (ii) testing the link between prospecting and social information gathering and (iii) testing the link between prospecting and subsequent breeding habitat patch choice. To do so, we experimentally manipulated sources of information about habitat quality available to individuals and monitored subsequent responses in prospecting movements of different categories of individuals. In the year following the manipulation, breeding habitat selection of individuals was recorded. To monitor post-fledging prospecting behaviour, we took advantage of recently developed miniaturized radio-tracking devices to obtain detailed information on individuals' movements between experimental patches (Naef-Daenzer 1993; Naef-Daenzer, Widmer & Nuber 2001b; Naef-Daenzer *et al.* 2005).

Manipulation of information. Two sources of information previously shown to affect individuals' breeding habitat selection decisions in this flycatcher were simultaneously manipulated: (i) personal breeding performance (failure *vs.* success in fledging at least one young; Pärt & Gustafsson 1989; Doligez *et al.* 1999) and (ii) local breeding performance of conspecifics in a patch ('public information'; Doligez *et al.* 1999; Doligez *et al.* 2002b; Doligez *et al.* 2004b). The assessment by individuals of local breeding habitat patch quality was experimentally manipulated by creating high- and low-breeding success patches, corresponding to high- and low-quality patches. Personal and local breeding success were again manipulated by transferring nestlings between nests. Two patch treatments were performed, with 5 to 6 replicates per treatment, in small-size plots (60 to 70 nest boxes with 22 to 25 breeding pairs per patch). In 'increased' patches (I), apparent local breeding success was increased by adding 2 to 3 nestlings to 60-80% of active nests (i.e. 14 to 18 experimental nests in each plot). In 'decreased' patches (D), apparent local success was reduced by removing 2 to 4 nestlings from 60-80% of nests. Because the aim of the experiment was not specifically testing for the use of public information, we choose not to use a control group but rather increase the number of replicates for the two treatments to maximise our power to detect effects. Nestlings were transferred from decreased (D) to increased (I) patches in pairs of nests matched for hatching date. In natural situations, the mean number of fledglings per nest varies depending on patch and year between 3 and 4.5 (Doncaster *et al.* 1997). The patch treatment manipulation thus aimed at inducing a change (increase or decrease) of 30%, within the natural range of variation in fledgling success, and similar to the level used in the previous experimental manipulation of conspecific local breeding success in this population (Doligez *et al.* 2002b). In addition, in each experimental patches, up to three nests were artificially put into apparent total failure ('failed nests') by removing all nestlings (and transferring them to other nests in experimental or non-experimental patches), in order to create failed breeders (Doligez & Clobert 2003). In each patch, approx. 5 nests thus remained non-manipulated. Nest treatments (i.e. decreased/increased brood size, complete failure, no manipulation) were assigned at random with respect to the spatial location of nests within patches and time of the season. Patch treatments were alternated in space to ensure that a patch of a given treatment neighboured patches of

the other treatment (i.e. to avoid spatial aggregation of a given treatment). The quality of experimental patches can also be assessed using local characteristics such as patch breeding density, mean timing of breeding (laying date) and clutch size, mean proportion of yearlings among breeders (Doligez *et al.* 2004b). These measures, as well as parental feeding rates in experimental patches (approx. 10 nests per patch per year; Pärt & Doligez 2003; Doligez *et al.* 2004a), were recorded as part of the population monitoring and will be included in analyses to account for potential variation in intrinsic habitat quality between experimental replicates and in prospecting behaviour. The experiment was conducted in two years (2008 and 2009).

Monitoring prospecting activity and subsequent breeding patch choice. Prospecting behaviour of (i) failed breeders and (ii) successful breeders and fledged juveniles was monitored using radio-tracking (Naef-Daenzer 1993; Kenward 2001; Naef-Daenzer *et al.* 2001b). The miniaturised radio-tags used emit a signal that can be recorded (using a portable receiver and antenna) from up to 200 m of distance approx. in a forest environment. Tags were attached on birds using a leg-loop harness with rubber thread insuring loss of the tag before birds depart on migration (Rappole & Tipton 1991; Naef-Daenzer 2007). In order to explore changes in prospecting behaviour with time of the season, individuals were equipped with radio-tags over the main breeding time window (i.e. a period of 20 days). We aimed at equipping a large number of individuals to ensure large enough numbers of individuals recaptured in the next year. We equipped different categories of individuals to explore the influence of different constraints on prospecting activity:

- a) failed breeders:** on the day before removing all nestlings from the failed nests (usually day 10 after hatching), parents were caught in boxes using swing-door traps and equipped with radio-tags (46 females and 45 males over the two years). In most cases, both pair members were equipped.
- b) successful breeders:** as close to fledging as possible (i.e. on day 14 or 15), parents of the chosen nests (both non manipulated and manipulated nests) were caught using mist net (to reduce disturbance for nestlings) and equipped with radio-tags (97 females and 94 males over the two years). Again, both parents were equipped in most cases.
- c) fledglings:** in the same nests as above, two fledglings per nest were equipped with radio-tags on day 14-15 (171 fledglings in total). We choose to equip four members of each family to maximise the time during which family movements could be detected in a species where fledgling daily mortality is likely to peak during a few days post-fledging mostly due to predation (see Naef-Daenzer *et al.* 2001a for survival estimates in the great tit). Because this high mortality rate should be linked to fledgling condition (Lindén, Gustafsson & Pärt 1992), the families to be equipped and the fledglings to be equipped within families were not randomly chosen; we favoured high condition fledglings in order to maximise the chances to detect prospecting movements.
- d)** additionally, we equipped all **prospecting birds** that could be caught in mist nets when catching parents (6 males and 7 females over the two years).

Whenever possible, we choose to equip already ringed birds, i.e. whose previous dispersal history was known. For most equipped adults, we video-recorded parental activity at the nest on the day following the attachment of the tag, in order to assess short-term tag loss. This also allowed us to catch again some of the parents that had lost the tag and equip them with a new one (or the same if it could be found in the nest). The presence and movements within and between patches of radio-tagged individuals were monitored by scanning entirely each experimental patch for 2 hours twice a day, in a random order. Tracking sessions were conducted from the day when the first radio-tag was attached on a bird (Mid-June) until most radio-tag batteries were empty (end of July). In the two years following the manipulation (because many young recruit when 2 years old; Gustafsson 1989), breeding adults were caught and identified throughout the study area, and breeding patch selection decisions (emigration and immigration) were determined.

Analyses. Presence or absence of signal from each radio-tagged individual was recorded during tracking sessions. For each breeder or juvenile, we therefore obtained a series of presence/absence data that will be used to build individual radio-tracking 'capture-recapture histories' and will be analysed using multi-state capture-recapture methods (Lebreton *et al.* 1992; Clobert 1995; Nichols & Kendall 1995; Pradel, Gimenez & Lebreton 2005; Gimenez *et al.* 2008) to account for individual detection

probability and its heterogeneity depending on different factors (sex, age, breeding status and success). In our case, signals from radio-tagged individuals could be missed during tracking sessions for several reasons (e.g. individuals foraging too high up in the dense canopy of trees to be detected, or temporarily emigrating from the study area). We will investigate individuals' probability of movement within and between patches, and choice of site or patch after a change, depending on (i) individual personal information, for breeders (Switzer 1997), and (ii) local reproductive success of conspecifics (patch treatment; Doligez *et al.* 2002b; Pärt & Doligez 2003; Doligez *et al.* 2004a). Time variables will be included to investigate (i) the delay before individuals start small- (within patch) and large-scale (between patch) prospecting activity after breeding failure or fledging, (ii) the rate of movement (how often they change patch, how long they stay in one patch after changing) and (iii) temporal changes in prospecting activity with time in the season. We will also investigate whether signals from (i) siblings and (ii) parents and offspring, respectively, coincide, that is, are always observed in the same site when both observed. Mismatches in signals could reflect family breaking-up after post-fledging parental care, and we will investigate whether break-up timing depends on parental personal information and public information. Prospecting strategies will be investigated (e.g. trading the number of patches visited against the time spent in each patch) between categories of individuals. Finally, to test the link between prospecting activity and future breeding habitat selection behaviour, we will investigate the correlation between (i) the number of times a patch has been visited and time spent on a patch and (ii) patch choice in the next year. We will also test which prospecting strategies allow individuals to make the best choice (i.e. here settle in 'increased' patches).

The timing of information gathering: information updating?

As mentioned above, the timing of gathering information *via* prospecting is a crucial issue in the context of the use of information for future decision-making. Most studies have focused on the breeding period (Reed *et al.* 1999), not only because prospecting was investigated in the context of breeding habitat selection, but also because observations of prospecting individuals outside this period are technically difficult, if not impossible, for most species. Individuals may however prospect both after the breeding season (see above) and before the next breeding season to collect and update information. In many seasonally breeding species, individuals have been suggested to gather information at the end of the breeding season for next year's breeding because the reliability of information may be maximal at this time (Lawn 1994; Boulinier *et al.* 1996; Boulinier & Danchin 1997; Reed *et al.* 1999; Danchin *et al.* 2001; Arlt & Pärt 2007). However, one of the main constraints acting on prospecting behaviour is the extent to which information temporal availability matches individuals' own temporal availability. The lower this match, the higher individuals have to trade time spent prospecting against time spent to other activities, and thus the higher the costs of information gathering. This explains why prospectors observed during the breeding season were mostly non-breeding individuals or failed breeders (Reed *et al.* 1999). Prospecting activities of breeders should indeed be spatially and temporally constrained (Danchin *et al.* 2001; Ottosson *et al.* 2001). However, such constraints will mostly apply to cues directly related to the breeding activity, e.g. social information such as the presence or breeding success of con- and heterospecifics. Other cues with different temporal availability may also provide reliable information about the expected success in a breeding patch / site. For instance, the density of safe nesting sites should reflect the expected level of competition in a breeding patch, and it may be accessible outside the breeding season. In many species, however, individuals may leave the breeding area once breeding is completed (migratory or partially migratory species), making the issue of the timing of prospecting even more complex. To what extent information may be updated outside the breeding season or at the beginning of next season for returning individuals remains unclear.

To investigate these issues, we experimentally manipulated a non social cue of local habitat quality, namely nest site availability, at different time periods in the study system of migratory collared flycatchers and sedentary tits (experiment described in box 4). These species differ in their accessibility to information outside the breeding season. By manipulating nest box availability either before or after the time when flycatchers depart on migration, we will test when individuals of both species gather information about nest site availability for future breeding habitat patch choice and

whether they can update the information before the next breeding season. This experiment will complement previous work on prospecting in this system, which focused mainly on intra- and inter-specific social information about habitat quality.

BOX 4: Timing of information gathering and information updating

(This experiment has been supervised by C. Meier as part of his PhD studies)

To test the relative influence of information available at the end of the breeding season and at the beginning of the next breeding season on subsequent breeding habitat selection, we conducted an experiment to manipulate one environmental cue at different time periods. The study species (great tits, blue tits and collared flycatchers) are cavity-nesters strongly constrained by the limited nest site availability in the wild. Therefore, they can be expected to cue on nest site availability to assess local habitat quality. In the long-term study site and in previous experiments, nest boxes were provided in excess to the number of breeding pairs (Doligez *et al.* 2004b). Thus this habitat characteristic has not been investigated as a factor influencing breeding habitat patch choice so far in this system. However, in the study area, most natural cavities can be found in dead birches and are ‘short-lived’ due to frequent winter storms. Therefore, the search for a nest site and strategies to secure a nest site are expected to be under strong selective pressure in the study species. Contrary to many socially acquired information sources linked to breeding, nest box availability can be assessed all year-round. Therefore resident species such as tits may be expected to be able to easily update this information in particular as the breeding season approaches. Conversely, migratory species such as flycatchers should be more time-constrained in decision-making upon arrival (e.g. Slagsvold *et al.* 1988), in particular as they start breeding after most tits and therefore experience strong competition for nest sites. Therefore they are expected to cue mostly on information available at the end of the previous breeding season and therefore make decisions about where to settle in the subsequent year before departing on migration (see above and Pärt & Doligez 2003).

We manipulated nest box availability at the patch scale at different time periods during the 2008 breeding season. Patches were randomly assigned one of the following treatments:

- **treatment A:** all unoccupied boxes were taken down by the end of May, at a time when most tits and flycatchers had started to breed (incubation stage for tits, nest building for flycatchers). Until the end of the season, boxes that became unoccupied after desertion, brood death or fledging were also taken down. One month after taking most boxes down, i.e. towards the end of June, at a time when most tit young and about half of the flycatcher young had fledged, these boxes were hang up on trees again. Thus, flycatchers were able to monitor the change in nest box availability back to normal before leaving on migration.
- **treatment B:** boxes were taken down as in treatment A, but continued to be taken down until the end of the breeding season (i.e. beginning of July), i.e. until no box was available anymore. Boxes were then hang up on trees again only at the end of October, i.e. at a time when all flycatchers have departed on migration.
- **treatment C:** control treatment, in which no box was taken down.

Overall, the availability of nest boxes was therefore similar in all three groups at the beginning of the next breeding season (2009). Each treatment was applied to 8 discrete replicate patches of similar size (around 50 boxes each) and separated by 0.5 to 30 km of unsuitable breeding habitat. All breeding attempts were monitored in the experimental patches to record breeding data and breeders were caught and identified for all species present (tits and flycatchers). In the next year, experimental patches were monitored to identify breeders and record breeding patch choices.

Differences in dispersal decisions (emigration and immigration rates) between treatments should reveal the use of nest box availability as a cue of local habitat quality in breeding habitat patch decisions and the timing of gathering information on nest box availability by prospecting individuals. The manipulation is expected to have an effect primarily on flycatchers, which are more time-

constrained and cannot update information during the non-breeding season compared to tits. If individuals prospect mostly during the breeding season (Boulinier *et al.* 1996; Reed *et al.* 1999; Doligez *et al.* 2004a), emigration is expected to be higher, and immigration lower, in patches of treatments A and B, which were made less attractive by removing nest boxes, compared to controls. If individuals prospect both during and after the breeding season, emigration is expected to be higher, and immigration lower, in patches of treatment B compared to A. Finally, if individuals update information at the beginning of the breeding season, no difference between treatments should be observed in terms of final breeding density, however, the dynamics of settlement (as well as age distribution) may differ between treatments. Prospecting individuals may indeed assess through nest box availability the expected level of local competition for nest sites. A shortage of nest sites may lead to increased expected competition level, thus individuals may return and settle earlier in patches with higher expected competition level. Yearlings usually start breeding later and may therefore have more opportunities to update information on nest site availability (accounting for already-settled older birds). Therefore, the arrival date of males (using both transects to record singing activity as an estimate of male density and nest building stage) and age distribution will also be compared between treatments. We will compare responses of both breeding adults and first-time breeders (local recruits or not), because the timing of prospecting may be expected to differ between adults and fledged young (see post-fledging experiment above).

C – The use of information to adjust other breeding strategies

The work presented so far focused on dispersal as a by-product of breeding habitat selection decisions made by individuals according to information about local habitat quality. However, breeding implies making a whole suite of decisions, starting with dispersal decisions (whether to leave the breeding patch / site and where to settle in that case) followed by many others in different contexts, e.g. mate choice, current investment vs. future investment, etc. Individuals make these many breeding decisions simultaneously and/or in sequence, and decisions may interact with each other. In particular, dispersal may affect the breeding strategies adopted by individuals by affecting their local knowledge of the environment and/or the consequences of their decisions. I conducted several experiments investigating some of these issues, which are presented below. However, the question of the interactions between dispersal and other breeding strategies depending on individual access to information is vast and complex, and should constitute one of the axes for my future research (see below).

Adjusting clutch size according to environmental conditions

According to life-history strategy, individuals should adjust their current reproductive investment to offspring survival prospects (Stearns 1992). In particular, birds should reduce clutch size when nestling mortality is high (Slagsvold 1982; Lima 1987). Nest predation is a major source of nestling mortality in birds (Ricklefs 1969), and should therefore be a prime determinant of clutch size. Interspecific comparisons have confirmed that clutch size variation is correlated with nest predation rate (Martin 1995; Martin & Clobert 1996). However this pattern can also be explained by other mechanisms (Martin *et al.* 2000), and correlative evidence does not allow to infer a possible causal relationship between clutch size variation and nest predation rate. A critical test of this ‘nest predation hypothesis’ of clutch size variation in birds was therefore needed, requiring an experimental manipulation of nest predation risk and observation of subsequent changes in clutch size. We performed this test in the collared flycatcher study population (Doligez & Clobert 2003). The perception of nest predation risk was experimentally manipulated by artificially depredating some of the nests in ‘high risk’ patches and leaving others (‘low risk’) unmanipulated. All nestlings from depredated nests were transferred to other nests while a stuffed nest predator was presented at the box. Additionally, the stuffed predator was presented to nests that were not subsequently depredated (see Doligez & Clobert 2003 for details).

In the year following the manipulation, we observed smaller clutches in the ‘high risk’ patches compared to the ‘low risk’ control patches, whereas clutch size did not differ between these patches before the manipulation (Doligez & Clobert 2003). Therefore, we confirmed a causal link between nest predation risk and subsequent clutch size decision. We discussed three potential, non-mutually exclusive, mechanisms to explain clutch size reduction. Interestingly, dispersal plays a role in all three cases, emphasizing the interactions between dispersal and other breeding decisions.

- 1 – Clutch size reduction could result from differential breeding habitat selection if individuals laying large clutches have a higher emigration probability, and/or individuals laying small clutches have a higher immigration probability, in the ‘high risk’ patches. No support for this mechanism was found: the probability that individuals change patch did not depend on previous clutch size. More generally, there was no difference in emigration and immigration rate depending on patch treatment, although the proportion of immigrants among breeders was lower in ‘high risk’ patches.
- 2 – Clutch size reduction could result from competitive interactions between individuals if all individuals try to avoid settling in ‘high risk’ patches but only the more competitive ones succeed, while subordinate, lower quality, individuals potentially laying smaller clutches are forced to settle in those patches. No support for this mechanism was found either: individuals breeding in ‘high risk’ patches showed no morphological difference with individuals in control patches for traits related to clutch size or to competitive ability in general and the two types of patches did not differ in mean laying date or proportion of yearlings among breeders.
- 3 – Finally, clutch size reduction could result from phenotypic plasticity of clutch size: in response to increased nest predation risk, individuals would make the decision to lay smaller clutches. In general, all breeding individuals showed the same reduction in clutch size in ‘high risk’ patches, supporting this interpretation, although a direct test using an intra-individual longitudinal analysis of clutch size was not powerful enough to detect a change. Interestingly, however, (i) females laid smaller clutches when mated to a non dispersing male compared to an immigrant male in ‘high risk’ patches and (ii) breeders that had experienced the presence of a stuffed predator at their nest box (irrespective of their subsequent fate, depredated or not) tended to leave ‘high risk’ patches with a higher probability than other breeders. Altogether, these results therefore suggest that adaptive responses to local environmental conditions, here nest predation risk, may depend on the information acquired by individuals, and thus their dispersal history.

Nest predation may therefore theoretically be a major factor of habitat quality influencing clutch size evolution in birds in varying environments. However, whether individuals can adaptively respond to nest predation will depend on both the spatio-temporal predictability patterns of nest predation risk and processes of information gathering by individuals, i.e. the ability of individuals to track such variation in nest predation risk (Doligez & Clobert 2003). Furthermore, the avoidance of ‘high risk’ patches by immigrants shows that reducing clutch size was not the only adaptive response to the experimental increase in nest predation risk. However, emigration rate was not higher from ‘high risk’ patches, which may reveal other constraints acting on individuals (e.g. other benefits linked to familiarity; Pärt 1994). In which conditions dispersing to safer patches is a better strategy than reducing clutch size in response to an increase in nest predation risk remains unknown. This experiment nicely illustrates the potential interactions between dispersal decisions and other breeding decisions, involving various potential mechanisms among which the issue of information.

Adjusting sex ratio according to environmental conditions: the role of spatial scale of habitat quality

Another nice illustration of a breeding decision that can interact with dispersal is sex allocation. Classical models of sex allocation predict that parents are expected to bias offspring sex ratio towards the sex that benefits most from parental investment depending on factors acting at a small spatial scale (e.g. territory quality, maternal condition or social rank, kin interactions; Trivers & Willard 1973; Clark 1978; Frank 1990). We tested this prediction in a population living in an extreme (desert) environment, where the returns from manipulating offspring sex ratio can be expected to outweigh the costs of evolving a sex-adjusting mechanism (Krackow 2002; West & Sheldon 2002).

Sex ratio was negatively correlated with female body condition (Oddie *et al.* in prep., MS(8)), a result in agreement with an experimental study on another desert-living passerine.

Recently, however, a model predicted that, in species where natal dispersal is sex-biased, parents may be expected to adjust offspring sex ratio when breeding habitat quality varies in space at the scale of natal dispersal but is temporally predictable (Julliard 2000). In this case, parents should bias offspring sex ratio towards the philopatric sex when breeding in a high quality habitat patch and towards the dispersing sex when breeding in a low quality patch, in order to maximise the probability that their offspring will settle in a high quality patch (the ‘natal dispersal’ model of offspring sex ratio adjustment; Julliard 2000). In the case of offspring sex ratio, the multiplicity of factors that may influence sex ratio adjustment was proposed to at least partly explain the low frequency of offspring sex ratio biases observed in vertebrate species (West & Sheldon 2002; Ewen, Cassey & Møller 2004). Surprisingly, however, most theoretical and empirical studies have investigated sex ratio as an isolated trait, on which one factor is acting at one spatial scale only. In particular, the ‘natal dispersal’ model, which deals with selective pressures potentially acting at large spatial scales in interaction in other breeding decisions, namely dispersal, had never been tested experimentally. Trade-offs resulting from conflicting environmental factors acting at different spatial scales are likely to affect the extent to which individuals will adjust different breeding decisions, such as offspring sex ratio in relation to parental and offspring dispersal and the directions of these adjustments, depending on the scales of habitat quality variation (Orians & Wittenberger 1991).

I conducted an experiment to test whether individuals adjusted sex ratio and other breeding decisions according to local quality at two different spatial scales, a large-scale (breeding patch) and a small-scale (breeding territory). One of the main aims of the study was to test experimentally the ‘natal dispersal’ model of offspring sex ratio adjustment. This experiment manipulating habitat quality at two spatial scales simultaneously was conducted in a study population of great tits (Doligez *et al.* 2008 - see also below for the description of the experiment). The results show that different breeding decisions are based on information about habitat quality at different spatial scales: laying date depended on large-scale (patch) but not small-scale (territory) quality; conversely, offspring sex ratio depended on small-scale (territory) but not large-scale (patch) quality. Finally, clutch size and territory occupancy did not depend on the experimental manipulation of territory quality (Doligez *et al.* 2008). The general prediction of the ‘natal dispersal’ model of offspring sex ratio adjustment was therefore not confirmed, but the results nevertheless suggest that integrating different decisions by breeders according to environmental variation at different spatial scales is required to understand patterns of breeding strategy adjustment, including dispersal decisions.

However, during this experiment, I also collected data on within-clutch sex ratio adjustment. Most studies on within-clutch sex ratio adjustment have been conducted on bird species with hatching asynchrony and/or small clutch sizes, because of the difficulty to obtain information on each nestling’s egg of origin in synchronously hatching species with large clutch sizes. However, evolutionary pressures on within-clutch competition and sex ratio adjustment are expected to strongly depend on these characteristics. Within-clutch adjustments of offspring sex ratio and/or egg components (e.g. yolk hormone deposition by females) have been suggested to either aim at favouring brood reduction when environmental conditions are poor, or enhancing competitive ability of last-hatched young to compensate for their later hatching. Within-clutch adjustments should therefore also depend on environmental conditions at different spatial scales. I will therefore experimentally test such within-clutch processes (box 5), and in particular relate potential within-clutch patterns to other breeding decisions including natal dispersal.

BOX 5: Information on habitat quality and within-clutch sex ratio adjustment

In order to test variation in within-clutch sex ratio adjustment according to local breeding habitat quality, we experimentally manipulated habitat quality and determined offspring sex depending on egg laying sequence in a population of great tits. The experiment, performed in spring 2003, consisted in manipulating (increasing or decreasing) local habitat quality through food availability and parasite prevalence at a small (territory) and a large (patch) scale simultaneously. Each nest box was

manipulated to either increase or decrease territory quality. Territory quality was either increased by supplementing nest boxes every three days with food or decreased by infesting nest boxes with fleas, the main ectoparasite of great tits. Both factors of habitat quality were manipulated simultaneously in different boxes in order to maximise the difference in quality between high- and low-quality territories. These treatments were applied to nest boxes in 21 forest patches of similar area and box density (with 30 boxes in each patch). Patches were assigned one of the three following treatments, depending on whether the quality of all territories in a patch was manipulated in the same or different ways: (i) high-quality patches containing high-quality territories only (6 patches), (ii) medium-quality patches containing 50% of high-quality and 50% of low-quality territories alternated in space (9 patches) and (iii) low-quality patches containing low-quality territories only (6 patches). A territory was therefore surrounded either by territories of the same quality (high- and low-quality patches) or territories of the opposite quality (medium-quality patches), thus creating four types of territories, high- and low-quality territories surrounded by either high- or low-quality territories on a local scale. Manipulation of habitat quality started two to four weeks before the peak of laying in order to influence breeding patch choice as little as possible (see Doligez *et al.* 2008 for more details).

Nest boxes were monitored every second day to record nest building activity. From the day when they were estimated to be ready, nests were checked every day for the presence of the first egg and subsequent eggs afterwards, until clutch size was complete (i.e. no further egg laid for three days in a row for clutches of 7 eggs or more) and incubation started (i.e. eggs were uncovered; great tit often delay the start of incubation by up to 8 days, especially in the beginning of the season). During these daily visits, eggs were marked with their number in the laying sequence, with a permanent marker. On the day before the expected hatch day (i.e. first day of incubation + 10 days), clutches were brought back to the laboratory, eggs were photographed and placed into an artificial incubator where eggs were individually separated until hatching. Clutches were replaced by dummy eggs in nests until hatching. The presence of newly hatched individuals was checked in the incubator at least once every hour during day time (i.e. from 7 am until 7 pm). Hatchlings were taken out of the incubator soon after hatching (except those hatched at night), they were weighed and individually marked by removing tuft feathers on the head, back and/or wings following a specific code; a blood sample (2-10 μ l) was taken from the superficial plantar metatarsal vein, transferred to 200 μ l of EDTA buffer for molecular sexing after the season, and frozen at -20°C on the same day. Hatchlings were then kept in a heated room for up to two hours maximum (unless they came from the last egg of the clutch), in order to wait for additional eggs of the same clutch to hatch. All hatchlings from the same clutch were then brought back to their nest, and the corresponding dummy eggs were removed, until all eggs in the clutch had hatched or we ensured that the remaining eggs would not hatch and were removed from the incubator (after a delay of 3 days after the last hatched egg). Unhatched eggs were dissected and dead embryos were transferred to EtOH abs and stored at -20°C for sexing. Sexing was performed using a DNA test following Griffiths *et al.* 1998. Nestlings were ringed on day 9, and the correspondence between ring number and hatchling code was noted. Remaining dummy eggs (if any) were also removed from nests upon ringing. Fledglings were measured on day 14 and fledging success was recorded. Therefore, both primary and secondary (at fledging) sex ratio will be known, together with fledgling body condition.

A total of 292 great tit nests were monitored in the experimental patches, among which nestling sex was known together with laying sequence and egg volume for 238 clutches (either the clutch had been transferred to the incubator or the nest was deserted and eggs were collected). The remaining clutches were either from nests located too far from the field station to bring eggs back to the incubator in good conditions (i.e. with less than 15 min of transport time, in a heated box), or where hatching had already begun on the day when clutches were planned to be transferred (most probably the start of incubation was badly estimated). This exceptional data set will allow us to powerfully test hypotheses about within-clutch sex ratio adjustment according to local habitat quality at two different spatial scales.

Signals and information use for resource allocation decisions by parents

The research work presented so far addressed the use of inadvertently produced social information or information directly gathered by individuals from the environment (personal information; Danchin *et al.* 2004; Dall *et al.* 2005). Information used in decision-making can also be obtained from signals advertised by other individuals in an intended communication process. I conducted an experiment in this context to investigate the role of juvenile plumage signals in parental decision-making about resource allocation to the offspring.

Elaborate colour traits in adults have usually evolved as honest signals of individual quality in the context of sexual selection or other social interactions (Hill 1991; Andersson 1994). This is in particular true of carotenoid-based traits because carotenoids cannot be synthesised by individuals and therefore have to be optimally allocated between coloured traits and immune (antioxidant) functions (Olson & Owens 1998). In juveniles, however, carotenoid-based ornaments are relatively rare compared to melanin-based ones (e.g. Harrison 1984), which are more cryptic and have therefore been suggested to confer a high selective advantage in the early stages of life by reducing predation risk. There are, however, a few bird species including the great tit (Cramp & Perrins 1993) where a conspicuous carotenoid-based colouration is expressed already in the nestling plumage, but the function of this colouration is poorly understood. It has been suggested that nestling ornamentation has evolved *via* parental preference for nestlings signalling their higher quality by carotenoid-based plumage colour (Lyon, Eadie & Hamilton 1994; Saino *et al.* 2000). Because great tit juveniles are subject to high post-fledging predation rates (Naef-Daenzer *et al.* 2001a), the conspicuous juvenile plumage colouration is likely to result from selective pressures counteracting the benefits of reducing juvenile detectability to predators. The carotenoid-based conspicuous plumage colouration of great tit juveniles may act as a signal of individual quality used by parents to make resource allocation decisions between offspring. Such a signalling function has been experimentally tested within the nest, i.e. during nestling growth, but no evidence was found that carotenoid-based colouration in nestling great tits has a signalling function in parent-offspring interactions in the nest (Tschirren, Fitze & Richner 2005). An explanation for these results was that parents were constrained in their perception of colour differences in the nest because of light restriction (Götmark & Olsson 1997; Heeb, Schwander & Faoro 2003; Tschirren *et al.* 2005). Thus carotenoid-based plumage colouration in juvenile great tits might have evolved in response to parent-offspring interactions after fledging rather than at the nestling stage, when the assessment of individual quality based on plumage signals becomes easy (Götmark & Olsson 1997; Tschirren *et al.* 2005). Great tits have high brood sizes (Cramp & Perrins 1993), thus juvenile experience high levels of sibling competition for parental care. I experimentally tested this hypothesis by manipulating the carotenoid-based plumage colouration of great tit fledglings and observing subsequent parental care decisions during the early post-fledging period (box 6). The results of the experiment are under analysis.

Interestingly, a similar experiment revealed that the UV reflectance of juvenile plumage in great tits affects maternal care after fledging (Tanner & Richner 2008). The influence of UV reflectance has however not been investigated within the nest. If the results confirm that parents use juvenile carotenoid-based plumage signals to make resource allocation decisions to offspring after fledging but not in the nest, this experiment will constitute another example of the constraints acting on information gathering processes. In general, studies tend to consider traits independently of their context and ignore the potential physical and/or social filters that can act upon these traits. This has been particularly well illustrated in the context of colour traits in the context of sexual selection or parent-offspring interactions (e.g. the role of the light environment on coloured traits; e.g. Endler & Théry 1996; Heeb *et al.* 2003), however the same processes could apply to any information source. It may therefore be crucial to consider information within the context it has been obtained, in order to fully understand its role in individual decision making. Finally, although we did not aim in this specific experiment at relating post-fledging parental care decisions based on juvenile plumage signals to dispersal behaviour, it would be particularly relevant to assess whether parental care decisions are also linked to subsequent offspring dispersal decisions and/or can be modulated by parental dispersal history. These issues are partly addressed in the next section.

BOX 6: The role of plumage signals in parental resource allocation between offspring

In order to test for the role of plumage signals, and more specifically the carotenoid-based ventral plumage coloration, in parental resource allocation between offspring in the post-fledging phase in the great tit, we experimentally manipulated this plumage trait during nestling development (or just before fledging) and tested the subsequent response of parents in terms of feeding decisions outside the nest box in conditions mimicking post-fledging parental care. The experiment was conducted in spring 2004.

From the end of April, great tit nests were monitored for recording breeding data (laying date, clutch size, hatching date). After hatching, experimental nests were chosen (among nests with at least 6 nestlings) and assigned one of the two experimental treatments at random. The yellow ventral coloration of fledgling plumage was experimentally enhanced either (i) by supplementing nestlings with carotenoids deposited in feathers (lutein and zeaxanthin; Partali *et al.* 1987) during growth and feather development, or (ii) by artificially painting juvenile belly plumage. In each nest, half of the nestlings were manipulated, while the other half received a control treatment (no carotenoid supplementation or neutral painting), controlling for weight. This intra-brood design allows controlling for variation in parental phenotypic quality and territory quality and breeding date. Blood samples were taken on day 4 nestlings for molecular sexing and paternity determination, to allow controlling for potential parental care differences according to fledgling sex and extra-pair paternity status. In the carotenoid supplemented group, nestlings were ranked according to body mass within each nest 4 days post-hatching. The heaviest nestling was randomly assigned to be carotenoid-supplemented or to receive a placebo. Feeding treatment was then alternated by decreasing mass rank within the nest. Starting 4 days post-hatching, nestlings were fed every second day for a total of six times (up to day 14). Nestlings of the carotenoid-supplemented group were fed with 20 mg of beadlets containing 1 mg of lutein and 0.08 mg of zeaxanthin per feeding, while nestlings of the control group were fed with 20 mg of placebo beadlets, a procedure used in previous studies on this species (Tschirren, Fitze & Richner 2003; Tschirren *et al.* 2005). In both treatments, experimental nestlings were weighed every fourth day during the growth period, in order to check for a potential influence of carotenoid supplementation at a time when parents should be unable to use nestling plumage colour as a signal (Heeb *et al.* 2003; Tschirren *et al.* 2005).

Just before fledging, on the early morning of day 19 or 20 (i.e. test day), between 05:30 and 07:15 am, fledgling ventral feathers were sampled, and fledglings were weighed and placed in individual adjacent cage compartments, simulating natural post-fledgling behaviour when begging for food (in a row or on close branches). Cages were hung up just above the nest boxes. In the artificially painted group, painting was performed on fledglings just before placing them in the cages. Three nestling treatments were performed: yellow painted (half of the nestlings), neutral painted (control 1; half of the remaining nestlings) and water painted (control 2; remaining nestlings). Water painted nestlings were treated as other nestlings, but water was used to cover ventral feathers to control for feather manipulation. In the painted group, fledgling feathers were sampled both before and after the manipulation to assess the effect of the treatment. The compartments allowed parents to feed fledglings individually and independently from each other. Placing the fledglings in the cages is expected to have an energetic cost because of heat loss (simulating true fledging). In order to limit the negative impact of this cost on fledging mass, we supplemented breeding pairs with food (live maggots and fat seed balls) placed upon the cages at the beginning of the afternoon. Feeding behaviour of both parents to each nestling was video recorded for 2h15 twice during the test day, once in the morning (starting 8:30 to 9:30 am; before food supplementation) and once in the afternoon (starting 16:00 to 16:30 pm; during food supplementation). In the evening of the test day, between 6:45 and 8:30 pm, with a minimum of 13h of fledgling presence in the cages, fledglings were weighed again and placed back in their nest box, and subsequently remain undisturbed until fledging (which could occur >24h after the end of the experiment - pers. obs.). The use of this cage design has also been used in another context (testing experimentally the role of UV reflectance plumage signals in post-fledging parental allocation - Tanner & Richner 2008). Finally, day 19 fledglings of additional

control broods were weighed at the same time of the day (both early morning and evening; 30 broods) to check for the natural variation of pre-fledging body mass.

A total of 71 nests were used in the experiment, 32 in the carotenoid-supplemented treatment and 39 in the painted treatment. Out of these experimental nests, 53 were video recorded on the test day (three cages but only two video recorders available). All parents but one male of experimental nests were caught and their ventral yellow feathers were sampled to assess the parent-offspring resemblance in feather spectra. Colour reflectance spectra of yellow feathers of fledglings and parents will be measured using a spectrophotometer in the laboratory. Video recordings will be analysed to determine feeding rate by each parent to each fledgling. Feeding rates and body mass changes will be compared between manipulated and control fledglings within broods, accounting for time in the season (linked to food availability), brood size (linked to the level of within-brood competition), fledgling behaviour (begging) and position in the cage (edge vs. centre). If parents use the yellow ventral plumage colour as a signal of fledgling condition to adjust parental care allocation decisions, we expect that they feed preferentially manipulated fledglings (i.e. carotenoid supplemented or yellow painted). Consequently, the body mass of manipulated fledglings should increase more (or decrease less) compared to control fledglings in the same brood at the end of the test day. Male and female parents have been shown to adjust feeding decisions based on different criteria (e.g. Richner, Christe & Oppliger 1995; Tanner & Richner 2008; Ruuskanen *et al.* 2009) and can therefore be expected to differ in their response to treatment. By comparing results for the two experimental treatments (carotenoid supplementation and artificial painting), we will be able to test whether potential differences between manipulated and control fledglings within broods can be attributed to the use of the carotenoid-based plumage colour signal by parents to make feeding decisions, or to other parameters also modified by carotenoid supplementation. In the next years, great tit population has been monitored and breeding adults caught and identified. Therefore, the long-term effects of differential parental resource allocation during the post-fledging phase on future offspring and parental local survival and breeding success can also be investigated.

Perspectives: linking breeding habitat selection and other breeding decisions

Starting from tests of the use of public information as a specific source of information about local habitat quality by individuals in breeding habitat selection decisions, my research work has emphasized or suggested that (i) individuals are likely to use several sources of information (e.g. intra- and inter-specific social information) in a context-dependent way, (ii) the behavioural processes of information acquisition constrain information accessibility and thus information use and the evolution of individual strategies and (iii) breeding habitat selection decisions are not made independently from other breeding decisions, involving a two-way feedback process: dispersal can affect other breeding decisions, for instance *via* the information available to individuals about local conditions (e.g. Pärt 1994; Doligez & Clobert 2003); but other breeding decisions can also affect dispersal, *via* for instance strategies of reproductive investment depending on potential fitness rewards when dispersing or not (e.g. Julliard, Perret & Blondel 1996; Tschirren, Fitze & Richner 2007).

My previous work therefore stressed the potentially strong interactions between dispersal decisions and other decisions linked to breeding. Dispersal is a complex trait that has so far mostly been studied independently from other decisions adopted by individuals. Because it however represents a single response to multiple selective pressures (Clobert *et al.* 2001; Clobert *et al.* 2008) and because it involves complex proximal decision-making processes by individuals (breeding habitat selection decisions), there is no short cut in the study of dispersal. Rather, there is a clear need to consider this trait as part of a complex of traits resulting from simultaneously made individual decisions in the context of breeding, in response to multiple interacting and potentially conflicting choices. Perspectives for my work include going further in this direction, with a particular emphasis on linking breeding habitat selection and mate choice processes. I aim at developing collaborative projects to investigate the interactions between sexual signals and dispersal decisions, using the flycatcher as an empirical model (with A. Qvarnström from Uppsala University and C. Doutrelant from the CEFE in Montpellier - see also the 'research perspectives' section below).

RESEARCH AXIS 2: Determinism, ontogeny and consequences of dispersal

A – Within family resemblance in dispersal behaviour and its consequences

‘Heritability’ of dispersal probability

In many species, individual dispersal decisions are strongly influenced by external factors (intraspecific competition, variability in habitat quality, etc. - reviews in Clobert *et al.* 2001; Bullock *et al.* 2002; Clobert *et al.* 2004; Bowler & Benton 2005; Ronce 2007). Therefore dispersal has generally been considered as a highly plastic, condition-dependent behaviour, with a complex external multi-determinism and thus low heritability (Ims & Hjermann 2001). However, a genetic basis of dispersal is required for dispersal strategies to respond to selection (Roff & Fairbairn 2001) and dispersal strategies have indeed been shown to evolve in response to selective pressures in the field (Thomas *et al.* 2001; Kokko & López-Sepulcre 2006; Duckworth & Badyaev 2007). Evidence for heritability of dispersal traits has been found mainly in plants and insects, in particular with selection experiments on seed or pollen dispersal structures or wing morphology (Roff & Fairbairn 2001; Ronce 2007). In vertebrates, the question of dispersal heritability has recently received increased interest (e.g. Massot & Clobert 2000; Hansson, Bensch & Hasselquist 2003; Pasinelli, Schiegg & Walters 2004). Direct evidence supporting a genetic basis of dispersal traits in vertebrate species is rare, with only two well-documented examples so far (Trefilov *et al.* 2000; Sinervo & Clobert 2003), but indirect evidence includes in particular within-family (sibling and parent-offspring) resemblance in dispersal behaviour (reviews in Massot & Clobert 2000; Doligez & Pärt 2008 - see box 7) and correlation between dispersal behaviour and heritable traits (e.g. personality traits: Dingemanse *et al.* 2003; immune response: Snoeijs *et al.* 2004).

Obtaining unbiased estimates of heritability of realised dispersal events in natural populations can prove difficult because of the need to track an unbiased sample of parent and offspring movements (see below - van Noordwijk 1984; Kokko & López-Sepulcre 2006; Doligez & Pärt 2008). It has been suggested that such unbiased estimates of dispersal heritability can only be obtained from data on dispersal between sub-populations (Hansson *et al.* 2003). In particular, when dispersal distances are used to compute heritability estimates (e.g. McCleery *et al.* 2004; Pasinelli *et al.* 2004), they may lead to biased estimates as soon as true (rather than observed) dispersal distance in the population is large compared to the size of the study area (see below).

To reduce the problem of a constrained array of observable dispersal distances for each breeding site within a study area, we estimated the heritability of between-patch dispersal propensity in the study population of collared flycatchers (Doligez *et al.* 2009). Between-patch dispersal propensity should not be prone to biases due to spatial configuration constraints because settlement decisions at the patch scale should be relatively unconstrained. We used classical parent-offspring regressions in this study and obtained heritability levels of 0.30 ± 0.07 when mixing breeding and natal dispersal status of parents and 0.47 ± 0.10 when restricting parental dispersal to natal dispersal (Doligez *et al.* 2009). These values are within the range of values obtained by other studies (Hansson *et al.* 2003; McCleery *et al.* 2004; Pasinelli *et al.* 2004; reviews in Stirling, Réale & Roff 2002; Doligez & Pärt 2008). Furthermore, because local habitat quality had previously been found to influence dispersal decisions in this population (Doligez *et al.* 1999; Doligez *et al.* 2002b; Doligez *et al.* 2004b), we investigated the influence of parental dispersal status on subsequent offspring natal dispersal probability while accounting for local quality (measured by breeding density and local reproductive success on a patch). Dispersal status of both parents influenced offspring natal dispersal probability, in an additive way when parental natal dispersal status was considered (Doligez *et al.* 2009). We also found sibling resemblance in natal dispersal propensity and assortative mating with respect to dispersal status of individuals.

This first approach gave an estimate of dispersal heritability in this population, showing that the genetic basis for dispersal propensity should be relatively high, despite the influence of multiple environmental factors on dispersal behaviour shown in previous studies. Therefore, these results again stress the complex nature of dispersal as a trait and of its multiple determinism (in particular local environmental quality through breeding habitat selection and genetic effects). As a consequence, the assessment of the relative influence of each factor on dispersal needs further investigation.

However, the use of parent-offspring regressions to estimate heritability suffers from a number of methodological problems (see also below). One major issue is that, because quantitative genetics methods in general have been developed for studies on captive or domestic populations, they rely on the crucial hypothesis that all individuals in the population considered are detected. This assumption is unlikely to be met in natural populations (Lebreton *et al.* 1992; Clobert 1995; Cam 2009), where detection and/or capture probability often depends on individual phenotype such as morphology, behaviour (e.g. breeding behaviour - Gustafsson & Pärt 1990 - or personality - Biro & Dingemanse 2009), health status (e.g. Hawley, Davis & Dhondt 2007), etc. Therefore, the phenotypic variance of many traits of interest is also unlikely to be identical among marked and unmarked individuals (Cam 2009). Violating the hypothesis of perfect individual detection can however not only lead to biased estimates of the demographical parameters of interest but also to flawed inferences on the biological processes revealed by relations between these estimates and other factors, as shown for survival patterns (see e.g. Martin, Clobert & Anderson 1995; Gimenez *et al.* 2008), and this issue can therefore not be ignored (Cam 2009). Capture-recapture (CMR) methods have been specifically developed to account for imperfect detection probability and its heterogeneity among individuals, but they remain largely ignored in the context of estimating trait heritability (Cam 2009). The main difficulty in using CMR models to estimate heritability lies in the integration of random effects into CMR to built ‘CMR mixed models’ (Cam 2009) or ‘capture-recapture animal models’ (Papaix *et al.* in press), which has only very recently been undertaken (Royle 2008; Papaix *et al.* in press).

Until such models become fully available, the question remains to what extent ignoring imperfect individual detection probability may bias heritability estimates in wild populations. The issue is particularly crucial in the context of dispersal, where strong biases may be expected because detection probability is likely to differ between dispersing and non-dispersing individuals due in particular to differences in (i) future dispersal probability, and thus chances to temporarily leave the study area (see below and Doligez & Pärt 2008) and/or (ii) breeding status, in particular mating success (e.g. Pärt 1994; Bensch *et al.* 1998). Accordingly, dispersing individuals may be expected to show lower detection probability, and estimations of dispersal heritability may be affected not only by imperfect individual detection but also by the heterogeneity of detection probability among individuals depending on the trait of interest, here dispersal status, and other traits linked to dispersal (e.g. sex and age; Greenwood & Harvey 1982). In order to explore this question, we attempted to compare parent-offspring resemblance levels obtained via both quantitative genetics methods and CMR models separately for dispersal probability (Doligez *et al.* in revision, MS(1)). Our study showed that accounting for imperfect detection did not seem to influence the observed pattern of parent-offspring resemblance in dispersal probability, despite detection probability is both sensibly lower than 1 and highly heterogeneous among individuals according to dispersal status (Doligez *et al.* in revision, MS(1)). However, to obtain unbiased heritability estimates, combining quantitative genetic and capture-recapture models is needed (see below).

BOX 7: Causes of within-family resemblance in dispersal behaviour in vertebrates

(Part of this discussion constituted a master student's work that I supervised in 2009)

Within-family resemblance in dispersal behaviour has been investigated in 27 studies so far (reviews in Massot & Clobert 2000; Doligez & Pärt 2008; Lahaye, Gutierrez & Dunk 2001; Forero, Donazar & Hiraldo 2002; Massot *et al.* 2003; Sharp *et al.* 2008; Doligez *et al.* 2009). We did not consider here group dispersal (such as observed for sibling lions or some antelope species), but only within-family resemblance after independent dispersal events. Three main categories of within-family resemblance in dispersal have been found: (i) sibling resemblance (16 studies out of 24 where it was

investigated), (ii) parent-offspring resemblance (5 studies out of 12, plus 3 additional studies suggesting it, among which only 2 studies distinguished the relative role of both parents) and (iii) within-pair resemblance (very few studies). As expected, sample size influenced the probability to detect resemblance in these studies (mean sample size in studies detecting resemblance: $N = 264.1$, and studies not detecting it: $N = 62.9$; $t=2.54$, $df=77$, $p=0.015$) Thus within-family resemblance in dispersal behaviour is frequently observed but may require relatively large sample size, i.e. data over sufficiently large spatial and temporal scales, to be detected.

Different factors may cause some families to be more dispersive than others. First, parent and offspring share genes. In order for dispersal strategies to evolve in response to selective pressures, a genetic basis is needed. The aim of most studies investigating within-family resemblance was indeed to show such a basis. In particular, studies comparing dispersal behaviour between parents and offspring often provide an estimate of the heritability of the measure of dispersal used (probability or distance). These estimates vary between 0.04 (Waser & Jones 1989) and 0.88 (Pasinelli *et al.* 2004) among studies, with an average effect size of parent-offspring resemblance of 0.15 (CI: 0.07-0.22) that did not depend on sex (Doligez & Pärt 2008). This value was lower than mean heritability values found for behavioural traits (0.31 ± 0.01), and movement traits more specifically (0.30 ± 0.03) (Stirling *et al.* 2002). Most of these heritability estimates have however been obtained using simple parent-offspring regressions, which do not allow clearly separating genetic from maternal and environmental effects. Only one study so far (except our work on the collared flycatcher, MS(1)) - has estimated heritability of dispersal distance using the more powerful 'animal' models (quantitative genetic mixed models; Kruuk 2004) that account for full pedigree relationships between individuals to quantify heritability. Heritability values obtained using parent-offspring relationships are often higher than those obtained by animal models because they mix genetic with part of parental and environmental effects (Kruuk 2004). In the only example using both methods on the same population, the estimates were however comparable (Greenwood, Harvey & Perrins 1978; McCleery *et al.* 2004). In conclusion, a genetic basis of dispersal is likely, but its quantification requires more investigation in future studies (see in particular the problem of accounting for imperfect individual detection in natural populations in the theme A of perspectives).

Second, siblings share the same parents. Parental effects can also have a genetic basis, thus parent-offspring resemblance in dispersal can also involve maternal effects (Mousseau & Fox 1998). Maternal effects have now repeatedly been shown to affect offspring phenotype and behaviour, and constitute a powerful means for the females to quickly and optimally adjust their offspring responses to local environmental conditions (see references in Tschirren *et al.* 2009a). From another point of view, early maternal effects also constitute cheap information for offspring on the quality of their natal environment. The effect of different maternal factors has now been shown to affect natal dispersal (e.g. Ronce, Clobert & Massot 1998), including long-term effects acting on the mother before the beginning of gestation or egg laying (Massot & Clobert 2000). Such maternal effects can be mediated for instance by hormones transferred by females to embryos or eggs. (Meylan *et al.* 2002; Tschirren *et al.* 2007). Later parental effects can also generate sibling resemblance in dispersal, including after young have left the natal site. For instance, bird families often remain grouped for weeks after fledging (e.g. Naef-Daenzer *et al.* 2001a), and parents have the possibility to influence the movements and spatial zones explored by their offspring (Gosler 1993), thereby potentially affecting their future dispersal decisions in a non-independent way.

Third, parents and offspring partly share the same environment before making dispersal decisions and thus experience the same conditions during their development or breeding. Individuals use information about their local habitat quality to make dispersal decisions (Cody 1985b; Reed *et al.* 1999). If parents and offspring or siblings use the same information sources, they can independently make the same dispersal decisions. Environmental effects can therefore generate 'true' within-family resemblance in dispersal behaviour. They can also generate apparent resemblance when dispersal distance is used as the measure of dispersal, a problem that has been discussed thoroughly in the case of the great tit population in Whytham wood (Greenwood, Harvey & Perrins 1979b; van Noordwijk 1984). In a finite study site, the probability to detect long distance dispersal events depends on the position within the area, i.e. is higher towards the edges compared to the centre. This implies that long parental dispersal distances can only be detected for offspring originating from sites near the edges of

the study area, which are themselves the only offspring for which long distance dispersal can be detected. On average, offspring originating from the centre of the study area will have (i) shorter parental dispersal distances and (ii) shorter dispersal distances themselves. This spatial heterogeneity in detecting long distance dispersal events within the study area bias can therefore create an apparent resemblance between parents and offspring in dispersal distance, i.e. artificially inflate the estimate of heritability of dispersal distance (van Noordwijk 1984). This problem could be frequent since in most cases, study areas remain small compared to potential long distance dispersal events, i.e. the distribution of observable dispersal distances is always right-truncated, even when study areas are supposed to be large compared to average dispersal distance (see e.g. Winkler *et al.* 2005; discussion in Doligez & Pärt 2008). Environmental effects could also explain within-pair resemblance in dispersal behaviour if individuals choose breeding sites according to different criteria depending on their dispersal status (e.g. spatial localisation, habitat characteristics). This would generate an environment-mediated assortative mating with respect to dispersal status.

Finally, within-pair resemblance in dispersal behaviour could also arise from sexual selection processes based on phenotypic (morphological or behavioural) differences between individuals differing in their dispersal history. Dispersing and non-dispersing individuals have been found to differ in many phenotypic traits, ranging from physiology and morphology to behaviour (Clobert *et al.* 2009), defining possible dispersal syndromes (Sih, Bell & Johnson 2004). Because such syndromes have the potential to strongly affect individual fitness (e.g. Duckworth & Badyaev 2007), they could also influence the evolution of mate choice processes and favour assortative mating by dispersal status, whenever individuals can recognize the origin of individuals within a population. Such a recognition process has already been shown (Cote & Clobert 2007) and could be based on either sexual signals (e.g. songs, mating displays, secondary sexual morphological characters such as new ornaments) or more general traits (e.g. behavioural traits such as aggressiveness).

Methodological consequences of non random dispersal: estimating individual fitness

Within-family resemblance in dispersal behaviour may have both methodological and evolutionary consequences. On a methodological point of view, a major issue concerns the estimation of fitness correlates of dispersal. Many studies aimed at investigating fitness consequences of dispersal by comparing fitness estimates between individuals differing in their dispersal history (see Doligez & Pärt 2008 for a full discussion about the validity of this approach). Parent-offspring resemblance, but also individual consistency in dispersal propensity are two key issues for a reliable estimation of fitness with respect to dispersal status. First, if individuals display a lifetime consistency in dispersal propensity, dispersers are more likely to disperse again, and thus leave the study area and be considered dead, than philopatric individuals. Such differential dispersal propensity will lead to the underestimation of local adult survival of dispersing compared to philopatric individuals. Second, if offspring resemble parents in terms of dispersal propensity, dispersing parents produce young that are more likely to disperse, and thus leave the study area and be considered dead, than philopatric parents. As a result, local recruitment rate of dispersers' offspring will be underestimated in comparison to that of philopatric individuals (Doligez & Pärt 2008). In both cases, differences are only apparent, i.e. linked to the spatial scale under consideration and the impossibility to distinguish emigration out of the study area from mortality. We highlighted this problem, already recognized in previous studies (e.g. Greenwood *et al.* 1979b; Clobert *et al.* 1988; McCleery & Clobert 1990; Bélichon, Clobert & Massot 1996; Verhulst & van Eck 1996; van der Castele 2002) but still largely ignored. We reviewed the literature to assess the frequency and importance of within-individual consistency and within-family similarities in dispersal propensity (Doligez & Pärt 2008). Box 7 summarizes the evidence of within-family similarities. Individual consistency in dispersal behaviour has rarely been investigated (only three studies on bird species testing for within-individual consistency, two of which find significant consistency, and two additional indirectly suggesting no consistency; Doligez & Pärt 2008). More data are therefore needed regarding within-individual consistency in dispersal behaviour.

We used a simple simulation approach to assess the potential underestimation of lifetime reproductive success (LRS) for dispersing compared to philopatric individuals and obtained a level of underestimation of LRS ranging from 2 to 40 % depending in particular on the species longevity (see

details in Doligez & Pärt 2008). Thus, non-random dispersal can possibly generate a large underestimation of LRS of dispersing compared to philopatric individuals when these are based on estimates of local survival rates. As a consequence, we reinterpreted comparisons of fitness estimates between dispersing and philopatric individuals in previous studies for which both fitness correlates of dispersal and within-individual consistency or parent-offspring resemblance in dispersal are available. About a third of the differences in fitness components reported between dispersing and philopatric individuals are open to the alternative explanation of biased fitness estimates (Doligez & Pärt 2008).

Whether parent-offspring resemblance and within-individual lifetime consistency in dispersal propensity arise from a genetic component of dispersal, parental effects, or a shared environment, is not known in most cases (Massot & Clobert 2000; Massot *et al.* 2003; Clobert *et al.* 2004). Importantly, however, the main issue here is not the causes of such phenotypic associations, but whether they exist and may generate biases in fitness estimates with respect to dispersal status of individuals. Apparent parent-offspring resemblance (or within-individual consistency) in dispersal may be artificially created by a simple ‘common environment’ effect, for example breeding site location within a limited study area, which constrains the array of distances observable from each site (van Noordwijk 1984 - see above). In such situations of no true parent-offspring resemblance, however, offspring of dispersers may still have a higher probability to leave the study area compared to those of philopatric individuals, for instance if dispersers are more likely to breed on the edge of the study area. Parent-offspring resemblance in dispersal propensity may therefore not always be a prerequisite of biased offspring dispersal depending on parental dispersal. Another potential example of this is sex-biased dispersal, which could also create biases in fitness estimates based on number of local recruits produced when dispersing and philopatric individuals adjust offspring sex-ratio differently, depending e.g. on individual condition or environment. If dispersers overproduce the most dispersive sex, their fitness estimate is at risk of being underestimated. In this case, while no sex-specific parent-offspring (i.e. parent-son or parent-daughter) resemblance in dispersal propensity exists, an overall resemblance (i.e. mid-parent - mid-offspring) should however be suggested due to offspring sex-ratio bias (Doligez & Pärt 2008).

Evolutionary consequences of non random dispersal: kin interactions, gene flow and Fisher’s theorem

Within-family resemblance in dispersal behaviour can lead individuals of the same families to disperse similar distances in the same direction and, as a consequence, settle close to each other. Negative kin interactions (kin competition, inbreeding) have long been proposed as major evolutionary forces explaining the evolution of dispersal (Hamilton & May 1977; reviews in Clobert *et al.* 2001; Clobert *et al.* 2004; Bowler & Benton 2005; Ronce 2007; Clobert *et al.* 2008). Within-family resemblance in dispersal behaviour may therefore be constrained by such selective pressures and could be expected to evolve mainly in species / populations where inbreeding cost and/or competition level are low. However, empirical studies in which both within-family resemblance in dispersal and the risk of inbreeding have been assessed show that inbreeding remained low (e.g. Arcese 1989; Forero *et al.* 2002). Even when family members show resemblance in dispersal behaviour, the risk of inbreeding can be reduced by sex-biased dispersal (e.g. Greenwood, Harvey & Perrins 1979a; Newton & Marquiss 1983; Sharp *et al.* 2008) and/or by kin recognition based on e.g. olfactory cues (Léna *et al.* 1998) or songs (Wheelwright & Mauck 1998). More generally, the overall influence of inbreeding as a selective force acting on dispersal has been challenged on the basis of empirical studies (Clobert *et al.* 2008). Conversely, within-family resemblance in dispersal could be favoured in species with cooperative breeding among kins (Hatchwell & Komdeur 2000). The evolution of helping behaviour was suggested to be linked to resemblance in dispersal behaviour among kin, up to group dispersal events by family members (observed e.g. in lions, antelopes), leading kin to settle on neighbouring territories. This can reduce competition level and favour helping behaviour in caring for the young or defending territories (Sharp *et al.* 2008).

Within-family resemblance in dispersal could also affect gene flow between populations. Because kin share alleles, effective population size of immigrants into a patch could be reduced. The existence and quantitative importance of such biases due to within-family resemblance in dispersal and more generally non-random dispersal processes has not been explored so far. However, such

processes have been suggested to explain patterns of genetic differentiation in marine invertebrates, where small-scale (down to a few meters) can be higher than large-scale differentiation (tens or hundreds of km).

Finally, within-family resemblance in dispersal behaviour is likely to reflect a genetic basis for dispersal (see box 7). The mean heritability value of traits linked to movement and dispersal found in previous studies is 0.30 ± 0.03 (Stirling *et al.* 2002; see also Doligez & Pärt 2008). Such heritability values have implications regarding the relative fitness of dispersing and philopatric individuals, since medium heritability levels such as here are typically associated with low proportions of fitness explained by the trait considered (<5%, e.g. Gustafsson 1986b; Mousseau & Roff 1987; Kruuk *et al.* 2000; Merilä & Sheldon 2000; Stirling *et al.* 2002; McCleery *et al.* 2004 - the negative relation between heritability level of a trait and between-individual variation in fitness explained by the trait is known as the 'Fisher's fundamental theorem of natural selection': Fisher 1958; Falconer & Mackay 1996). If the genetic contribution to the observed heritability of dispersal traits is sufficiently high, dispersal should therefore not be expected to have general lifetime fitness consequences, and observed fitness differences according to dispersal status (reviews in Béchichon *et al.* 1996; Doligez & Pärt 2008) may in fact be due to confounding effects, e.g. within-family resemblance in dispersal generating systematic underestimation of dispersers' fitness (see above and Doligez & Pärt 2008 for a full discussion). Observed fitness differences according to dispersal status may also be due to compensation between fitness components over individuals' lifetime, since most studies investigate single or limited components rather than lifetime fitness (Béchichon *et al.* 1996; Doligez & Pärt 2008). Other possible explanations for the frequently observed apparent fitness differences according to dispersal status are (i) an overestimation of dispersal heritability levels, mainly obtained using parent-offspring regressions (except McCleery *et al.* 2004; see below; Kruuk 2004), (ii) quantitatively small, despite significant, fitness differences according to dispersal status and/or (iii) an evolutionary stable genetic polymorphism in spatio-temporally varying environments (Hansson *et al.* 2003; Ronce 2007; see Kruuk 2004; Kruuk, Slate & Wilson 2008 for more discussion).

B – The relative influence of genetic, parental and environmental effects in dispersal determinism

The relative influence of genetic, maternal and environmental effects: animal models

Based on capture-recapture data, many evolutionary studies have used quantitative genetic models to estimate heritability of morphological, physiological and behavioural traits and address related evolutionary questions in natural populations (Kruuk 2004; Kruuk *et al.* 2008). However, until recently, most studies used simple parent-offspring regressions (or sib analyses) to estimate the heritability level of a trait (Kruuk 2004). One major problem with these simple approaches is the impossibility to obtain precise estimates of different components of variance, i.e. to fully discriminate between genetic, parental and environmental effects of various origins. Recently, however, a major change in the study of quantitative genetics of natural populations was operated with the use of generalised linear mixed models ('animal models'; Kruuk 2004). These models incorporate full multigenerational information about parentage relationships between individuals from complex pedigrees and thereby allow the partitioning of the observed phenotypic variance in a trait into a range of causal components of variance. They are also free from constraints imposed by the presence of assortative mating, inbreeding or unbalanced data sets. As a consequence, they have recently received increasing interest in evolutionary studies and are now largely preferred over parent-offspring regressions or sib analyses whenever a deep enough pedigree is available for the study population (Kruuk *et al.* 2008).

In the case of our study population of collared flycatchers, we have evidence that both genetic and various environmental effects influence between-patch dispersal probability. We also suspect maternal effects to potentially influence natal dispersal behaviour (Mousseau & Fox 1998; Tschirren *et al.* 2007; see below). The relative influence of these effects, however, is unknown. Therefore, in collaboration with D. Réale, we have started analyses of dispersal heritability in collared flycatchers using mixed quantitative genetics models (Doligez *et al.* in revision, MS(2)). The estimates obtained

in preliminary analyses were 17 to 37 % lower than estimates obtained with parent-offspring regressions: 0.19 (0.16-0.21) and 0.39 (0.31-0.47) for all parental dispersal events and parental natal dispersal events only, respectively; corresponding figures from parent-offspring regressions were: 0.30 (0.16-0.44) and 0.47 (0.28-0.66) (Doligez *et al.* 2009; Doligez *et al.* in revision, MS(1)). Nevertheless, they remain significantly larger than 0, confirming the influence of genetic effects in the determinism of dispersal probability. Analyses of dispersal heritability in the collared flycatcher using mixed quantitative genetics models will be continued, in particular to incorporate maternal effects in the models to assess their contribution in the determinism of natal dispersal (see below). We also aim at estimating genetic correlations between dispersal and other traits, in particular breeding and life-history traits, revealing potential trade-offs (see below).

The relative influence of early and late development effects: an experimental approach

Although animal models are powerful in partitioning total phenotypic variance into genetic, parental, environmental components of variance when long-term pedigree information is available (Kruuk 2004; Kruuk *et al.* 2008), they remain correlative. I therefore decided to complement the analysis of the determinism of natal dispersal in the study population of collared flycatchers using the long-term data and animal models by performing a field experiment to estimate the relative influence of early (i.e. before hatching) and late (i.e. after hatching) factors during nestling development on subsequent natal dispersal behaviour (description in Box 8). The experiment consists in cross-fostering hatchlings between nests whose parents (especially females) differ in their dispersal status, and was performed at a large spatial and temporal scale to allow large sample sizes and high statistical power to be obtained (box 8). This experiment will not allow separating different types of effects (in particular genetic and maternal effects, on the one hand, and late parental and environmental effects, on the other hand). However, it will provide a complementary view of natal dispersal determinism besides the analysis of the long-term correlative data.

Furthermore, several large-scale cross-fostering experiments have been performed in the past in this population. Although they addressed questions such as the existence of reproductive costs (Gustafsson & Sutherland 1988), i.e. not related to dispersal, these experiments could provide additional data to test for the relative influence of early and late factors during development on subsequent natal dispersal behaviour. In most cases, however, cross-fosterings were performed in the context of brood size manipulation experiments (i.e. unequal numbers of nestlings exchanged between nests, except in control treatments). Unlike the experiment recently conducted, therefore, rearing conditions in the nest (here, brood size) were changed as a result of cross-fostering. Previous results in this population indicate that natal dispersal distance decreased with increasing brood size at fledging in females, while no clear link was found in males (Pärt 1990). The influence of brood size on dispersal probability, however, has not been tested yet. We will therefore first check the relation between brood size and dispersal probability in the general population and in nests where brood size has been manipulated. In a second step, this second data set of cross-fostered recruits (approx. 700 recruits, of which 200 to 300 should have parents of known dispersal status) will be analysed together with the first data set obtained from the experiment described below, including brood size and manipulations as covariates in the models to account for the consequences of differences in experimental designs.

BOX 8: The relative influence of early and late factors in dispersal determinism

In order to experimentally assess the relative influence of early (e.g. genetic and early maternal effects) and late (e.g. parental and environmental effects during nestling rearing) factors during development on future natal dispersal behaviour, I conducted a large-scale cross-fostering experiment aiming at breaking down the link between biological and rearing parents in the study population of collared flycatchers. In this population, females are caught and identified during incubation. Therefore, their dispersal status can be determined before hatching day. Each year between 2005 and 2009, nestlings were exchanged between nests of females differing in their dispersal status. Four treatments were applied: (1) nestlings of dispersing females transferred to nests of non dispersing females, (2) reverse transfer, i.e. nestlings of non dispersing females transferred to nests of dispersing females, (3)

and (4) control transfers: nestlings of dispersing females transferred to nests of other dispersing females and nestlings of non dispersing females transferred to nests of other non dispersing females. Nestling transfers occurred mostly on day 2, with further adjustments up to day 5. Before transfer, nestlings were individually marked by clipping nails so that their nest of origin was known. Whenever possible, all nestlings of a given nest were cross-fostered to increase the sample of expected manipulated recruits; although such a design would be particularly interesting, it would indeed be extremely difficult to cross-foster only half of the nestlings in a given nest to compare transferred and non transferred nestlings, since recruitment is low (10% approx.; Doncaster *et al.* 1997) and the proportion of nests from which two or more nestlings recruit is therefore very low (Gustafsson 1989 – not even accounting for the fact that these multiple recruits would need to originate from different treatments within a nest). Given these constraints, I choose to cross-foster the maximum possible number of nestlings in all nests involved in the experiment. Nestlings were cross-fostered between nests matched for (i) hatching date (i.e. nestling age), (ii) brood size at the age of transfer and (iii) habitat patch, so as to modify as few environmental effects as possible. When brood sizes differed between nests, or depending on the total number of nests hatched on a given day, transfers were performed between three or more nests to cross-foster all possible nestlings. When no recipient nest was available in the same patch on a given day, nestlings were transferred between nests in different but as close-by as possible, patches.

Large samples are needed for this experiment because of (i) low overall recruitment rate and (ii) low expected effect size given the level of heritability assessed using parent-offspring regressions (Doligez *et al.* 2009). Over the 5 years of the experiment (2005-2009), more than 800 nests and 2000 nestlings were manipulated. Recruits are caught each year during the general monitoring of the population, and experimental recruits will be identified from 2006 until 2011 included, since many individuals only recruit when 2 years old (Gustafsson & Pärt 1990; Doligez *et al.* 2009). Approximately 200 recruits of both sexes are therefore expected to be found during the period 2006-2011. The dispersal behaviour of the recruits will be determined and analysed with respect to treatment, i.e. dispersal status of the mother, accounting for age of both parents, dispersal status of the male in the nest of origin and nest of rearing, age at recruitment and other covariates (fixed effects: hatching date, brood size, fledging area characteristics such as breeding density and local success; random effects: year and fledging area). Depending on the relative influence of the dispersal status of biological and foster parents on the natal dispersal of experimental recruits, we will be able to determine the relative influence of early (i.e. dispersal status of biological parents) and late (i.e. dispersal status of foster parents) factors on subsequent natal dispersal, explaining the observed parent-offspring resemblance in dispersal behaviour in this population.

The role of maternal effects in natal dispersal behaviour: yolk androgens

The work presented so far mainly addressed genetic and environmental effects on dispersal behaviour in the study population of collared flycatchers. However, maternal effects may also be expected to play a prominent yet so far neglected role in shaping natal dispersal. Maternal effects occur when the phenotype of the mother or the environment she encounters modifies her offspring's phenotype (Mousseau & Fox 1998). Maternal effects are a powerful and flexible tool for females to adjust their offspring phenotype to local conditions. They can significantly contribute to fitness variation by modifying offspring phenotype, thereby altering the genotype-phenotype relationship and potentially accelerating or impeding the response to selection (Mousseau & Fox 1998; Wolf *et al.* 1998). They are therefore a major evolutionary force, in particular when females make a high investment in their offspring. Oviparous species are particularly interesting models to study early (prenatal) maternal effects. Maternal investment into the egg, reflected by egg size and/or composition, has been shown to critically influence offspring development in a variety of taxa, including birds. Recently, there has been an increased interest in androgen hormones of maternal origin transferred to the yolk (Schwabl 1993). Androgen hormones have been shown to be an important component of egg quality, in particular a main determinant of developmental plasticity (Groothuis *et al.* 2005b; Gil 2008). Studies revealed that maternal yolk hormones have both short- and

long-term effects on postnatal growth, begging intensity and competitiveness, but also phenotype and behaviour at adulthood (aggressiveness, neophobia, social status, sexual traits - reviews in Groothuis *et al.* 2005b; Gil 2008). Most studies have found beneficial effects of maternal yolk androgens on offspring. However, elevated levels of yolk androgens may imply physiological costs for the mother and potentially the young, for instance through their immuno-suppressive effects (Groothuis *et al.* 2005a). These opposing costs and benefits therefore indicate that the optimal allocation of maternal yolk androgens depends on current and/or future environmental or social local conditions, as found in many studies (review in Tschirren *et al.* 2009b). It may also depend on other decisions taken by the female during breeding. Yolk androgens of maternal origin therefore have the potential to optimally shape offspring natal dispersal in response to local conditions and to female investment. In a natural population of great tits, natal dispersal distance increased with experimentally increased yolk androgens and this adjustment was suggested to be adaptive with respect to parasitism (Tschirren *et al.* 2007). Indeed, fledglings reared in nests infested with ectoparasitic hen fleas had higher reproductive success when dispersing short distances, suggesting local adaptation processes; because females transferred lower concentrations of yolk androgens to their eggs when their nest was infested with fleas, they may adaptively adjust offspring natal dispersal behaviour (Tschirren *et al.* 2007). However, this is the only study on the effects of yolk androgens on dispersal in the wild so far, thus these effects remain poorly investigated.

Using several combined approaches, we explored these issues in the study population of collared flycatchers. First, we performed a spatially and temporally large-scale egg sampling scheme (see box 9) to investigate the links between yolk androgens of maternal origin, female dispersal history and offspring future dispersal. We aimed at testing whether maternal effects in the form of yolk androgens could at least partly explain the parent-offspring resemblance in dispersal behaviour observed in the flycatcher population (Doligez *et al.* 2009). Yolk androgens could mediate parent-offspring resemblance if three conditions are met:

- 1 - Females should transfer different amounts of yolk androgens depending on their dispersal history;
- 2 - Maternal transfer of yolk androgen should be heritable;
- 3 - And finally, offspring natal dispersal should be related to yolk androgen concentration in the same direction as observed in condition 1 (i.e. offspring natal dispersal should increase with increasing yolk androgens if dispersing females transfer higher androgen concentrations to their eggs than philopatric females).

Because measuring of yolk androgen concentrations implies the destruction of one egg in our case, condition 3 can only be tested indirectly by investigating a relation between yolk androgen concentration in the sampled egg and natal dispersal of the siblings, assuming that the sampled egg is representative of the whole clutch (see Michl *et al.* 2005; Tobler, Granbom & Sandell 2007; Ruuskanen *et al.* 2009 for within- vs. between-clutch variation in yolk androgen hormones). Only a sub-sample of eggs has been analysed so far, therefore the set of analyses is not complete yet. Regarding condition 1, preliminary results (N=346 eggs from 2005 to 2007) indicate that dispersing females indeed transferred higher androgen concentrations to their eggs ($F=5.41$, $p=0.021$) accounting for a year effect ($F=3.17$, $p=0.024$); yolk androgen concentration also decreased with increasing female age ($F=5.45$, $p=0.020$; Doligez *et al.* in prep.). Regarding condition 2, we were able to show that female transfer of yolk androgen is heritable in this population ($h^2=0.75$ (0.23-1.26), $F_{1,50}=8.09$, $p=0.006$; Tschirren *et al.* 2009a). Condition 3 has not been tested yet. Therefore, the analyses need to be completed before any conclusion regarding the links between maternally transferred yolk androgens and dispersal behaviour can be drawn, although such links are likely to exist.

Second, we experimentally manipulated yolk androgens in eggs of flycatchers to test the long-term effects of elevated yolk androgens on offspring phenotype, behaviour (including dispersal) and ultimately fitness. This experiment was performed in spring 2007 on 240 nests from which 610 young fledged (Ruuskanen *et al.* 2009; Ruuskanen *et al.* in prep., MS(4)) and experimental recruits have been caught from 2008 until 2010. We first investigated short-term effects of experimentally increased yolk androgens on sexual conflicts over parental investment (Ruuskanen *et al.* 2009) and nestling growth and immune function (Pitala *et al.* 2009). Long-term effects on offspring phenotype and fitness are currently under analysis. The first results indicate that yolk androgen elevation decreased the recruitment rate of male, but not female offspring (Ruuskanen *et al.* in prep., MS(4)). The manipulation had no effect on the breeding success of offspring of either sex. Furthermore, elevation

of yolk androgens had no effect on return rate or breeding success of the parents (Ruuskanen *et al.* in prep., MS(4)). These results thus indicate that high yolk androgen levels can impose a potential direct fitness cost for male offspring, but no long-lasting additional fitness costs arising via the future reproductive success of the parents. The influence of the treatment on offspring phenotype, including dispersal behaviour, needs to be analysed.

Finally, while we focused so far on maternally transferred yolk androgens, other egg components may play an important role in the adjustment of offspring phenotype to local conditions *via* maternal effects in the eggs. Among these components, antibodies are of specific interest because they are linked to responses to parasites (e.g. Gasparini *et al.* 2001; Buechler *et al.* 2002) and therefore may affect local adaptation processes in interaction with natal dispersal behaviour (see Tschirren *et al.* 2007 and below). The links between different egg components, but also between egg components and other breeding variables reflecting decisions by the female will also be investigated in relation to female past and offspring subsequent dispersal behaviour, to test whether dispersal may be linked to different breeding strategies involving egg components. Similar responses will be investigated in the sympatric great tit population in order to compare the two study species (see box 9).

BOX 9: Maternal effects on natal dispersal: transfer of androgen hormones and antibodies of maternal origin to the eggs

In order to measure egg components in relation to parent and offspring dispersal behaviour, and more specifically androgen hormones and immunological proteins (antibodies) of maternal origin, a large-scale egg sampling scheme was performed from 2005 until 2010, in both the collared flycatcher and the great tit study populations. One egg per clutch was sampled, except in 2005 when 8 complete clutches of each species were collected to investigate within-clutch variation in egg components according to laying sequence in these populations. In sampled nests, we aimed at collecting one of the middle eggs of the clutch, i.e. avoid clutch extremes, to obtain a clutch average value (see Tschirren, Schwable & Richner 2004; Tobler *et al.* 2007). Average clutch sizes in these populations are approx. 6-7 for the flycatcher and 8-9 for the great tit. Therefore we choose to collect the third egg for collared flycatchers and the fourth egg for great tits. Nest boxes were visited every second day in the patches where sampling occurred, and new clutches with one or two eggs were marked with a permanent marker. In the next day, these nests were visited again to either mark the second or third egg when one or two eggs were present in the previous day (for flycatchers and great tits respectively) or collect the third or fourth egg when two or three eggs were present in the previous day (again, for flycatchers and great tits respectively). Complete sampled clutches were chosen at random among nests visited on the day of laying the first egg. These nests were subsequently visited daily to collect eggs on the laying day. Except in 2010, all sampled eggs have been replaced by dummy eggs in order not to modify the original clutch size laid by the female. In 2010, sampled eggs (in flycatchers only) were not replaced, and the egg replacement rate by sampled females will be assessed by comparing final clutch size between sampled females and non sampled females that started to lay on the same day.

In 2006 and 2007, we aimed at collecting eggs specifically for estimating heritability of androgen hormones transfer to egg yolk. In the flycatcher, we therefore identified the females before laying to target daughters of already sampled females. We caught females in nest boxes during nest building and only nests of the target females were subsequently sampled. Early catching had already been performed in this population and the disturbance induced is low: few nest box shifts occurred following catching during nest building, most of which may be due to catching a prospecting female rather than the owner of the nest. In 2008 and 2009, egg sampling increased again in relation to the post-fledging prospecting experiment (see box 3). Individuals equipped with radio-tags were chosen preferentially among nests where an egg had been sampled in order to test for a potential relation between androgen hormone and antibody transfer to the yolk and post-fledging prospecting behaviour.

Sampled eggs were brought back to the laboratory, and processed on the same day. Yolk, albumen and shell were separated, weighed to the nearest mg and stored frozen at -18°C until the end of the field season. They were subsequently transferred to -80°C for analyses of components in the laboratory.

Androgen hormone concentrations are measured using radio-immuno assays described in Tschirren *et al.* 2004 and Tschirren *et al.* 2009a for the great tit and flycatcher respectively. Antibody concentrations will be analysed using ELISA tests following Buechler *et al.* 2002 and Tschirren *et al.* 2009b. A total of 661 flycatcher (2005 to 2010) and 980 great tit (2005 to 2009) nests were sampled. Additionally, 243 flycatcher nests had been sampled in 2003 (no nest sampled in 2004), and the 8 complete clutches collected in 2005 correspond to 50 flycatcher and 66 great tit eggs.

Sampled nests of both species were monitored as part of the long term population monitoring on the study site, allowing us to test for the influence of nest and parental characteristics (including dispersal status) on female transfer of androgen hormones and antibodies to the eggs. Recruits from the sampled nests are also caught as part of the population monitoring, allowing us to test the link between egg components (androgen hormones and antibodies) and natal dispersal (and other characteristics), i.e. test whether females can adjust offspring dispersal phenotype according to local conditions (Tschirren *et al.* 2007) and the fitness consequences of these maternal effects. All flycatcher nestlings from sampled nests and about half of the great tit nestlings have been cross-fostered to break the link between the conditions in the nest of origin and in the rearing nest. Therefore, any relationship detected between egg components and sibling subsequent natal dispersal behaviour (or other traits) must relate to early effects in the egg (or incubation). Finally, using the parentage relationships between individuals whose eggs have been sampled, we have recently assessed the heritability of androgen hormone transfer to the eggs in the flycatcher *via* parent-offspring regressions (Tschirren *et al.* 2009a). The same approach will be conducted on great tit eggs to estimate the heritability of androgen hormone transfer to the eggs and compare the levels between the two study species living in the same general environment, and to estimate the heritability of antibody transfer in both study species. Using the full collection of eggs and full pedigree relationships in the flycatcher population, we also aim at using a more powerful method, i.e. mixed quantitative genetic models ('animal models'), to partition phenotypic variance in androgen hormones and antibody transfer to the eggs between genetic, parental and environmental effects.

C – Individual and population consequences of dispersal

Breeding and life-history strategies linked to dispersal: quantifying breeding decisions in relation to dispersal

Even when individuals engage in (potentially high) prospecting activity to gather information about habitat quality (see above), time and energy constraints are likely to restrain the quantity and/or quality of information available to individuals - hence making the use of integrative cues such as public information particularly relevant (Danchin *et al.* 2001). Dispersing individuals may therefore be expected to be less well informed about their new breeding habitat than non dispersing individuals. Individuals have been shown to optimize their current breeding investment to local conditions (see e.g. Pettifor, Perrins & McCleery 1988; Both, Visser & Verboven 1999). Therefore, individuals differing in their knowledge about local conditions because of their dispersal history may be expected to make different breeding decisions, as a result of different risk-taking breeding strategies. Dispersing parents may for instance choose to reduce offspring number but invest more in parental care to each offspring (e.g. Julliard *et al.* 1996); in species with sex-biased natal dispersal, they may also adjust offspring sex ratio to produce both dispersing and non dispersing offspring, i.e. spread the risk related to offspring natal dispersal and local recruitment (Julliard 1996; Julliard 2000). Many such adjustments of breeding strategies may be expected in relation to parental dispersal status. Differences in breeding decisions between dispersing and non dispersing individuals have been described in many species (reviews in Bélíchon *et al.* 1996; Doligez & Pärt 2008); however such differences are generally interpreted as consequences of dispersal, reflecting costs (when breeding variables are lower for dispersers compared to non dispersers) or benefits (when they are higher), and rarely as breeding strategy adjustment according to individual knowledge of local conditions as a result of dispersal history. In general, the

interactions between dispersal and other breeding decisions and their life-history consequences at the individual level have been poorly investigated.

Such interactions however have the potential to drastically change the interpretation of results. An example is provided by the study we conducted about estimating reproductive costs in collared flycatchers and great tits using multi-state capture-recapture models to estimate transition probabilities between dispersing and reproductive investment (i.e. clutch sizes) states (Doligez *et al.* 2002a). We aimed at testing reproductive costs while accounting for dispersal, which had been neglected so far. However, reproductive costs may affect not only life history traits (future survival and reproduction) but also behavioural traits that can affect subsequent individual detection probability, such as dispersal. We re-analysed data from brood size manipulation in both species (Gustafsson & Sutherland 1988) to test whether experimental manipulation affected future survival, clutch size and/or dispersal probability (Doligez *et al.* 2002a). The results may at first suggest reproductive costs on future survival (decreased survival after increasing reproductive effort and *vice-versa*), but these differences could be explained by differential dispersal in response to the manipulation (increased dispersal after increasing reproductive effort and *vice-versa*). Thus we did not confirm the existence of reproductive costs in these populations (Doligez *et al.* 2002a). Interestingly, the effect of the manipulation of reproductive effort on future dispersal probability was shown to depend on individual initial dispersal status, suggesting that individuals with different knowledge about the environment made different future decisions in response to the manipulation (Doligez *et al.* 2002a). Accounting for dispersal history and thus information available to individuals can therefore change the conclusions drawn about future breeding decisions by individuals.

I aimed at exploring further differences in breeding strategies depending on individual dispersal history in the study population of collared flycatchers (and, to a lesser extent, great tits, for which knowledge about dispersal status is lower). Using information about as many and as fine breeding traits as possible, I also intended to investigate potential compensatory mechanisms between decisions made by individuals within a breeding event. The breeding traits on which information was collected over the past few years are described in box 10. Preliminary analyses of these breeding traits depending on parental dispersal status have been conducted during the course of several first and second year of master research trainings in the past years, and they revealed differences in many breeding traits between dispersing and non dispersing individuals, with (as expected) interactions with individual sex and age. However, no general picture of these differences can be given so far, as these analyses require further work. This will be done as part of a PhD project starting in autumn 2010 (see perspectives).

BOX 10: Dispersal and breeding decisions: refined strategies?

In order to test for differences in breeding strategies between dispersing and non dispersing individuals, we collected data on early and late breeding decisions in the study population of collared flycatchers over 5 years (2005-2009). We aimed at obtaining precise information on different breeding traits, revealing as refined as possible breeding decision-making by individuals. The information collected comprises the following data and samples:

- 1 - Female weight before laying:** in spring 2006 and 2007, most females (i.e. > 600) were caught before laying (see box 9) and weighed. Because (i) body mass in birds impairs flying and predator escaping ability (Adriansen *et al.* 1998) but may reduce risk of starvation, (ii) metabolic reserves may affect female investment in eggs and (iii) dispersing and non-dispersing individuals may differ in their knowledge or familiarity with their environment (Pärt 1994) and in particular with food resources, differences between females depending on their dispersal history may be expected in body mass before laying, but also during incubation and during nestling rearing, which can be tested using the long-term data base and body mass data collected since 2005.
- 2 - Female investment in eggs:** from 2005 until 2009, a random sample of clutches was monitored daily to mark and weigh egg along the laying sequence (>500 clutches over the 5 years). In 2006, 2008 and 2009, clutches from a sample of these monitored nests were photographed to allow

assessing egg volume (>300 clutches over the three years). These measures of female investment decisions in eggs will be related to her dispersal history. From the long-term population monitoring, we will be able to assess the relation between egg mass and size and subsequent offspring survival and natal dispersal behaviour, on a clutch scale (indeed, the egg of origin of the nestlings within the clutch is unknown).

- 3 - Egg components:** in 2003 and from 2005 until 2010, one egg was sampled from a random subset of nests on the laying day and yolk, albumen and shells were weighed and frozen on the same day (see box 9; >900 eggs over the 7 years). From these eggs, maternal transfer of androgen hormones and antibodies (see above), but also total protein concentration, total calorific contents, yolk carotenoids, shell colour pigments can be measured and compared between dispersing and non dispersing individuals as further measures of female investment decisions in eggs.
- 4 - Nestling sex ratio and extra-pair paternity:** from 2005 until 2009 (except 2007), nestlings were blood sampled on day 2 (hatching day = day 0); 2-5 μ l of blood was taken on the metatarsal vein for molecular sexing and paternity determination in the laboratory (>400 broods over the 4 years). A preliminary study has been performed in 2008, with the identification of 6 polymorphic microsatellite markers that can be used for paternity determination in this population (with an exclusion power of >98% - in collaboration with D. Lepetit, lab engineer at the LBBE). Analyses will focus on nests for which all nestlings have been sampled (primary sex ratio), and differential mortality until fledging will be analysed.
- 5 - Parental care at the nest and feeding rates:** from 2006 until 2009, parental feeding rates have been recorded from outside the nest box (5-8m of distance) in the morning of day 9 (2h per nest, >400 nests over the 5 years). Additionally, recordings have been performed from within the nest box in 2004 (by J. Sendekka; 65 nests all with known female), providing data about prey type for each parent. This information about food quality can be used to refine comparisons of feeding decisions by parents depending on their dispersal history.
- 6 - Nestling growth rate:** from 2006 until 2009, nestling growth was monitored in a random sample of nests (>200 nests over the 4 years). Nestlings were individually marked on day 2 (by clipping nails) and weighed every second day until day 12 (i.e. 6 times over the growing period); correspondence between individual code and ring number was made on day 8.

All these measures of parental breeding decisions will be compared between dispersing and non dispersing parents and the long-term consequences of differences in breeding strategies can be assessed on parent and offspring subsequent fitness and dispersal behaviour using the long-term monitoring of the population.

Part of these data (egg weight and volume, egg components, nestling sex ratio and paternity) was also collected on great tits. My aim would be to try and compare both species in as many respects as possible, to identify possible differences in strategies relating to migratory vs. sedentary characteristic in the two species sharing a lot of breeding features. In particular, the two species clearly differ with respect to dispersal mode (probability and distance, life-long dispersal dynamics) and spatial knowledge of their environment. Testing whether such differences relate to differences in breeding strategies associated with dispersal would therefore be particularly relevant.

The dynamics of a patchy population: balanced dispersal vs. source-sink systems

In collaboration with C.P. Doncaster

The dispersal of individuals between populations directly affects the spatial distribution and temporal dynamics of populations in a fragmented landscape, and therefore affects the overall functioning of the general population (Clobert *et al.* 2001). Different types of fragmented population functioning have been proposed according to local mortality, reproduction, emigration and immigration rates and models have explored the evolution of dispersal between populations depending on the spatio-temporal patterns of environmental variability. Two main contradictory theoretical population functioning modes have been described:

- 1 – In source-sink systems, populations are divided between source populations, producing an excess of individuals (i.e. local reproduction > local mortality), and sink populations, with a demographic deficit (i.e. local reproduction < local mortality; Pulliam & Danielson 1991; Dias 1996; Pulliam 1996). Sink populations only maintain themselves in the long-term due to continuous immigration of individuals from sources compensating for the demographic loss of individuals (i.e. in sinks, local reproduction + local immigration from sources = local mortality; in sources, local reproduction = local emigration to sinks + local mortality). Source-sink systems are therefore characterised by constant demographic differences between populations and highly asymmetrical dispersal rates (Pulliam & Danielson 1991; Dias 1996).
- 2 – Alternatively, populations may vary in space and time, favouring dynamic dispersal between populations, with an average balanced dispersal on the long-term between the different populations (McPeck & Holt 1992). In this system, no overall demographic differences are expected between populations, and dispersal rates between populations are symmetrical.

The implications of these two types of population functioning greatly differ, in particular regarding the evolution of dispersal strategies. They have been largely debated and tested (Diffendorfer 1998). Empirical studies have mainly identified source-sink system on the basis of demographic variables, in particular because obtaining detailed information about dispersal rates between different populations can prove difficult. We tested whether the patchy population of flycatchers functions as a source-sink system or the alternative system with balanced dispersal (Doncaster *et al.* 1997). We characterised the demographic functioning of populations without accounting of dispersal, by assessing local reproduction and survival rates. Most of the populations in the study system have a growth rate of 1 or close to 1, i.e. they are at demographic equilibrium without dispersal (Doncaster *et al.* 1997). Furthermore, the average number of dispersal events between pairs of populations in the system is balanced (i.e. number of individuals dispersing from population i to population j = number of individuals dispersing from population j to population i). The study population therefore represented the first example of a balanced demographic functioning in which dispersal evolved due to spatio-temporal variation of populations exchanging individuals (Doncaster *et al.* 1997). We discussed the implications of these results in terms of individual decision-making in the context of breeding habitat selection.

D – Dispersal, local adaptation and specialisation in a host-parasite system

(This section constitutes the PhD work of M. Lemoine, in codirection with H. Richner)

Among major consequences of dispersal, gene flow linked to individual movements have crucial consequences on the genetic structuration of populations (Clobert *et al.* 2001; Garant *et al.* 2005; Postma & van Noordwijk 2005) and thus on local adaptation processes (Gandon *et al.* 1996). Using experimental approaches in a well-known host-parasite system (the great tit and its main ectoparasite the hen flea; Richner, Oppliger & Christe 1993; Tripet & Richner 1997), we explored (i) the link between local adaptation and relative dispersal ability of hosts and parasites and (ii) the mechanisms of parasite specialisation, with a potential role for parasites as mediators of interspecific competition for nest sites between host species.

Dispersal, local adaptation and its spatial scale in a host-parasite system

Traditionally, parasites are thought to win the host-parasite coevolutionary arms race due to shorter generation times and higher reproductive rates. Thus parasites have been expected to be locally adapted to exploit sympatric (local) host populations more efficiently than allopatric (foreign) ones (Ebert 1994; Gandon & van Zandt 1998; Gandon & Michalakis 2002). However, several experimental tests using reciprocal transplant experiments failed to detect local adaptation of parasites, or have even found local maladaptation (Kaltz & Shykoff 1998; Greischar & Koskella 2007). Possible reasons proposed to explain this apparent contradiction include (i) spatio-temporal variability of host populations in resistance to infection and parasite populations in the ability to infect (Greischar & Koskella 2007) and (ii) gene flow due to dispersal, with the relative dispersal rates of hosts and parasites determining the potential for local adaptation: the partner with higher relative dispersal rate

should be locally adapted, with no local adaptation expected when parasites and hosts disperse at an equal rate (Gandon *et al.* 1996; Gandon & Michalakis 2002). While gene flow may be expected to limit local adaptation by counteracting gene frequency changes as a result of selection, it can also introduce novel resistance and virulence alleles, favour asymmetry in coevolutionary processes through the increase of the evolutionary potential of one partner only and thus facilitate the establishment of local adaptation. A recent review showed that when parasites disperse more than hosts, they are indeed more likely to be locally adapted to their hosts, confirming theoretical predictions (Greischar & Koskella 2007). However the six cases of parasite maladaptation or host local adaptation were not explained by lower relative dispersal in parasites compared to hosts (Greischar & Koskella 2007). Understanding parasite local maladaptation or host local adaptation therefore requires further investigation. The geographic mosaic theory of co-evolution (Thompson 1994; Thompson 1999) stressed that measuring local adaptation requires averaging fitness estimates of hosts and parasites on their local or foreign partners over several sub-populations in one metapopulation to take the spatio-temporal variation in local environment and coevolutionary processes into account.

We conducted an experiment to measure local adaptation over several subpopulations using reciprocal infestations in the great tit - hen flea host-parasite system (Lemoine *et al.* in prep., MS(5)). We also aimed at assessing the spatial scale at which potential local adaptation processes may occur. Indirect evidence for local adaptation of great tits to hen fleas has been provided in another population (Tschirren *et al.* 2007; see above) but a direct experimental test performed at a very large scale failed to reveal such local adaptation (Dufva 1996). We performed reciprocal flea infestations between pairs of patches located at various distances in a fragmented landscape and compared the performance of hosts and parasites when hosts nests were (i) free of fleas or infested with fleas (ii) from the same patch (local fleas) or (iii) from the paired patch (foreign fleas). Results show that, when fitness is measured *via* reproductive rates (i.e. offspring number), (i) parasites were locally maladapted and (ii) hosts seemed locally adapted, although the absence of host local adaptation cannot be excluded (Lemoine *et al.* in prep., MS(5)). However, patterns observed for fledgling morphological measurements differed from host reproductive rate, and could potentially show host maladaptation. Depending on the relation between these measurements and future offspring fitness, the results could reveal (i) a trade-off between offspring number and quality, (ii) a trade-off between host resistance and tolerance levels or (iii) differential resource allocation strategies to offspring depending on flea origin, involving e.g. accelerated growth with delayed costs or dispersal strategies (Lemoine *et al.* in prep., MS(5)). These results therefore stress the need to identify the relevant host and parasite fitness traits before conclusions about local adaptation can be drawn. Furthermore, the differences in reproductive performance between nests infested with local and foreign fleas increased with distance between the paired patches, suggesting that local adaptation processes occur at a given spatial scale. These analyses on the spatial scale of local adaptation processes however require further work.

Our aim was also to link observed local adaptation patterns to host and parasite relative dispersal rates. In many host-parasite systems, parasite dispersal regime is poorly known. In our system, while great tit dispersal has been described in different populations and is thus relatively well known (Verhulst, Perrins & Riddington 1997; Tinbergen 2005; Doligez *et al.* 2008; but see above for potential methodological problems), flea dispersal is indeed largely unknown. High immigration rates into previously deparasitized nests suggests high rates of flea dispersal movements (Heeb *et al.* 1996), however flea dispersal distances remain unknown. In our system as in many others, while host dispersal may be measured by direct observations (e.g. capture-recapture studies), parasite dispersal patterns can only be investigated indirectly. We aimed at obtaining information about the relative host and parasite dispersal rates using population genetic tools on both host and parasite populations simultaneously. An exhaustive sampling of natural flea and great tit populations over Gotland was conducted in 2007 and 2008 to characterise their genetic structure at various spatial scales. Technical difficulties have however slowed the genetic analyses based on microsatellite markers (e.g. Binz *et al.* 2003) in the lab. In addition to assessing the genetic structure of Gotland subpopulations, we will investigate (i) smaller spatial scale in fleas (i.e. within nests and between nests within patches) and (ii) larger spatial scales in great tits (i.e. between European populations). These scales will provide additional information about dispersal patterns in this host-parasite system. Testing whether within-nest flea populations are composed mainly of few families or are as diverse as between-nests

populations will inform about parasite immigration rates at small scales; testing population differentiation at large scales will inform about long-distance dispersal events in hosts.

Parasite specialisation and role as mediators of between-host species interactions

While most parasites can exploit different host species, host-parasite coevolutionary processes are expected to be both stronger and faster when parasites are specialised, i.e. when exploiting a single or few host species (Kawecki 1998; Woolhouse, Taylor & Haydon 2001). Parasite specialisation could result from both the need for the parasite to first locate and infest the different hosts and/or its ability to exploit them. Host-parasite encounter implies appropriate spatial and temporal overlap between host and parasite populations, which may be affected by the spatial distribution of hosts, thus by their dispersal behaviour (Tripet & Richner 1997; McCoy *et al.* 2001; Tripet, Christe & Moller 2002), while parasite exploitation of a given host depends on the balance between host defences and resources needed for parasite development, i.e. host profitability (Combes 2001; Bize *et al.* 2008b). The ability of a parasite to exploit different hosts will therefore depend on its ability to address the functional trade-offs posed by different hosts (Joshi & Thompson 1995).

In the study population, fleas can exploit their main host, the great tit, but also an alternative host, the collared flycatcher (Tripet & Richner 1997). The two host species strongly differ in flea infestation intensity (Harper, Marchant & Boddington 1992). Three potential explanations can be proposed:

- (1) a difference between the two host species in the balance between nutritive resources and defences (Møller & Erritzoe 2001; Krasnov 2008);
- (2) a difference in microenvironmental conditions created by nest material affecting the efficiency with which fleas can exploit their host (Heeb, Kölliker & Richner 2000; Moreno *et al.* 2009);
- (3) a difference in encounter probability linked to differences in the timing and/or length of the breeding period (Harper *et al.* 1992; Tripet & Richner 1999).

We addressed the first two hypotheses regarding host profitability, by (i) measuring fitness of two host species infested by the same parasite, and (ii) disentangling the effects of host nutritive resource and immune defences from the effects of microenvironmental nest conditions on fitness differences of fleas infesting the main or an alternative host (Lemoine *et al.* submitted, MS(3)). We simultaneously manipulated parasite infestation (presence or absence of fleas) and nest material (tit or flycatcher nest) in two sympatric flea host populations of tits and flycatchers (Lemoine *et al.* submitted, MS(3)). The results show that flea reproductive success was similar on both host species when hosts bred in nests of their own species, suggesting that fleas did not specialise on great tits. However, in flea-infested nests, fledging success of both host species was higher on great tit nests, suggesting that the microenvironment offered by a great tit nest may alleviate the cost of parasitism. Overall, the results suggest different evolutionary responses of the main and the alternative host to fleas, with a higher tolerance to fleas in great tits and a higher resistance in collared flycatchers (Lemoine *et al.*, submitted, MS(3)). However, these results cannot explain the higher parasite load observed in great tit nests in natural situations. The difference in flea infestation level between host species could be due to differences in the timing of breeding between host species (Lemoine *et al.*, submitted, MS(3)).

Our results also have interesting consequences for the role of fleas as modulators of the competition between collared flycatchers and great tits for nest sites depending on environmental conditions (Gustafsson 1987; Merilä & Wiggins 1995; Ahola *et al.* 2007) in natural settings where old nests and parasites remain present in nesting sites from one year to the following one. Because the impact of fleas may depend on the presence of great tit material in the box and because the two host species can use the same nest sites, the asymmetric selective pressure created by the presence of fleas could differently affect processes of nest site selection by the two host species. Fleas therefore have the potential to modulate the competitive interactions between great tits and collared flycatchers by restricting optimal nesting sites and thus increasing the level of competition for nest sites in the alternative, but most abundant, host species in this population. To what extent fleas may affect the interactions between the two host species, and possibly their spatial distribution, needs further experimental investigation. Finally, differential selection may apply to fleas depending on the host species and therefore could lead to the specialisation of different flea 'races' on the two hosts (see

McCoy *et al.* 2001). Because host species alternate in the same nest sites both within- and between-years, this system could constitute a good model for exploring the consequences of rapidly fluctuating environmental selection, involving potential dispersal and host selection processes (McCoy *et al.* 2003).

OTHER RESEARCH WORK

A – Oxidative stress and the link between life-history traits

In collaboration with P. Bize

Major life-history traits, such as fecundity and survival, have been consistently shown to covary positively in nature, ‘high quality’ individuals having more resources than ‘low quality’ ones to allocate to all life history steps (Stearns 1992). Which resources may account for such variation remains poorly known. Evidence is growing that the ability to resist oxidative stress may play an important role (Finkel & Holbrook 2000). Oxidative stress occurs when the production of reactive oxygen species (ROS) exceeds antioxidant defences and it can have deleterious effects on both fecundity and survival. Still, very little is known about the link between resistance to oxidative stress and reproductive success and survival in the wild. Using long-term data from a colonial bird, the Alpine swift, we investigated whether between-individual variation in fecundity (clutch size and hatchability) and annual survival is related to between-individual variation in red cell resistance to oxidative stress, controlling for individual known age (Bize *et al.* 2008a). As predicted, we detected positive relationship between life-history traits and resistance to oxidative stress, but relations differed between sexes: males that survived to the next breeding season tended to be more resistant to oxidative stress, and females with higher resistance to oxidative stress laid larger clutches and had a higher hatching rate. A clutch swapping experiment revealed that the higher hatching rate was due to the higher quality of eggs laid by females with a high resistance level rather than better parental care during incubation. The positive relations between resistance to oxidative stress, survival and fecundity occurred independently of age although resistance covaried with age (Bize *et al.* 2008a). These results suggest that resistance to oxidative stress may indeed play a role in shaping between-individual variation in fecundity and survival in natural populations, and therefore it can provide information about individual state and life-history trajectory. The covariation between resistance to oxidative stress and life history traits may be sex-specific, with high resistance covarying primarily with fecundity in females and survival in males (Bize *et al.* 2008a).

We now aim at developing collaborative work on oxidative stress and metabolic activity in the context of life-history evolution and dispersal decisions. A first series of samples has been collected in the flycatcher study population to measure the link between oxidative stress and senescence processes in a comparative study involving a total of 8 bird species differing in their life-history traits (see also box 11). Furthermore, we aim at developing the exploration of the specific links between dispersal decisions, oxidative stress and the evolution of life-history strategies within a co-supervised PhD project (see below).

B – Estimating consequences of conservation measures on life-history and behavioural traits in a reintroduced population

Understanding the consequences of conservation and management actions on the long-term population functioning is crucial both to validate past actions and explore new conservation and management scenarios. The White stork in the Netherlands has been the object of an intensive and successful reintroduction programme after the population had nearly gone extinct at the end of the 1960s. A captive breeding programme coupled with an intensive feeding programme was started in 1969 at several breeding stations throughout the country. This programme resulted in restoring the white stork population in the Netherland back to its level before 1945. The active breeding phase (during which the juveniles produced were released) ended in 1995. Free birds, including previously

released juveniles and a gradually increasing proportion of birds born free, were found to feed at the stations, where food was provided all year-round, when breeding close to the stations. Thus food provided may have influenced life-history and behavioural traits of both captive and free birds. In particular, food supplementation led to a modification of migratory behaviour, fed individuals becoming sedentary and escaping mortality linked to the migratory journey (collisions with power lines) and the stay on the breeding grounds (drought, hunting). However, feeding actions were stopped in some stations while they continued in others, although their potential long-term influence had not been assessed. Furthermore, many individuals departing on migration were found to stop along their migration route in Spain, where open garbage dumps provided food during the non-breeding season. Such dumps were however planned to close due to new European regulations in the early 2000s. The consequences of these changes on the long-term dynamics of the white stork in the Netherlands are unknown. This work therefore aimed at quantifying the consequences of conservation measures on life-history (survival and breeding probability) and behavioural (dispersal and migration) traits in this reintroduced population, using large-scale long-term capture-recapture data collected on this population over the whole country. I aimed at implementing multi-state capture-recapture models to investigate the links between food supplementation, survival and migratory behaviour, in order to provide tools to assess the long-term consequences on population dynamics of past conservation actions and help validating future potential conservation actions.

In a first step, I modelled life-history traits (survival and breeding probability) and simplified their structure with age and time (i.e. decreased the number of parameters in the models) in order to be able to implement multi-state models including behavioural traits (Doligez, Thomson & van Noordwijk 2004c). Starting from a simple model describing time and age variation in survival and capture probability (Doligez *et al.* 2004c), I showed that, as expected, the influence of food supplementation on survival was indirect *via* the disappearance of migratory behaviour. Indeed, the distance between the nest and the feeding station (directly linked to the probability that the bird fed at the station) influences the probability to depart on migration, but not survival; however, migration probability influences survival, migratory birds showing lower survival rate (Doligez *et al.* unpublished results).

C – Environmental modulation of parasite impact on host breeding

The strong selective pressures imposed by parasites on their hosts (Combes 2001) lead to the evolution of host responses to reduce exploitation by parasites (i.e. increase resistance) and/or to compensate for the damages due to parasites (i.e. increase tolerance). Host adaptations in turn select for parasite counter-adaptations. This coevolutionary ‘arms race’ process may involve processes acting at various levels (genetic, physiology, behaviour; e.g. Oppliger, Richner & Christe 1994; Christe, Richner & Oppliger 1996; Gasparini *et al.* 2001; Tschirren & Richner 2006). Behavioural strategies in particular provide flexible and efficient ways for individuals to adapt to variations in local conditions (Duckworth & Badyaev 2007). When parasitism risk can change rapidly and individuals may not be able to predict the expected level of parasitism before starting to breed, behavioural adjustments may allow individuals to adaptively respond to parasites when other strategies cannot be used anymore (e.g. transferring antibodies to the eggs to protect nestlings) but may be too costly to adopt in the absence of parasites. In tit species, parents have been suggested to increase feeding rate to the nestlings to compensate for the detrimental effect of nest ectoparasites feeding on nestling blood when food availability is high (Tripet, Glaser & Richner 2002). Parasitism cost would in this case decrease on nestlings but potentially increase on adults, with potential consequences *via* life-history trade-offs. I experimentally tested the hypothesis of compensation by increased feeding rate and the associated short-term costs for nestlings and parents in a natural population of great tits. I cross-manipulated nest infestation and resource availability; experimental nests thus were assigned one of the four following experimental treatments: (i) flea-free food supplemented, (ii) flea-infested food supplemented, (iii) flea-free no supplementation and (iv) flea-infested no supplementation (approx. 100 experimental nests in total). The results show that the negative impact of parasites on nestling growth is strongly reduced when environmental conditions are favourable (high food availability level;

Doligez et al, unpublished results). The underlying mechanism is however not completely clear since feeding rate does not increase to compensate for parasite impact in food supplemented infested nests. The quality rather than quantity of food brought to the nestlings may be affected. Further analyses are required before the compensatory mechanism used by tits can be identified.

PART B – RESEARCH PERSPECTIVES

The main perspectives for my future work are based on the research work presented above that I have conducted or collaborated to in the past 12 years. They include five main topics. The first three constitute three PhD projects that I will supervise (in all cases together with a collaborator), two of which have now been funded and will start next autumn. The last two topics will be addressed through collaborations, within the framework of a PhD started in 2010 and a master's project in spring 2011.

A – Estimating heritability of dispersal and its consequences on individual fitness

PhD project “Evolution of dispersal in natural populations: estimating the heritability of dispersal and its consequences on individual fitness” (2010-2013)

This PhD project has been funded via a PhD grant received from the Ministry of Higher Education and Research in July 2010 (to Marion GERMAIN). O. Gimenez (CEFE, CNRS, Montpellier) will be cosupervising the PhD.

As mentioned above, the evolution of dispersal has been addressed through very many theoretical studies in the past, which identified the selective pressures acting on dispersal. However, the empirical study of dispersal evolution in natural populations remains a crucial challenge for many evolutionary and conservation processes (Thomas *et al.* 2001; Kokko & López-Sepulcre 2006; Duckworth & Badyaev 2007). The response of a trait to selective pressures directly depends on:

- (1) the variation of the trait in the population,
- (2) the strength of selection acting upon this trait, i.e. the relation between this trait and individual fitness,
- (3) its genetic basis, i.e. heritability (Fairbairn & Reeve 2001).

Understanding the evolution of dispersal behaviour therefore involves analysing its link with individual fitness, on the one hand, and quantifying its heritability, on the other hand. These two issues remain poorly investigated in natural populations. The link between dispersal and individual fitness was addressed mainly using direct comparisons of rough fitness components (e.g. offspring number) between individuals differing in their dispersal behaviour (reviews in Béchichon *et al.* 1996; Clobert *et al.* 2004; Doligez & Pärt 2008). Such correlative approaches are however incomplete and subject to methodological problems often ignored (see above; Doligez & Pärt 2008). No general understanding of fitness consequences, or even correlates, of dispersal has been reached so far at the interspecific level, and one reason may be the lack of within-species thorough testing of such consequences, except for a very limited number of study species (e.g. Massot *et al.* 2002; Sinervo & Clobert 2003; Hansson, Bensch & Hasselquist 2004).

Furthermore, the genetic basis of dispersal remains poorly known in vertebrate species because few studies have addressed this question (Doligez & Pärt 2008; Doligez *et al.* 2009). Most studies provide indirect evidence for a genetic basis of dispersal in the form of within-family resemblance in dispersal behaviour or correlations between dispersal behaviour and heritable traits (see above; Dingemans *et al.* 2003; Snoeijs *et al.* 2004; Doligez *et al.* 2009; Duckworth & Kruuk 2009). These studies are however also subject to methodological problems, in particular because they ignore to a large extent the fact that all individuals are not observed in natural populations (Cam 2009). The analysis of the link between dispersal and individual fitness and the estimation of the genetic basis of dispersal using appropriate methods are the two research axes that constitute the main objectives of the PhD project. We will use the study population of flycatchers as a model system.

Objective 1: Estimating consequences of dispersal on individual fitness

1 - Analysing refined breeding strategies: within-breeding events trade-offs

The fitness differences between dispersing and non dispersing individuals are poorly known partly because many studies so far focused on relatively rough fitness components (including the study population; Pärt & Gustafsson 1989; Pärt 1990; Pärt 1991) and/or investigated only a few independent

components reflecting a particular process such as mate or nest site acquisition, clutch size or recruitment (Bélichon *et al.* 1996; Doligez & Pärt 2008). However, because dispersers and residents may adopt different strategies (e.g. Julliard *et al.* 1996; Spear, Pyle & Nur 1998; Marr, Keller & Arcese 2002) and compensation may occur between different fitness components (Bélichon *et al.* 1996; Lemel *et al.* 1997; Clobert *et al.* 2001), in particular between traits within a breeding event, comparisons of separate fitness traits may be misleading. The first aim of the PhD project will therefore be to investigate the links between individual dispersal status and as refined as possible reproductive components, in order to test for possible compensation mechanisms between decisions within a breeding event. Ultimately, the complete set individual decisions on different breeding traits will be confronted to identify breeding strategies depending on dispersal status (and environmental variation) and their consequences for individual fitness. To do so, we will analyse the detailed breeding data collected on the study population regarding (1) early breeding decisions (mate choice, laying date, investment in eggs: number, size and components, offspring sex ratio and paternity) and (2) late breeding decisions (investment in parental care, territory and nest defence, nestling growth). Detailed data has been collected in the past years (see box 10), and will be completed during the PhD (data on song, mate choice, territory defence).

2 - Quantifying LRS according to lifetime dispersal history: between-breeding events trade-offs

Conversely, few studies have quantified lifetime reproductive success (LRS) in relation to dispersal behaviour and its potential lifetime dynamics (Bélichon *et al.* 1996; Doligez & Pärt 2008). However, compensatory strategies may also occur between fitness components between breeding events, or between breeding and survival. Beyond the methodological issues described above that are usually neglected when estimating LRS (Doligez & Pärt 2008), in most cases individual dispersal status is considered fixed (e.g. when comparing immigrants into a population and locally born individuals; Bélichon *et al.* 1996; Bensch *et al.* 1998; Hansson *et al.* 2004) and LRS estimates are compared between these individuals' categories. In our system, between-patch dispersal behaviour can occur life-long (Pärt & Gustafsson 1989; Doligez *et al.* 1999). Because the selective pressures acting upon dispersal may change through life (e.g. between natal and breeding dispersal events), accounting for dispersal history and temporal dynamics with age appears particularly relevant when estimating fitness correlates of dispersal. The second aim of the PhD project will be to use the long-term data base on the study population to quantify LRS depending on the dispersal history of individuals (number and temporal dynamics of dispersal events). This analysis will be implemented using recently proposed capture-recapture models (Rouan *et al.* 2009) generalised to multi-state situations, in order to account for individual detection probability and its heterogeneity between individuals, a crucial problem when dealing with dispersal (see above; Doligez *et al.* in revision, MS(1)).

3 - Experimentally testing the consequences of artificial dispersal on fitness components

Finally, most previous studies (including the first two parts of this PhD) have analysed correlates of dispersal but interpreted them as consequences (Doligez & Pärt 2008). However, experiments are needed to reveal causal relationships. In order to reveal dispersal consequences on individual fitness, we will conduct a translocation experiment in the study population (see Pärt 1995). Individuals of known age and dispersal status will be displaced between habitat patches and the subsequent breeding success (collecting as refined as possible breeding traits) and survival will be monitored and compared between displaced and control individuals. In this type of experiment, the dispersal 'motivation' is artificial and may not reflect 'true' dispersal events, i.e. decided by individuals depending on internal and external factors. Therefore the results need to be interpreted with caution. Nevertheless, the experiment should provide information about costs and benefits of settling in a new environment, which is one of the dispersal steps.

Objective 2: Assessing the genetic basis of dispersal accounting for imperfect detection of individuals in natural populations

As mentioned above, the use of mixed quantitative genetics models has recently received an increased interest in evolutionary ecology studies for estimating heritability of various traits, among

which behavioural traits (Stirling *et al.* 2002; Kruuk 2004; Kruuk *et al.* 2008; Cam 2009). However, these models assume that all individuals are detected, an assumption rarely met in natural populations (Gimenez *et al.* 2008; Cam 2009; see above). Imperfect detection of individuals is however susceptible to bias parameter estimates and therefore lead to flawed inferences about biological processes described from variation observed in these parameters (Gimenez *et al.* 2008). The second main objective of the PhD project will therefore be to obtain an unbiased estimate of between-patch dispersal probability in the study population, by developing methods allowing the combination of mixed quantitative genetics and multi-state capture-recapture models. Mixed quantitative genetics models estimate heritability based on information about full parentage relationships between individuals in a population from multigenerational pedigrees, while multi-state models estimate demographic parameters and between-state transition probabilities accounting for imperfect individual detection and its heterogeneity between individuals (Nichols & Kendall 1995; Lebreton & Pradel 2002). This approach may be crucial in the case of dispersal since individual detection probability should strongly depend on dispersal behaviour in spatially limited study areas (Doligez & Pärt 2008). The combination of these two model families requires incorporating random effects into capture-recapture models, i.e. implementing mixed capture-recapture models (Royle 2008). This implementation has now been done for ‘one-state’ capture-recapture models (Papaix *et al.* in press). We aim at generalising it to multi-state models and apply these models to dispersal probability in our study population.

Does philopatry pay? An updated comparison of collared flycatcher siblings

Comparisons of fitness components of individuals differing in their dispersal behaviour provide fitness correlates of dispersal that may or may not reflect dispersal consequences. Ideally, assessing fitness consequences of dispersal would require quantifying the fitness of the same individual having dispersed and not dispersed in exactly the same environmental conditions. This proves impossible except possibly for clonal organisms. However, comparing individuals that share genes and early environmental conditions, such as siblings, partially relieves from the methodological problem of confounding consequence and covariation and can therefore provide insights into dispersal fitness consequences. This method has been previously used in the flycatchers study population, where fitness components of sisters differing in their dispersal behaviour (here, long- and short-distance dispersal) were compared (Pärt 1991). Since this study was published, however, a great deal of additional data has been collected in the population, drastically increasing sample sizes, and refined statistical methods (generalised linear mixed models) have become widely available and used. We will therefore perform this analysis again using the full data and more powerful statistical models. We will check whether the previously observed results, which suggested reproductive benefits of philopatry, although no significant difference could be found in offspring recruitment rate, are confirmed (Pärt 1991).

B – Dispersing behavioural syndromes and their evolutionary consequences

PhD project “Interactions between dispersal and behavioural syndromes: causes and consequences – empirical approaches in fragmented population of a passerine bird” (2010-2013)

This PhD project has been funded via a research contract and PhD grant received from the Region Rhône-Alpes (programme CIBLE) in July 2010. D. Réale (Université du Québec à Montréal, Canada), will be cosupervising the PhD.

Despite the many studies addressing the factors affecting dispersal behaviour (Clobert *et al.* 2001; Clobert *et al.* 2004; Bowler & Benton 2005; Ronce 2007), the proximate mechanisms and ontogeny of dispersal remain poorly known in natural populations (see above). In particular, although dispersal represents the same evolutionary response to different selective pressures (Clobert *et al.* 2004; Bowler & Benton 2005; Ronce 2007), empirical studies have often considered dispersal

independently from the other behavioural traits of an individual, and independently from the other decisions that an individual has to make during its life. However, phenotypic differences between dispersers and non-dispersers have been described in many species, and recent studies have stressed behavioural differences between individuals depending on their dispersal behaviour (Dingemanse *et al.* 2003; Duckworth & Badyaev 2007; see review in Clobert *et al.* 2009). In order to understand dispersal consequences, it is necessary to investigate the phenotypic and genetic relations between dispersal ability and the other behaviours and strategies adopted by individuals, in other words, investigate behavioural syndromes (Dall, Houston & McNamara 2004; Sih *et al.* 2004) involving dispersal (Clobert *et al.* 2009; see also Dingemanse *et al.* 2010). Natural selection can favour certain combinations between these behaviours, and thus lead to the evolution of functional integration among traits at the individual level and generate genetic correlations between these traits at the population level, which will in return affect the response to selective pressures (Duckworth & Kruuk 2009). Such feedback effects remain largely unexplored in dispersal studies so far; however they could strongly modify the success of dispersal strategies and must therefore be better understood. Because of such interactions between traits, dispersing individuals are unlikely to be a random sample of a population in many respects, which can have crucial implications for evolutionary processes leading to population differentiation (e.g. gene flow, local adaptation).

The aim of this PhD project is to characterise empirically the interactions between dispersal and personality traits and assess their consequences for individual fitness according to local environmental conditions, thus identify the constraints that these interactions can exert on the evolution of dispersal strategies in natural populations. The project will be based on a combined series of correlative and experimental approaches in the study population of collared flycatchers.

Objective 1: Characterising the interactions between dispersal and personality traits

In animal populations, personality traits are defined as consistent differences between individuals in levels of aggressiveness, neophobia, exploratory behaviour (Dall *et al.* 2004; Dingemanse *et al.* 2010), which can represent adaptive variation. The first aim of the PhD project will be to measure these personality traits in the study population using the standard protocols described and validated by previous studies (e.g. Dingemanse *et al.* 2002; Dingemanse & de Goede 2004; Duckworth & Badyaev 2007; Fidler *et al.* 2007), by placing individuals in novel situations (presence of novel objects) or risky situations (presence of conspecifics or predators on the territory). We will measure as many individuals as possible; then the heritability of personality traits and the genetic covariance between these traits and dispersal behaviour, along with the selective gradients acting on these traits, will be quantified using mixed quantitative genetics models ('animal models'; Kruuk 2004 and see above). Furthermore, the polymorphism in the dopamine receptor *Drd4* gene was recently found to correlate with personality traits in natural bird populations (Fidler *et al.* 2007). This polymorphism will therefore be quantified here and the link between *Drd4* polymorphism and dispersal behaviour will be tested. These analyses will shed light on the joint evolution of dispersal and personality traits in the study population (Duckworth & Badyaev 2007; Duckworth & Kruuk 2009).

Objective 2: Experimentally testing the consequences of these interactions

In parallel to the analyses based on the long-term data set and measurement of personality traits in the study population, two experimental approaches will be used in order to better understand the consequences of interactions between personality traits and dispersal behaviour in terms of colonisation ability and settlement success in new habitats.

Colonisation experiment: new habitat patches will be installed at the periphery of the study area, and the characteristics of pioneer individuals settling there in terms of dispersal history, personality traits and *Drd4* gene polymorphism will be compared between the year of patch installation (no pre-existing social information available on the patch) and two years later. Fitness components (reproductive success and survival) of colonisers will be monitored and the link between fitness components, personality traits and dispersal will be investigated.

Translocation experiment: in a second experiment conducted in different patches, individuals will be caught early, identified and their personality traits and *Drd4* gene polymorphism will be measured; these individuals will then be experimentally displaced and their reproductive success and survival will be measured in relation to personality traits and dispersal history. (This experiment will be common to the two PhD projects, although they focus on different aspects of the experiment; here we focus on the links between personality traits and the success of settlement after displacement).

These two experiments will allow us to show causal relationships between dispersal behaviour, personality traits and fitness components during the course of habitat colonisation.

C – Dispersing physiological syndrome and senescence: dispersal and life-history strategies

PhD project “Dispersal and physiological syndromes: consequences on life-history strategies” (planned 2011-2015)

Funding for this PhD project will be applied for during winter 2010-2011. P. Bize (Department of Ecology and Evolution, Lausanne, Suisse) will cosupervise the PhD.

Recently, links between dispersal ability and other phenotypic traits have been shown, defining syndromes (i.e. consistent differences between individuals in suites of traits) with potentially major evolutionary consequences (Sih *et al.* 2004; review in Clobert *et al.* 2009). Dispersing individuals can in particular show higher levels of aggressiveness and higher propensity to explore their environment (e.g. Dingemanse *et al.* 2003), which can favour colonisation success (Duckworth & Badyaev 2007). In addition, dispersing individuals can be larger (O’Rian, Jarvis & Faulkes 1996), show higher circulating hormonal levels (in particular steroids) (Clobert *et al.* 2009) and mount higher immune responses (Snoeijs *et al.* 2004) than non dispersing individuals. All these characteristics have in common to be energetically demanding, thus phenotypic differences described between dispersing and non dispersing individuals could involve differences in metabolic activity. However, the existence of physiological syndromes involving dispersal remains poorly investigated, although their consequences could be as crucial as behavioural syndromes. Energy production during mitochondrial respiration also produces reactive oxygen species (ROS), highly unstable compounds that can damage biomolecules such as DNA, proteins and lipids (Finkel & Holbrook 2000). When ROS production exceeds antioxidant defences, metabolic activity generates oxidative stress that can affect gene expression, tissue functioning and ultimately survival and reproductive success of individuals. The existence of ‘physiological dispersal syndromes’ involving a link between dispersal behaviour and metabolic activity could therefore have major consequences on life history traits *via* oxidative stress (Brown *et al.* 2004), and possibly shape the diversity of life-history strategies between dispersing and non dispersing individuals (Finkel & Holbrook 2000; Monaghan, Metcalfe & Torres 2008; Dowling & Simmons 2009). Life-long differences in metabolic activity of individuals in relation to dispersal decisions can indeed lead to an increased exposition to oxidative stress in dispersing individuals. This could possibly generate different feed-back selective pressures according to dispersal strategies on major life-history traits such as age at first breeding, investment in current reproduction and, ultimately, senescence dynamics. The role of oxidative stress as a mediator of interactions between metabolism, dispersal behaviour and life-history strategies has not been investigated so far.

The PhD project will aim at empirically (and possibly theoretically) exploring the role of oxidative stress in the diversification of life-history strategies in relation to dispersal behaviour. The first objective of the PhD will be to explore the link between dispersal, metabolic activity and oxidative stress in the study population of flycatchers using both indirect and direct measures of metabolism. The second objective will be to investigate (empirically and possibly theoretically) the potential consequences of the observed links on life-history trajectories in relation to dispersal. The third objective will be to manipulate experimentally the level of oxidative stress to test individual responses in reproductive strategies depending on their dispersal status. This interdisciplinary project

should allow us to provide insights into individual responses to selective pressures in terms of combined dispersal and life-history strategies.

Objective 1: exploring the links between dispersal, metabolic activity and oxidative stress

To test for the existence of a physiological dispersal syndrome linking metabolic activity, oxidative stress and dispersal behaviour, we will measure metabolic activity and oxidative stress on individuals of known dispersal status and age in the study population. These traits will be measured both indirectly and directly. Indirect measures will be performed on blood samples and are described in box 11; blood samples have been collected during spring 2009 and 2010 on all birds of known origin (i.e. ringed prior to capture); blood sampling will continue in the next springs. Direct measures of metabolic activity will be performed using a metabolic field chamber on the site. We will test whether dispersing and non dispersing adult individuals differ in their basal metabolic activity, but also whether the basal metabolic activity of nestlings is a predictor of their future natal dispersal behaviour. Due to low local recruitment rate in this short-lived species (approx. 10%), a large sample of nestlings will be measured. We also plan to measure metabolic activity and ROS production of a large number of adult individuals over several years in the study population in order to analyse the heritability of these traits and estimate the level of genetic correlation with dispersal using mixed quantitative genetic models (animal models).

Finally, because oxidative stress results from an imbalance between the levels of antioxidant defences and ROS production, an important challenge is to evaluate the relative contribution of variation in antioxidant defences and in ROS production in driving the diversification of life-histories (Criscuolo *et al.* 2005). We will also try to investigate this issue using uncoupling proteins (Criscuolo *et al.* 2005).

Objective 2: investigating the consequences of these links on life-history strategies

The consequences of a physiological dispersal syndrome on evolutionary trade-offs in life-history strategies will be explored empirically in the study population. First, we will test whether damages due to an increased exposition to oxidative stress in dispersing individuals lead to differences in senescence dynamics between dispersing and non dispersing individuals. Using the same samples as above, we will analyse telomere dynamics longitudinally to assess senescence and survival prospects of dispersing and non dispersing individuals of known age (Bize *et al.* 2009). Second, we will use the long-term data base to assess senescence in survival and reproductive success in relation to dispersal. Senescence has been suggested in this population (Gustafsson & Pärt 1990; Sendecka 2007); however, the previous analyses did not account for individual detection probability, which is crucial when investigating survival patterns (Martin *et al.* 1995; Gimenez *et al.* 2008). We will therefore use multi-state capture-recapture models to investigate the consequences of dispersal on senescence patterns in the study population.

Finally, modelling can be used to assess the evolutionary consequences of physiological dispersal syndromes mediated by oxidative stress on the diversification of life-history strategies in relation to dispersal.

Objective 3: experimentally testing the role of oxidative stress on breeding strategies in relation to dispersal

The last aim of the PhD project will be to assess the consequences of variation in oxidative stress between dispersing and non dispersing individuals on their reproductive strategies depending on age (see Pärt, Gustafsson & Moreno 1992). We will experimentally manipulate oxidative stress by manipulating (increasing and decreasing) reproductive investment, i.e. brood size, for individuals of known age and dispersal status. Behavioural responses (e.g. feeding rates and nestling body mass changes) as well as metabolic activity, damages due to oxidative stress, and subsequent reproductive success and survival will be measured, and we will test how individuals face variation in oxidative

stress depending on their dispersal status and how this affects their breeding strategies and, consequently, life-history trajectories.

BOX 11: Dispersal, metabolic activity and oxidative stress

In order to explore (i) the links between dispersal behaviour, metabolic activity and damages due to oxidative stress and (ii) potential consequences of these links on life-history strategies related to dispersal, we collected blood samples in the fragmented study population of collared flycatchers in the 2009 and 2010 breeding seasons. We will measure metabolic activity and damages due to oxidative stress on breeding individuals whose dispersal history and age are known. Each year, adults breeding in nest boxes and young are individually ringed and these data are grouped in the long-term general data base from which individual age and dispersal (and breeding) history can be determined. Around 400 to 500 breeding pairs are present in the study population every year, among which 2/3 of individuals successfully breed and are therefore caught and identified (see above). Among identified individuals, around half (i.e. 130 to 150 individuals of each sex) have been ringed in their natal year or as yearlings, and are therefore of known age. Natal and breeding dispersal are frequent in this population (Pärt & Gustafsson 1989; Pärt 1990; Doligez *et al.* 1999; Doligez *et al.* 2004b), thus about half of ringed individuals are dispersers. During the last two breeding seasons, we sampled all ringed adults for blood (females during incubation, males during nestling feeding); 100 to 150 μ l were sampled per individual for the different physiological analyses. Sampling such a relatively large quantity of blood had been shown previously to generate no desertion or mortality in this population (J. Sendecka, pers. comm.). A total of 340 and 280 (approx.) blood samples were collected in 2009 and 2010 respectively on adults whose age and dispersal status is known (see Table B2). Blood samples were processed on the day of sampling by centrifuging samples (4 min to 6000 r/min) to separate plasma and red cells, and were then frozen to -18°C until the end of the season, when they were transferred and stored at -80°C .

Using these samples, metabolic activity will be assessed indirectly for a minimum of 15 to 20 individuals of each sex and age class between 1 and 6 years or more, by measuring the metabolism of glucose (glucose in plasma and glycated haemoglobin in red cells), proteins (albumin, allantoin and uric acid) and lipids (triglycerids and free fatty acids) (see e.g. Ardia 2006). Damages due to oxidative stress will be assessed on the same blood samples by measuring lipid peroxidation (in plasma) and telomere degradation (on DNA; Bize *et al.* 2009). We will compare variables measuring metabolic activity and damages due to oxidative stress between dispersing and non dispersing individuals according to their age and sex, and accounting for past and present reproductive investment in the analyses in order to control for potential reproductive costs. In the next years (2010 to 2012), during the general long-term population monitoring, survival and reproductive success of sampled individuals (with an observed adult return rate of 35 to 50% approx.; Sendecka 2007) will be determined and related to the variables measuring metabolic activity and oxidative stress damages in the previous year as well as dispersal status.

D – Towards cognitive mechanisms of decision making: exploring the link between cognitive ability and dispersal decisions

In collaboration with L. Cauchard, L. Lefebvre and J. Forsman

To make optimal dispersal decisions, individuals have been shown to use information about local habitat quality to assess their relative expected fitness in the alternative habitat patches / sites (e.g. Schjørring, Gregersen & Bregnballe 1999; Doligez *et al.* 2002b; Ward 2005; Boulinier *et al.*

2008). In environments varying at different spatio-temporal scales, available information can be multiple, from different simultaneous (internal and external) sources and used in a context-dependent way. In other words, information can be complex. Therefore, adaptive dispersal decision-making based on information use by individuals requires cognitive abilities allowing individuals to associate cues with local habitat quality, store the information gathered, prioritize the different information sources, update information and retrieve it after a given period of time. Some of these cognitive processes have been studied in the context of foraging habitat selection (e.g. food caching; Dally, Emery & Clayton 2006). In the context of dispersal decisions, however, little is known about how these different cognitive processes determine and potentially constrain individual dispersal strategies by constraining information management in the brain. Dispersal decisions usually involve larger spatial and temporal scales than foraging habitat selection, and therefore may require different cognitive processes to store and retrieve information; in particular, information is expected to be stored for longer periods of time, thus long-term memory processes are of particular interest. Comparative studies have shown that brain size relates to both cognitive abilities and life-history strategies on an interspecific level, affects many fitness components and is under natural selection (Garamszegi *et al.* 2005; Sol, Lefebvre & Rodríguez-Teijeiro 2005; Sol *et al.* 2007). Such interspecific differences suggest that variation in brain size and selection on this trait among individuals within species may also occur; however such variation and its effects on decision-making on an intraspecific level remains poorly investigated so far. We aim at exploring the link between cognitive ability and dispersal decisions in the study population of collared flycatchers and great tits. Two approaches will be used.

(1) First, we will test how cognitive ability relates to nest site choice decisions in the two species using the experimental design described above, based on artificial symbols attached to nest boxes to create associations with biologically relevant variables. We will test whether between-individual variation in the ability to learn and memorise environmental cues (here, artificial symbols) for future nest site choice is linked to cognitive ability. Cognitive ability could be measured either by brain size or by innovation rate (Shettleworth 2001), defined by the frequency of new, complex or unusual behaviours (Lefebvre, Reader & Sol 2004), which can be assessed using problem-solving tasks proposed to individuals (Roth & Dick 2005). We will (i) measure brain size and innovation (and learning) rate on the individuals involved in the experiment and (ii) test for a link between these measures of cognitive ability and the ability to make the ‘right’ decisions when using artificial cues for nest site selection. External measurements of the head of living birds will be used as a proxy for brain size (after checking the level of repeatability of these measurements), since head size scales closely to brain size on an interspecific level (Brooke, Hanley & Laughlin 1999). The within-species association between external measurements and brain size may be expected to be even stronger because the effect of different head shapes and skull thickness is controlled for.

(2) Second, we will investigate potential links between individual cognitive ability, personality traits and dispersal behaviour, and test for fitness consequences of these links. So far, the within-species links between cognitive ability, other traits and fitness components remain poorly investigated, with only one example showing that males with higher innovation ability were more likely to be preferred by females (Keagy, Jean-François Savard & Borgia 2009). Cognitive ability (innovation and learning rate, and brain size) and personality traits (neophobia, temerity; Dall *et al.* 2004) have been measured in spring 2010 on the great tit study population in a pilot experiment that will allow exploring the link between these traits and individuals fitness (see box 12). We aim at developing this approach and measure cognitive ability in the flycatcher population, for which individual parentage relationships (pedigree) are better known. Our aim is to measure a large number of individuals in order to test for a link between cognitive ability, personality traits and dispersal behaviour using mixed quantitative genetic models in this population. Such relations may be expected if dispersers have to compensate their lower familiarity with (i.e. their lower knowledge of) the local habitat by a higher ability to exploit the environment. Higher cognitive ability or higher aggressiveness / exploration levels may however impose costs to dispersers (e.g. higher predation risk or physiological costs).

This work should provide insights into the cognitive processes involved in decision-making in the context of dispersal; however, a more thorough understanding of such cognitive processes will

require further work, potentially on different study species (e.g. insects) allowing more controlled experimental designs in the lab.

BOX 12: Innovation ability, personality traits and individual fitness

(This project is supervised by L. Cauchard as part of his PhD studies)

We measured innovation and learning ability and personality traits during breeding in the study population of great tits to investigate the links between these behavioural traits and components of fitness in a wild population. The aim of the study is to assess whether (i) personality traits (neophobia, exploration, aggressiveness) are correlated to each other and to cognitive ability (innovation and learning) and (ii) these traits are correlated to fitness components: breeding success and survival. This pilot experiment was conducted in spring 2010 to validate protocols for measuring the behavioural traits of interest. Several adjustments of the initial protocols regarding the timing of the tests and the source of motivation were needed in the field before a valid test could be found. Behavioural tests could be measured on 52 (out of approximately 250) breeding pairs.

Great tit nests were monitored regularly to record breeding data (laying date, clutch size, hatching date). Neophobia and temerity were measured when nestlings were 5 day old, by recording the time needed for parents to return to their nest to feed nestlings after disturbance by an observer in absence or presence of a novel object near the nest box entrance hole. The time needed to return in the absence of a novel object measures temerity, and the difference between the time needed to return in presence and in absence of the novel object measures neophobia. To perform the test, an observer placed a video recorder 5-6 m away from the box, then approached the nest box to either place the novel object (a small red- and blue-coloured toy 5 cm high) or not close to the entrance hole, before returning to the video recorder, starting the recording and leaving the area. The observer also noted alarming behaviour of the parents during the period when close to the box. After one hour, the observer came back to the box and proceeded in the same way with the second test, either removing the novel object if it was present or placing it if it was absent, and video recording birds' behaviour for an additional hour. The order of the tests (with and without a novel object) was randomly determined. Neophobia and temerity of both pair members will be determined from the videos (males and females can be identified from a distance using the sexually dimorphic size of the black breast stripe).

On the next day (i.e. when nestlings were 6 days old), cognitive ability was measured by proposing an innovation task to the parents and recording the time to solve the task for the first time (innovation ability) and subsequent times (learning ability). The innovation task consisted of blocking the entrance hole of the nest box using a reversed swing-door trap placed outside the box. The trap was in closed position when the parent arrives to the box. To open the trap, the parent had to pull a piece of string hanging besides the trap door. Once the parent had entered, the trap closed again, but the parent could get out of the box. The parents' motivation for this innovation task was therefore to enter the box to feed nestlings. To perform the test, an observer placed a video recorder 5-6 m away from the box, attached the innovation task on the box and started the video recording before leaving the area. After an hour, the recording was stopped and the task was taken down. In the evening, the video was checked to see if parents had succeeded to solve the task at least once during the test. If not, the test was performed again in the following day. Innovation and learning ability of both pair members will be determined again from the videos.

All behavioural tests were performed before catching adults (when feeding day 7 to 15 nestlings) to avoid any perturbation. Nestlings were ringed and weighed on day 9, and measured (tarsus length, body mass) on day 14 to estimate condition at fledging. Fledging success was recorded. In the next years (2011 and 2012), all breeding adults in the study population will be caught to assess local survival rate of parents (and offspring) in relation to personality traits and cognitive ability. The relation between the different fitness components (measures of reproductive success and survival probability) and personality traits and cognitive ability will be estimated.

The perspectives of this work include:

(i) testing the established protocols and adjusting them to flycatchers to measure the same traits. In particular, the innovation task may not apply to flycatchers because of lower ability to hang on and lower leg strength compared to great tits due to different foraging modes. For flycatchers, the innovation test may have to be based on the motivation initially planned for great tits, i.e. obtaining food. Measuring personality traits and cognitive ability in the flycatcher will be done in direct collaboration with the PhD student working on behavioural syndromes involving dispersal. Taking advantage of the higher local recruitment rate and higher quality of the pedigree for flycatchers compared to great tits, the aim of measuring personality traits and cognitive ability in the flycatcher will be to assess the heritability of these traits and their genetic correlation to dispersal behaviour using mixed quantitative genetic models ('animal models');

(ii) experimentally testing the link between cognitive ability and ability to cope with stressful situations. Cognitive abilities are expected to allow individuals to make optimal decisions to exploit their environment. Therefore, individuals with larger cognitive abilities are expected cope better when facing unfavourable situations. This prediction can be tested by manipulating (increasing or decreasing) the required parental investment, for instance by manipulating brood size and/or providing supplementary feeding.

E – Reversed sexual selection: female choice by males based on signals of female quality

In collaboration with C. Doutrelant (CEFE, Montpellier)

This research topic will be investigated during a Master 2 research training (January-June 2011), and depending on the results obtained, may continue with a PhD project.

Sexual selection is based on within-sex differential ability of individuals to acquire mates. Traditionally, sexual selection was considered to be a direct consequence of the asymmetry between sexes: females are assumed to contribute most or all of the energy necessary to produce offspring while males would contribute only by their genes. Thus most models assume that the fecundity of a female depends only on her physiological limits, while the one of males is proportional to the number of mates they get and to the fecundity of these mates. For this reason exaggerated secondary sexual signals (armaments and ornaments) that increase mating success are typically considered as male traits, and choosiness as a female trait (Andersson 1994). Yet, although male displays and female choosiness are indeed frequent in nature, they are by no means universal. Although sexual dimorphism has been equated to sexual selection, there is increasing evidence that (i) sexual selection operates also in non-dimorphic and dimorphic species where female also display conspicuous traits (Admunsen 2000; Kraaijeveld, Kraaijeveld-Smit & Komdeur 2007), and (ii) sexual displays can occur simultaneously in both sexes. In many species males and females may be of similar appearance not because neither of them displays secondary sexually-selected traits, but rather because both of them display such traits (Kraaijeveld *et al.* 2007). Recently, a new paradigm was proposed, with a symmetrical sexual selection between sexes, i.e. males would also choose mates using signals revealing female quality and her capacity to breed successfully, in particular in non dimorphic and monogamous species (Admunsen 2000; Clutton-Brock 2007).

The aim of the master's project is to test this hypothesis and investigate some of its mechanisms on the study population of flycatchers, using the long-term data set combining morphological and breeding data. In this species, white plumage patches on the wings and forehead have been shown to be secondary sexual characters displayed by males and selected by females (Qvarnström 1997; Qvarnström, Pärt & Sheldon 2000). However, white patches are also present in females, with a high

inter-individual variation. The first objective of the project will be to test whether wing patch size can be a signal of female quality; we will investigate the link between wing patch size and fitness components (reproductive success, survival) in females. Female breeding quality can be measured by global variables of reproductive success (laying date, clutch size, fledgling number, recruitment rate) as well as more detailed breeding variables such as egg size, mass and coloration, egg components, feeding rates that have been collected in the past few years (see box 10). A second step will be to test the honesty of this signal using experimental data on brood size manipulations that have been performed for several years during the course of the long-term population study. Following the manipulation, within-female variation in wing white patch size will be related to the reproductive cost paid by experimental females in the preceding year. These analyses will allow determining whether white patch size is an honest signal of female quality that males can use to choose mate. If this is the case, this master project will therefore open perspectives for a PhD project during which (i) the mechanisms of such mate selection can be experimentally tested and (ii) the heritability of wing patch size and the genetic correlation between male and female trait can be quantified using mixed quantitative genetics models.

Perspectives: linking breeding habitat selection and sexual selection

As mentioned above, individuals make a suite of interacting decisions in the context of breeding, in response to multiple interacting and potentially conflicting information sources. In particular, breeding habitat selection and mate choice have repeatedly been suggested to be intimately related in bird species (see e.g. Alatalo, Lundberg & Glynn 1986; Slagsvold 1986; Slagsvold & Lifjeld 1986; Alatalo, Lundberg & Carlson 1988). In many cases, these decisions are made simultaneously, or influence each other since breeding site choice may result from mate choice or mate choice is constraint by breeding site choice. I would therefore like to develop in the future research projects addressing the interactions between breeding habitat selection and sexual selection, based on empirical studies using the collared flycatcher study population as a model. To start with, I would investigate the links between breeding habitat selection based on public information and mate choice. Previous results on the use of public information in this population suggest such a link *via* male competitiveness. Less competitive males (yearling and failed males) make a different use of public information in their emigration decisions compared to females and more competitive males (Doligez *et al.* 1999). Because patches where local reproductive success is high should be more attractive in the next year, less competitive individuals may trade breeding patch quality against the probability to access a breeding site and/or mate, and choose to emigrate from high quality patches (Doligez *et al.* 1999). Therefore, spatio-temporal patterns of habitat quality and mate quality are not independent. The consequences of such interactions need to be assessed. In a first step, I would investigate the link between secondary sexual traits and dispersal decisions (emigration, immigration).

Interactions between breeding strategies, sexual selection and dispersal are probably complex, resulting from a suite of simultaneously made and temporally constrained decisions, which potentially involve compensatory and/or trade-offs processes between decisions. However, understanding these interactions also appears crucial to fully estimate consequences and evolution of dispersal strategies.

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APPENDICES

Curriculum Vitae

Blandine DOLIGEZ

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Professional address: Department of Biometry and Evolutionary Biology
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Nationality: French.

Date and place of birth: 10 / 04 / 1973, at Thiais (Val-de-Marne, France)

Status: married, two children

University studies and diplomas

2001: PhD of the University Pierre and Marie Curie (Paris VI) in Ecology. Department of Ecology (“Functioning and Evolution of Ecological Systems”, Director: Jean CLOBERT) - CNRS UMR 7625, Université Pierre et Marie Curie (Paris VI), 7 quai Saint Bernard - Case 237, F - 75252, Paris Cedex 05, France. Supervisors: Dr. Etienne DANCHIN and Dr. Jean CLOBERT. PhD obtained on the 29th of January 2001, with distinction.

Title: Breeding habitat selection mechanisms in birds: local reproductive success and other cues of local environmental quality - information gathering and use in the collared flycatcher (*Ficedula albicollis*).

1996: DEA in Ecology (Ecole Normale Supérieure (ENS), Universities Paris VI, Paris XI, and INA-PG), equivalent to a Master of Sciences, awarded in September 1996 with distinction.

DEA research project: Breeding habitat selection in the Collared flycatcher *Ficedula albicollis*: demographic consequences and behavioural mechanisms. Supervised by Jean CLOBERT and Etienne DANCHIN, Department of Ecology - CNRS UMR 7625, University Paris VI, France.

Magistère Inter-universitaire of Biology-Biochemistry (ENS, Universities Paris VI, VII et XI), awarded in September 1996 with distinction.

1995: Maîtrise in cellular biology (Paris VI), equivalent to a Bachelor of Science, Honours, awarded in June 1995 with distinction.

Maîtrise research project: Early juvenile dispersal in the Great tit *Parus major*: an empirical approach in a population in Northern Belgium. Supervised by André A. DHONDT, Department of Biology, University of Antwerp, Belgium.

1994: Licence of cellular biology and animal physiology (Paris VI), equivalent to a Bachelor of Sciences, awarded in June 1994 with distinction.

1991 - 1993: Classes Préparatoires aux Grandes Ecoles, in Versailles (Yvelines). Subjects: mathematics, biology, physics and chemistry.

Admitted in June 1993 to the **Ecole Normale Supérieure**, Paris (section Biology, Geology and Chemistry), after a national competition, with rank: 5th.

Professional research experience

2008 (October) – present:

Permanent CR1 researcher at the CNRS - University Lyon I, Department of Biometry and Evolutionary Biology (Lyon, France), Behavioural Ecology research group.

Research projects: Information gathering, integration and use for breeding habitat selection. Maternal effects and their role in natal dispersal. Dispersal determinism.

2007 (January) – 2008 (September):

Permanent researcher at the CNRS - University Lyon I, Department of Biometry and Evolutionary Biology (Lyon, France), Behavioural Ecology research group.

Research projects: Information gathering, integration and use for breeding habitat selection. Maternal effects and their role in natal dispersal. Dispersal determinism.

2004 (February) – 2006 (December):

Permanent researcher at the CNRS - University Lyon I, Department of Biometry and Evolutionary Biology (Lyon, France), Evolutionary Population Biology research group.

Research projects: Maternal effects and their role in natal dispersal. Dispersal determinism. Sex ratio adjustment according to local breeding habitat quality.

2001 (November) – 2004 (February):

Post-doctoral research at the University of Bern, Institute of Zoology, Department of Evolutionary Ecology (Bern, Switzerland), in collaboration with Prof. Heinz Richner. Research associate contract funded by the University of Bern and the Swiss National Fund for Scientific Research.

Research project: Behavioural breeding strategies in response to variation in local habitat quality: resistance of hosts to their parasites - Experimental approaches in the hen flea - tit species system.

2001 (June to October):

Post-doctoral research at the Centre for Terrestrial Ecology, Netherlands Centre for Ecological Research - KNAW NIOO-CTO (Heteren, the Netherlands), in collaboration with Dr. David L. Thomson and Prof. Arie van Noordwijk. Research contract funded by Vogelbescherming (partner of BirdLife International for the Netherlands).

Research project: Modelling of population dynamics of the White Stork *Ciconia ciconia* in the Netherlands - Applications in conservation biology: assessment of the consequences of reintroduction measures on life-history and behavioural traits.

1996 (October) - 2001 (January):

Post-graduate research at the Department of Ecology (CNRS UMR 7625), University Pierre and Marie Curie, Paris, under the supervision of Dr. Etienne Danchin and Dr. Jean Clobert. Research contract funded by the French Ministry of Higher Education and Research, and teaching contract funded by the University Pierre and Marie Curie, Paris VI.

Research project: Breeding habitat selection mechanisms in birds: gathering and use of public information - Theoretical, correlative and experimental approaches.

List of publications

22 publications: 17 articles in international peer-reviewed journals, 5 chapters in peer-reviewed books

Articles published or accepted in international journals or reviewed book chapters

- (1) Morand-Ferron, J., **Doligez, B.**, Dall, S. and Reader, S. 2010. Social information use. In *Encyclopedia of Animal Behaviour*. (M. Breed and J. Moore eds.), Elsevier. In press.
- (2) Tschirren, B. Sendekka, J. Groothuis, T. G. G., Gustafsson, L. and **Doligez, B.** 2009. Heritable variation in maternal yolk hormone deposition in a wild bird population. *The American Naturalist*, 174:557-564.

- (3) **Doligez, B.**, Gustafsson, L. and Pärt, T. 2009. 'Heritability' of dispersal propensity in a patchy population. *Proceedings of the Royal Society London B*, 276:2829-2836.
- (4) Boulinier, T. and **Doligez, B.** 2009. Evolution et implications des comportements de choix de l'habitat. In, *Biologie Evolutive*, chapitre *Ecologie Comportementale: une approche évolutive du comportement* (F. Thomas, M. Raymond and T. Lefefre, eds.), De Boeck Université, in press.
- (5) Ruuskanen, S., **Doligez, B.**, Tschirren, B., Pitala, N., Gustafsson, L., Groothuis, A. G. G. and Laaksonen, T. 2009. Yolk androgens do not appear to mediate sexual conflict over parental investment in the collared flycatcher. *Hormones and Behavior*, 55:514-519.
- (6) Pitala, N., Ruuskanen, S., Laaksonen, T., **Doligez, B.**, Tschirren, B. and Gustafsson, L. 2009. The effects of experimentally manipulated yolk androgens on growth and immune function of male and female nestling collared flycatchers. *Journal of Avian Biology*, 40:225-230.
- (7) **Doligez, B.** and Pärt, T. 2008. Estimating fitness consequences of dispersal – A road to 'know-where'? Non-random dispersal and the underestimation of dispersers' fitness. *Journal of Animal Ecology*, 77:1199-1211.
- (8) **Doligez, B.**, Berthouly, A., Doligez, D., Tanner, M., Saladin, V., Bonfils, D. and Richner, H. 2008. Spatial scale of local breeding habitat quality and adjustment of breeding decisions in a wild tit population. *Ecology*, 89:1436-1444.
- (9) Bize, P., Devevey, G. Monaghan, P., **Doligez, B.**, and Christe, P. 2008. Fecundity and survival in relation to resistance to oxidative stress in a free living bird. *Ecology*, 89:2584-2593.
- (10) **Doligez, B.** and Boulinier, T. 2008. Habitat selection and habitat suitability preferences. In S. E. Jorgensen and B. D. Fath, Behavioral Ecology. *Encyclopedia of Ecology*, vol. 3 pp. 1810-1830. Oxford: Elsevier.
- (11) Boulinier, T., Mariette, M., **Doligez, B.** and Danchin, E. 2008. Choosing where to breed - Breeding habitat choice. In *Behavioural Ecology: An Evolutionary Perspective on Behaviour*. Eds. Danchin, E., Giraldeau, L.-A. and Cézilly, F. pp. 285-322. Oxford University Press.
- (12) **Doligez, B.**, Thomson, D. L. and van Noordwijk, A. 2004. Using large-scale data analysis to assess life history and behavioural traits: the case of the reintroduced White stork *Ciconia ciconia* population in the Netherlands. *Animal Biodiversity and Conservation* 27:387-402 (Proceedings of the EURING 2003 conference).
- (13) **Doligez, B.**, Pärt, T. and Danchin, E. 2004. Informed breeding habitat selection: prospecting and public information in the collared flycatcher. *Animal Behaviour* 67:457-466.
- (14) **Doligez, B.**, Pärt, T., Danchin, E., Clobert, J and Gustafsson, L. 2004. Availability and use of public information and conspecific density for settlement decisions in the collared flycatcher. *Journal of Animal Ecology* 73:75-87.
- (15) **Doligez, B.** and Clobert, J. 2003. Clutch size reduction as a response to increased nest predation rate in the collared flycatcher. *Ecology* 84, 2582-2588.
- (16) **Doligez, B.**, Cadet, C., Danchin, E. and Boulinier, T. 2003. When to use public information for breeding habitat selection? The role of environmental predictability and density dependence. *Animal Behaviour* 66:973-988.
- (17) Pärt, T. and **Doligez, B.** 2003. Public information and habitat selection: prospecting birds cue on parental activity. *Proceedings of the Royal Society London B* 270:1809-1813.
- (18) **Doligez, B.**, Danchin, E. and Clobert, J. 2002. Public information and breeding habitat selection in a wild bird population. *Science* 297: 1168-1170.
- (19) **Doligez, B.**, Clobert, J., Pettifor, R. A., Rowcliffe, M., Gustafsson, L., Perrins, C. M. and McCleery, R. H. 2002. Costs of reproduction: assessing responses to brood size manipulations on life-history and behavioural traits using multi-state capture-recapture models. *Journal of Applied Statistics* 29: 407-423.
- (20) Danchin, E., Heg, D. and **Doligez, B.** 2001. Public information and breeding habitat selection. pp. 243-258 in: *Dispersal*. Eds: J. Clobert, E. Danchin, A. A. Dhondt and J. D. Nichols. Oxford University Press.

- (21) **Doligez, B.**, Danchin, E., Clobert, J. and Gustafsson, L. 1999. The use of conspecific reproductive success for breeding habitat selection in a non-colonial, hole-nesting species, the collared flycatcher. *Journal of Animal Ecology* 68: 1193-1206.
- (22) Doncaster, C. P., Clobert, J., **Doligez, B.**, Gustafsson, L., and Danchin, E. 1997. Balanced dispersal between spatially varying local populations: an alternative to the source-sink model. *American Naturalist* 150: 425-445.

Articles submitted and in revision

- (23) **Doligez, B.**, Daniel, G., Warin, P. Pärt, T. Gustafsson, L. and Réale, D. 2010. A comparison of methods based on capture-recapture data to estimate heritability of dispersal propensity: the collared flycatcher as a case study. *Journal of Ornithology*. In revision.
- (24) Pärt, T., Arlt, D. **Doligez, B.** and Qvarnström, A. Territory-specific prospecting and subsequent choice of breeding site: the use of multiple cues and the constraint of territory owner survival. Submitted to *Ecology*.
- (25) Lemoine, M. **Doligez, B.**, Passereault, M. and Richner, H. Influence of host profitability and microenvironmental conditions on parasite specialisation in main and alternative hosts. Submitted to *Journal of Animal Ecology*.

Articles in preparation

- (26) Ruuskanen, S. **Doligez, B.**, Pitala, N. Gustafsson, L. and Laaksonen, T. Long-term fitness consequences of high yolk androgen levels for parents and offspring in collared flycatchers: sons pay the costs.
- (27) **Doligez, B.** Public information as a selective force for breeding synchrony.
- (28) Oddie, K. R., **Doligez, B.** and Devaadorj, E.. Effects of female body condition on egg sex ratio in a desert breeding Mongolian Passerine *Passer ammodendri*.
- (29) Lemoine, M., **Doligez, B.** and Richner, H. Does parasite local maladaptation equals host local adaptation? An experimental test in the great tit - hen flea system.
- (30) Seppanen, J.-T., Forsman, J. T., Mönkönen, M., **Doligez, B.** and Gustafsson, L. Intra- and interspecific neighbourhood effects on nest-site choice of collared flycatcher.
- (31) **Doligez, B.**, Sendecka, J. Groothuis, T. G. G. and Tschirren, B. Do yolk androgens mediate parent-offspring resemblance in dispersal propensity in a patchy bird population?
- (32) **Doligez, B.**, and Pärt, T. Public information and intraspecific competition: breeding habitat selection decisions in yearling collared flycatchers.
- (33) **Doligez, B.** and Richner, H. Carotenoid-based plumage coloration as a signal for post-fledging parental care decisions: an experimental approach in the great tit *Parus major*.

Reports

- (34) **Doligez, B.** 2009. *Récolte d'informations sur la qualité locale de l'habitat: relier le comportement de prospection et la sélection de l'habitat de reproduction chez une espèce aviaire: Scientific report on the project funded by the Fyssen Foundation, France.* (21 pages).
- (35) **Doligez, B.**, Deerenberg, C., Thomson, D. L., and van Noordwijk, A. 2001. *White Stork conservation in the Netherlands: Report on the project funded by BirdLife/Vogelbescherming Nederland.* KNAW- NIOO, CTO, Heteren, Pays-Bas. (34 pages).
- (36) **Doligez, B.** 2001. *Mécanismes de sélection de l'habitat de reproduction chez les oiseaux: succès reproducteur local et autres indices de la qualité locale de l'environnement - récolte et utilisation de l'information chez le Gobe-mouche à collier (Ficedula albicollis).* Thèse de Doctorat de l'Université Pierre et Marie Curie (Paris VI).
- (37) **Doligez, B.** 1996. *Sélection de l'habitat de reproduction chez le Gobe-mouche à collier (Ficedula albicollis): conséquences démographiques et mécanismes comportementaux.* DEA d'Ecologie, Université Pierre et Marie Curie (Paris VI).

Oral communications at conferences and meetings

Oral communications

- M. Lemoine, **B. Doligez** and H. Richner. *13th International Congress of the ISBE*, Perth, Australia, 26th - 30th of September 2010.
- B. Doligez**, G. Daniel and L. Gustafsson. *13th International Congress of the International Society for Behavioural Ecology (ISBE)*, Perth, Australia, 26th - 30th of September 2010.
- S. Ruuskanen, **B. Doligez**, N. Pitala, L. Gustafsson and T. Laaksonen. *25th International Ornithological Congress*, Campos de Jordao, Bresil, 22nd - 28th of August 2010.
- M. Lemoine, **B. Doligez** and H. Richner. *6th International hole-nesting bird conference*, Oxford, UK, 13th - 15th of July 2010.
- B. Doligez**, G. Daniel, P. Warin, T. Pärt, L. Gustafsson and D. Réale. EURING analytical meeting, Pescara, Italy, 14th - 20th of September 2009.
- B. Doligez**. "Ecology and behaviour" meeting, Lyon, France, 6th - 10th of April 2009 (invited talk).
- B. Doligez**. International workshop on Social information use, Montréal, Canada, 1st-5th of December 2008.
- B. Doligez**, T. Pärt and L. Gustafsson. International conference on Dispersal, Paris, France, 5th-6th of December 2007.
- B. Doligez** and T. Pärt. *11th International Congress of the International Society for Behavioural Ecology (ISBE)*, Tours, France, 23rd - 29th of July 2006.
- J.-T. Seppanen, J. Forsman, **B. Doligez**, and L. Gustafsson. *11th International Congress of the ISBE*, Tours, France, 23rd - 29th of July 2006.
- B. Tschirren and **B. Doligez**. *11th International Congress of the ISBE*, Tours, France, 23rd - 29th of July 2006.
- B. Doligez**. *12th Belgium Congress of Zoology*, Wageningen, the Netherlands, 26th - 28th of October 2005 (invited talk).
- B. Doligez** and T. Boulinier. "Ecology and behaviour" meeting, Chizé, France, 16th - 18th of March 2005 (invited talk).
- B. Doligez**, A. Berthouly, M. Tanner, D. Doligez and H. Richner. *10th meeting of the International Society for Behavioral Ecology (ISBE)*, Jyväskylä, Finland, 10th - 15th of July 2004.
- B. Doligez** and T. Pärt. *10th meeting of the International Society for Behavioral Ecology (ISBE)*, Jyväskylä, Finland, 10th - 15th of July 2004.
- B. Doligez**, D. L. Thomson and A. van Noordwijk. *EURING Conference*, Radolfzell, Germany, 6th - 11th of October 2003.
- B. Doligez**, A. Berthouly, M. Tanner, D. Doligez and H. Richner. *25th Conference on Population Genetics and Biology*, Toulouse, France, 26th - 28th of August 2003.
- E. Danchin, T. Boulinier and **B. Doligez**. *International Ornithological Conference (IOC)*, Beijing, China, 12th - 20th of August 2002.
- B. Doligez**, E. Danchin and J. Clobert. *9th meeting of the International Society for Behavioral Ecology (ISBE)*, Montréal, Canada, 7th - 12th of July 2002.
- B. Doligez**, E. Danchin and J. Clobert. *Meeting of the Swiss Zoological, Botanical and Mycological Societies*, Bern, Switzerland, 14th - 15th of February 2002.
- B. Doligez**, D. L. Thomson and A. van Noordwijk. *International meeting "Capture-recapture methodology and Ecology"*, Alterra, Wageningen, the Netherlands, 27th of September 2001.
- B. Doligez** and Jean Clobert. *23rd Conference on Population Genetics and Biology*, Orsay, France, 27th - 29th of August 2001.
- B. Doligez**, E. Danchin and J. Clobert. *3rd Behavioural Ecology Meeting*, Montpellier, France, 15th - 17st of March 2001.
- B. Doligez**, J. Clobert, R. A. Pettifor and M. Rowcliffe. *EURING Conference*, Pt. Reyes, California, United States, 2nd - 7th of October 2000.

- B. Doligez**, E. Danchin and T. Boulinier. *1st Conference of the A.F.E.E.E. (Association Francophone d'Ecologie, Ethologie et Evolution)*, Rennes, France, 31th of August - 3rd of September 1999.
- B. Doligez**, E. Danchin and T. Boulinier. *International Conference "Evolution of Dispersal"*, Roscoff, France, 24th - 30th of April 1999.
- B. Doligez**, E. Danchin and T. Boulinier. *52nd EGI (Edward Grey Institute) Student Conference on Bird Biology*, Oxford, United Kingdom, 4th - 8th of January 1999.
- B. Doligez**, E. Danchin and T. Boulinier. *20th Conference on Population Genetics and Biology*, Lille, France, 14th - 17th of September 1998.
- B. Doligez**, E. Danchin and J. Clobert. *1st Behavioural Ecology Meeting*, Dijon, France, 19th - 21st of March 1998.
- B. Doligez**, E. Danchin and J. Clobert. *3rd European Meeting of PhD Students in Evolutionary Biology*, Barcelona, Spain, 26th - 28th of February 1997.

Posters

- J. Forsman, T. Jaakkonen, J.-T. Seppänen, **B. Doligez** and L. Gustafsson. *12th International Congress of the ISBE*, Ithaca, USA, 9th - 16th of August 2008.
- T. Boulinier, **B. Doligez** and E. Danchin. *Meeting of the European Society for Evolutionary Biology (ESEB)*, Barcelona, Spain, 23rd - 28th of August 1999.

Invited seminars

- Lausanne**, Institute of Zoology, University of Lausanne, Switzerland, 25th of March 2009. "Causes and consequences of within-family resemblance in dispersal behaviour: the case of the collared flycatcher".
- Dijon**, Department of Biology, University of Bourgogne, France, 13th of March 2009. "Causes and consequences of within-family resemblance in dispersal behaviour: the case of the collared flycatcher".
- Montréal**, Department of Biology, University of Québec in Montréal, Canada, 4th of December 2008. "Social information, breeding habitat selection and dispersal: information gathering and use in the collared flycatcher".
- Oulu**, Department of Biology, University of Oulu, Finland, 6th of November 2008. "Social information, dispersal and breeding habitat selection: information gathering and use in the collared flycatcher".
- Groningen**, Department of Behavioural Biology, University of Groningen, The Netherlands, 4th of October 2005. "Brood sex ratio adjustment according to local breeding habitat quality: the role of sex-biased natal dispersal - an experimental approach in tit species".
- Bern**, Institute of Zoology, University of Bern, Switzerland, 23rd of November 2004. "Brood sex ratio adjustment according to local breeding habitat quality: the role of sex-biased natal dispersal - an experimental approach in tit species".
- Uppsala**, Centre of Evolutionary Biology, University of Uppsala, Sweden, 15th of January 2004. "Adjustment of sex ratio according to local breeding habitat quality: the role of sex-biased natal dispersal - an experimental approach in tit species".
- Lausanne**, Institute of Zoology, University of Lausanne, Switzerland, 19th of June 2002. "Public information and breeding habitat selection: information gathering and use in the collared flycatcher".
- Lyon**, Department of Biometry and Evolutionary Biology, France, 21st of March 2002. "The use of local reproductive success of conspecifics for breeding habitat selection - the case of the collared flycatcher".
- Uppsala**, Centre of Evolutionary Biology, University of Uppsala, Sweden, 28th of February 2002. "Local reproductive success of conspecifics and breeding habitat selection: information gathering and use in the collared flycatcher".

Heteren, Centre for Terrestrial Ecology, Netherlands Institute for Ecological Research (KNAW-NIOO, CTO), the Netherlands, 19th of September 2001. "Population dynamics of the White Stork in the Netherlands: modelling survival rate and assessing the impact of conservation measures".

Bern, Institute of Zoology, University of Bern, Switzerland, 2nd of July 2001. "The use of local reproductive success of conspecifics in breeding habitat selection - the collared flycatcher as a case study".

London, Institute of Zoology, London, United Kingdom, 6th of March 2001. "Breeding habitat selection mechanisms in birds: local reproductive success of conspecifics and other cues of local environmental variation - information gathering and use in the collared flycatcher".

Montpellier, Centre of Functional and Evolutionary Ecology (CEFE CNRS), Montpellier, France, 21st of February 2001. "Succès reproducteur local des congénères et sélection de l'habitat de reproduction - récolte et utilisation de l'information chez le gobe-mouche à collier".

Scientific techniques and research skills, courses, research assistantships

Referee for the following scientific international journals:

American Naturalist, Ecology, Proceedings of the Royal Society, London B, Journal of Animal Ecology, Animal Behaviour, Ecology Letters, Oecologia, Behavioral Ecology, Behavioral Ecology and Sociobiology, PLoSone, Ecography, Ecological Modelling, Behavioural Processes, Animal Biology, Ibis, Revue d'Ecologie

Referee for the NSERC (Canada), the NSF (USA) and for the ANR (French National Research Agency).

Chair of session "Dispersal, Movement and Migration" at the EURING Technical Meeting, 14-21 January 2007, Dunedin, New Zealand, and ***Associate Editor*** of the corresponding section in the Proceedings of the conference.

Member of PhD committee of P. Legouar, National Museum of Natural History (defence on the 6th of February 2007) and S. Varela, University Pierre and Marie Curie, Paris VI (defence on the 28th of September 2007) and ***member of the PhD board*** of J. Clavel, National Museum of Natural History, A. Boussier, University of Paris Sud, A. Midamegbe, University of Montpellier, and J. Geraci, University of Dijon.

Statistical knowledge: inferential statistics, ANOVAS, general linear models, multivariate statistics. SAS software. Preparation of experimental protocols.

Modelling techniques: programming (Pascal language). Population dynamics modelling: Capture-Mark-Recapture methodology (MARK, SURGE and U-CARE softwares) and matrix models (ULM software).

Field work skills in ornithology: ringing, observing and recording behaviour, organisation of field work, supervision of a research team of students and field assistants, monitoring of breeding populations of cavity-nesting birds, behavioural experimentation.

Courses:

1997: 4-day course on the use of the SAS statistical software. Session 1: "which tests for which type of data?" Session 2: generalised linear models.

June 2001: Summer school on Dynamic State Variable Modelling in Ecology, by Prof. Marc Mangel, University of California (12th - 15th June 2001, at University Claude Bernard - Lyon I).

November 2008: Workshop "Modelling individual histories with state uncertainty", by J.-D. Lebreton, O. Gimenez, R. Pradel, CNRS CEFE Montpellier (17th - 21st November 2008, at the CEFE Montpellier).

Research assistantships:

April- May 2001: Research assistantship for the project: "Evolution of brood sex ratios in extreme environments - the influence of environmental predictability on parental decisions in

the Saxaul sparrow" (directed by Dr. K. Oddie, CEFE, Montpellier, France), in Mongolia, Gobi desert.

October 2001: Research assistantship for the project: "Local adaptation and gene flow: determinism of laying date in two blue tit populations in Corsica - an experimental approach" (directed by Prof. Donald Thomas, Sherbrook University, Canada, and Dr. Marcel Lambrechts, CEFE, Montpellier, France - project funded by National Geographic), in Corsica, France.

Teaching experience

1998 - 2000: 192 hours in Formal Genetics, undergraduate level (2nd year biology students), at the University Pierre and Marie Curie, Paris, France (directed and practical work).

1998 - 1999: 20 hours in Ecology, undergraduate level, at the University Pierre et Marie Curie (DEUG, Magistère of Biology-Biochemistry, and DEA in ecology).

2001 - 2003: 130 hours in Evolutionary Ecology, undergraduate level (2nd and 3rd year biology students), at the University of Bern, Switzerland (courses and practical work). Responsible for the 3rd year course "Experimental design and statistics" (60 hours).

Supervising experience

1998 - 2000: supervision of **7 research training projects** for Bachelor of Sciences, Honours, students (Organism and Population Biology), at the University Pierre and Marie Curie (Paris VI) and for 2nd-year students of the ENSAM agronomic engineer school (Montpellier). Project titles: (1) *behavioural responses to nest predation in the collared flycatcher - field work and data analyses*; (2) *influence of sampling on the estimation of temporal environmental variation in local breeding patch quality - theoretical approach*; (3) *the role of public information in breeding habitat choice in the collared flycatcher - information gathering via prospecting*.

2002 - 2003: supervision of **6 research training projects** for Bachelor of Sciences, Honours, students (Organism and Population Biology), at the University of Poitiers, for 2nd-year students of the ENSAM, and for a 3rd-year IUP student (Institut Universitaire Professionnel - Subject: Environment), University of Corsica. Project titles: (1) *the role of constraints in time budget on resistance strategies of hosts (great tits) against their parasites (hen fleas)*; (2) *brood sex-ratio adjustment in relation to local habitat quality and sex-biased natal dispersal – an experimental approach in the great tit*.

2005-2010: supervision of **28 research training projects for 1st year Master of Sciences** students in Ecology (University of Lyon 1, University of 'Pau et Pays de l'Adour', University of Rennes, University of Saint-Etienne, University of Poitiers, University of Lille), for **2nd year students of agronomic engineer schools** (ENSAM and INA P-G - AgroParisTech), and for **2nd year IUT student** (Technology University, Toulon, Poitiers, Nantes, Caen). Projects title: (1) *processes at the origin of parent-offspring similarity in dispersal behaviour, and the role of maternal effects - experimental approaches in the collared flycatcher*; (2) *interspecific transfer of public information – an experimental approach in the system great tit-collared flycatcher*; (3) *prospecting behaviour and information gathering for future breeding habitat selection*; (4) *relation between innovation ability, personality traits and fitness components in the great tit*.

2003-2009: supervision of **7 research training projects for 2nd year Master of Sciences** students in Ecology, University Pierre and Marie Curie, Paris VI, University Claude Bernard, Lyon I, and University of Tours. Project titles: (1) *brood sex-ratio adjustment in relation to local habitat quality and sex-biased natal dispersal – an experimental approach in the great tit*; (2) *brood sex-ratio adjustment in relation to local habitat quality and sex-biased natal dispersal – a correlative approach in the collared flycatcher*; (3) *behavioural strategies involved in the resistance of hosts to parasites: temporal constraints in the great tit – hen flea system*; (4) *dispersal and breeding strategies in the collared flycatcher: early strategies (maternal effects,*

investment in eggs, sex-ratio and paternity) and late strategies (feeding rate, young growth, fledging success); (5) parent-offspring resemblance in dispersal behaviour in the flycatcher.

2006-2010: co-supervision of one **PhD project** in Ecology, Université Claude Bernard, Lyon I (in codirection with Prof. H. Richner, University of Bern, Switzerland). PhD title: Local adaptation in a host-parasite system – population genetics, behavioural and experimental approaches in the great tit-hen flea system (Mélicca Lemoine).

2010-2013: supervision of one **PhD project** in Ecology, Université Claude Bernard, Lyon I (in codirection with Denis Réale, Université du Québec à Montréal, Canada). PhD title: Interactions between dispersal and behavioural syndromes: causes and consequences – empirical approaches in a fragmented population of passerine birds (Grégory Daniel).

2010-2013: supervision of one **PhD project** in Ecology, Université Claude Bernard, Lyon I (in codirection with Olivier Gimenez, CNRS CEFE, Montpellier). PhD title: Evolution of dispersal in natural populations: estimating heritability and consequences of dispersal on individual fitness (Marion Germain).

Academic distinctions, fellowships and awards

2010-2013: Research grant and PhD grant from the Région Rhône-Alpes (programme CIBLE 2010).

2010: Grant for an Exploratory Interdisciplinary Project (PEPS) from the CNRS.

2010-2012: International Collaboration Research Project with Finland (PICS) from the CNRS, coordinated together with Jukka Forsman (University of Oulu, Finland).

2009-2011: Participation to a project funded by a research grant from the French National Research Agency (ANR) in collaboration with Dr. Claire Doutrelant, Montpellier, France.

2009-2011: Participation to a project funded by a research grant from the French National Research Agency (ANR) in collaboration with Prof. Franck Cézilly, Dijon, France.

2007-2009: Research grant from the French National Research Agency (ANR).

2007-2008: Research grant from the Fyssen Foundation.

2007: Research grant from the Région Rhône-Alpes (student mobility programme) for the PhD of Mélicca Lemoine (cosupervised with H. Richner in Switzerland).

2006: Research award from the Association for the Study of Animal Behaviour (ASAB)

2006: Research award from the British Ecological Society (Small Ecological Project Grant).

2005-2007: International Collaboration Research Project with Sweden (PICS n° 3054) from the CNRS, coordinated together with Lars Gustafsson (University of Uppsala, Sweden).

2005-2006: Research grant from a French Research Network in Behavioural Ecology with Dr. Thierry Boulinier (CEFE, Montpellier, France).

2005: Research award from the Association for the Study of Animal Behaviour (ASAB) for a collaborative project with Dr. Barbara Tschirren (Bern University, Switzerland).

2005: Research awards from the Animal Behavior Society, the American Ornithologists's Union and the Percy Sladen Memorial Fund (Linnean Society of London).

2001: Marie Curie post-doctoral fellowship for a research project in the Department of Zoology, University of Antwerp, Belgium, in collaboration with Erik Matthysen (withdrawn to accept another position).

2000: Research awards from the Animal Behavior Society and from Sigma Xi, The Scientific Research Society.

1999 - 2000: Honorary Student Membership to the Cooper Ornithological Society.

1998: Research award from the French Ministry of Foreign Affairs.

1997: PhD fellowship from the French Ministry of Higher Education and Research; teaching fellowship at the University of Pierre and Marie Curie (Paris VI).

1993: Admission to the Ecole Normale Supérieure, Paris (Biology, Geology and Chemistry section).

Manuscripts submitted, in revision and in preparation

This last section contains the manuscripts currently submitted, in revision and in an advanced preparation stage whose list is given p. 11.