MALADAPTIVE HABITAT SELECTION OF A MIGRATORY BIRD IN A HUMAN-MODIFIED LANDSCAPE

From patterns to mechanisms

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de l'obtention du grade de docteur en sciences

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Photo de couverture: *Pie-grièche écorcheur* - ©Arno ten Hoeve.nl

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SUMMARY OF THE THESIS

Habitat selection is an individual, behavioural, process during which organisms decide where to live and this decision-making ultimately affects their fitness. Organisms often exhibit preference for habitats that provide rewarding fitness consequences, but this adaptive link between habitat preference and habitat quality might become uncoupled in human-modified environments. Such ecological trapping has received both theoretical and empirical evidence, but the mechanisms leading to this form of maladaptive behaviour remain poorly understood.

This thesis focuses on the habitat selection of a migratory bird, the Red-backed shrike (*Lanius collurio*), breeding in mixed farmland-forest landscapes of southern Belgium. Agricultural activities in farmland and harvesting practices in plantation forests provide structurally different open habitats for shrikes and other open-habitat wildlife. This offers the opportunity to test whether habitat selection is adaptive or if there is evidence for an ecological trap in this study species. A three-year dataset was collected to document habitat preference and habitat quality for the shrikes. A series of key environmental conditions and resources for the shrikes were sampled and compared between both habitat types to examine the mechanisms of habitat selection.

Results indicate a preference for open areas in forest over farmland: the forest habitat was found to be valued as a territorial resource to a higher level by the shrikes and, on average, selected before farmland during the habitat selection phase. However, breeding shrikes showed lower reproductive performance in forest than in farmland. This ecological trapping pattern could be partly explained by two different functional components of habitat quality: predation rates and food resources. First, shrikes preferred to settle in the forest habitat with a lower amount of nest predators (i.e. corvids), but where nest predation rate was higher compared to farmland. Among the different factors that were tested to explain this pattern, the limited nest concealment in forest compared to farmland was found to be the best candidate. Second, food limitation offered an additional explanation for the mismatch between habitat preference and quality. Shrikes were shown to be unable to correctly evaluate and deal with the habitat quality in terms of food availability in the breeding sites.

This study indicates that open areas in plantation forests may be a less favourable habitat for farmland birds in contrast to what has been assumed previously in the literature. Beyond this applied contribution, this thesis also contributed to the conceptual development of the ecological trapping framework as it draw attention to the importance of food in addition to nest predation as a part of the functional mechanisms underlying this form of maladaptive habitat selection in the wild.

RÉSUMÉ DE LA THÈSE

La sélection d'habitat représente le choix d'un individu quant à l'endroit où vivre, affectant ses performances reproductrices. Il est fréquent d'observer que les organismes préfèrent des habitats liés à une performance élevée, mais des habitats modifiés par l'homme peuvent découpler ce lien adaptatif. Un tel piégeage écologique a reçu à la fois des preuves théoriques et empiriques, mais les mécanismes menant au piège écologique sont encore mal explorés.

Cette thèse se concentre sur la sélection d'habitat d'un oiseau migrateur, la Pie-grièche écorcheur (*Lanius collurio*), se reproduisant dans des paysages composés de prairies bocagères (habitat agricole) et de plantations d'épicéas (habitat forestier) dans le sud de la Belgique. Les activités agricoles et le régime de coupes forestières fournissent des habitats de reproduction pour les pies-grièches et d'autres espèces de milieux ouverts. Ce scénario offre l'opportunité de tester l'adaptivité de la sélection d'habitat chez cette espèce, ou au contraire l'existence du piégeage écologique. Pour ce faire, un jeu de données sur trois années a été échantillonné, portant sur la préférence et la qualité de l'habitat chez la pie-grièche écorcheur, ainsi que sur différentes conditions environnementales dans les deux habitats concernés.

Les résultats indiquent une préférence pour l'habitat forestier comparé à l'habitat agricole: l'habitat forestier est évalué à un plus haut degré en tant que ressource territoriale et les pies-grièches sélectionnent en moyenne l'habitat forestier avant l'habitat agricole. Cependant, la nidification dans l'habitat forestier a comme conséquence de diminuer les performances reproductrices de la pie-grièche écorcheur comparé à l'habitat agricole. Ce piégeage écologique pourrait être en partie expliqué par deux mécanismes différents. Tout d'abord, malgré que l'habitat forestier accueille une plus faible quantité de prédateurs, la prédation des nids y est plus élevée par rapport à l'habitat agricole. Le camouflage inférieur des nids pourrait expliquer le taux plus élevé de la prédation au nid dans l'habitat forestier. Deuxièmement, les résultats indiquent qu'une limitation en ressources nutritives peut expliquer la plus faible qualité corporelle de la progéniture dans l'habitat forestier.

Cette étude montre d'abord que les plantations d'épicéas peuvent constituer des habitats de faible qualité pour les oiseaux agraires contrairement à ce qui a été suggéré précédemment. Plus généralement, cette étude pointe également que des environnements anthropiques peuvent attirer certains organismes en leurs infligeant un coût sur leurs performances reproductrices. De ce fait, une meilleure compréhension conceptuelle du piégeage écologique fut atteinte, tout en attirant

l'attention sur l'importance de la variation en ressources nutritives et de la prédation au nid comme mécanismes fonctionnels au piège écologique.



Red-backed shrike (male), 30 June 2008, Lierneux. Picture: F. Hollander

Chapter 1

General introduction

One of the central aims in ecology is to understand how organisms are spatially distributed. Habitat selection studies investigate the (results of) decision-making of organisms relative to where to live and reproduce in the environment. Hence, this field addresses the ecological resources and (a)biotic conditions (or their proxies) in space and time for reproduction and survival. These resources and conditions are nested into a multidimensional biological space, which is typically referred to as the ecological niche (Whittaker et al. 1973, Pulliam 2000). The way animals exploit the conditions and resources of their ecological niche affects individual fitness, and potentially, population dynamics (Gaillard et al. 2010). The ecological conditions and resources vary naturally in space (e.g. heterogeneous environment) and time (e.g. seasonal changes), but human activities including amongst others urbanization or agricultural intensification, may considerably interfere with this variation, which in turn may have consequences for their distribution and organismal condition (Van Dyck 2012). Moreover, anthropogenic changes might also alter the information previously used by the organisms to make habitat choices and other life-history decisions (Kokko & Sutherland 2001, Tuomainen & Candolin 2011). In order to persist in human-modified landscapes, organisms might for instance adapt their niche requirements through behavioural flexibility (e.g. phenotypic plasticity) to cope with novel situations and environments (Sih et al. 2011). Although human activities are commonly leading to population declines and/or species extinctions, some species have been shown to adapt rapidly and they perform well in anthropogenic environments (e.g. Møller 2010, Sih et al. 2011). In this vein, habitat selection studies take a central place in ecology to understand how organisms cope with changing environments. Both from a theoretical and empirical viewpoint, habitat selection studies in human-modified environments have become an important component of both conservation and evolutionary biology (e.g. Battin 2004, Kawecki 2008, Morris 2011).

What is a habitat?

Habitat is one of the basic concepts in ecology, yet it is often used in an inconsistent and ambiguous way (Hall et al. 1997, Dennis et al. 2003, Mitchell 2005, Gaillard et al. 2010). The common, although vague, definition of the habitat is the place or vegetation type where an organism lives (Odum 1971, Collin 1988, Calow 1999, but see Dennis et al. 2003). This definition is actually that of the **structural habitat**, and typically perceives the habitat as a species-specific, homogeneous and spatially fixed entity (a 'patch') embedded within a biotope (i.e. a vegetation type such as a broad-leaved forest, a mountain lake or a city park). The part of the biotope a species occupies to live and survive corresponds to its (structural) habitat, often also referring to a (more detailed) vegetation type (i.e. a beech forest). In most studies, it remains however unclear at which spatial and temporal scale organisms are studied in their environment: from small (e.g. foraging patch) to large (e.g. landscape) spatial extents or under different seasonal conditions (Hall et al. 1997, Gaillard et al. 2010). More recently, there has been an interest to re-define the habitat from a functional, organism-centered viewpoint; the **functional habitat**. Both the 'niche-based' (Gaillard et al. 2010) and 'resource-based' (Dennis et al. 2003) definitions in the literature regard the functional habitat as the suite of resources (food, shelter) and environmental conditions (biotic and abiotic) that are important for the survival and reproduction of an organism at a given place and time. Hence, it can be seen as the combination of resources and conditions needed for an organism to live and function (Hall et al. 1997, Dennis et al. 2003). A slight difference in both concepts might be found in the fact that the niche-based definition also includes the use of resources and conditions as proxies to model and predict the occurrences of target species in given habitats, a research question less developed in the resource-based definition. This definition of the habitat is the 2D spatial projection of the n-dimensioned, hypervolumed niche as originally defined by Hutchinson several decades ago (Hutchinson 1957). Therefore, this abstracted n-dimensioned sphere containing all critical resources and conditions for a species to live (= niche) can be projected to field conditions in case these resources and conditions can be mapped (2D) in a bounded, functional space. The resource-based definition offers a strong tool for conservation strategies as it creates a functional link between resources and other environmental conditions used by the organisms, and individual fitness or population dynamics (Dennis et al. 2006, Gaillard et al. 2010). Throughout this PhD-thesis, the term 'habitat' and 'habitat type' refer to structural habitat (i.e. vegetation types), and in case we explicitly refer to functional habitat it is mentioned as such.

Habitat selection, quality, use, preference: definitions

Following Clobert et al. (2009), **habitat selection** is the behavioural process that results in a disproportional utilization of certain habitat types over others, and this choice affects the survival and reproduction of individuals. Habitat selection is assumed to occur as a hierarchical process in space and over time: e.g. selection of a region, a home range, a patch within a home range until the selection of a particular breeding site or food item, each step occurring at a distinctive period of the organisms' breeding cycle or lifetime (Johnson 1980, Gaillard et al. 2010). The first stages of habitat selection are often based on stimili such as structural elements of the landscape and features of the local terrain (Hildén 1965). A more detailed assessment of the ecological resources within habitats may then occur and influence decision-making for habitat selection. Routine movements (e.g. related to foraging), dispersal or migration events are all important drivers of habitat selection (Stamps 2001, Van Dyck & Baguette 2005, Morris 2011). Conceptually, **habitat quality** is defined as the ability of the environment to provide resources and conditions appropriate for individual and population persistence (Hall et al. 1997, Johnson 2007). Natural selection should favour the capacity for individuals to respond appropriately to low and high quality habitats given the predicted impact on fitness (Cody 1987, Clark & Shutler 1999). In the field, habitat quality is merely investigated throughout individual fitness measures (e.g. reproductive performance). Hence, habitat quality combines the concepts of habitat (population level) and fitness (individual level) into the notion that high-quality habitat confers high fitness for the occupants (Fretwell & Lucas 1970). **Habitat use** refers to the way an individual select (or accept) certain resources and how it deals with the environmental conditions present in its habitat in order to reproduce and/or survive (Gaillard et al. 2010). It may also be considered as the proportion of time animals spend in particular habitats, and use is said to be selective in case a habitat type or particular resources within these habitats are used disproportionally compared to the availability (Beyer et al. 2010). However, this definition is often confused with habitat preference, which is more related to a choice, not a use. **Habitat preference** is the likelihood of an animal selecting a given habitat (*sensu* a place or vegetation type) when offered alternative choices (Johnson 1980). Unfortunately, studying habitat preference by means of standardized choice experiments is most of the time only feasible under lab-controlled conditions (e.g. Johnsson 2000), although recently choice experiments have been conducted in the field for insects (Horváth et al. 2010). However, habitat preference in the field is most often identified indirectly and animal density has frequently been used as a surrogate for habitat preference; densely occupied habitat types are then regarded to be preferred over less densely occupied habitats. Several problems have been identified with this use of density since it does not reflect an individually-motivated behavioural choice (Van Horne 1983, Skagen & Yackel Adams 2010). Hence,

density should be used in the field as a surrogate of habitat preference only when its biological meaning in the study system has been tested priorly in the field or is at least correlated to other preference estimates (e.g. Chalfoun & Martin 2006). Interesting alternatives of indirect measures of habitat preference in the field are settlement patterns (arrival date in migratory organisms), distribution of dominant individuals or site fidelity (Robertson & Hutto 2006, Arlt & Pärt 2007). These alternatives better reflect the individual choice, and hence, they are likely to be better estimates of habitat preference in the field. Unfortunately, these parameters are rarely used as the requested field sampling is time-consuming. Moreover, very few studies experimentally tested whether alternatives indeed reflect a motivated choice. This is important to examine since habitat preference is a key factor to evaluate whether habitat selection is adaptive or not; flawed measures of habitat preference may bias the conclusions on the patterns of habitat selection (Robertson & Hutto 2006).

Habitat selection theory: from adaptive to maladaptive behaviour

Habitats often vary in quality as resources are not necessarily homogeneously distributed across the environment. Adaptive habitat selection refers to the process of maximizing fitness, and thus closely refers to a suitable choice during habitat selection given habitat availability. In such a case, habitat quality is thus correctly valuated during habitat selection. Evidence for this adaptive process has often been found in the wild (e.g. Petit & Petit 1996, Blondel et al. 1999, Haugen et al. 2006, Chalfoun & Martin 2009), and is the conceptual keystone for the development of habitat selection models. Maladaptive habitat selection occurs when an organism prefers a habitat of lower quality although higher-quality options are available, and this process received both empirical and theoretical support (Schlaepfer et al. 2002, Robertson & Hutto 2006).

Adaptive habitat selection models

Density-dependent competition can be an important aspect of habitat selection (Svärdson 1949, Fretwell & Lucas 1970, Rosenzweig 1981). The original seminal work developed by Fretwell & Lucas (1970) described density-dependent habitat selection and has been an important theoretical framework for ecology exploring the mechanisms of animal distribution in heterogeneous environments with non-uniformly distributed resources and conditions. In this system, settlement depends on the amount of resources in a habitat (originally labeled as a ‘patch’); density is directly proportional to the amount of resources of a habitat. The quality of a habitat is related to the number of individuals consuming the competing resources (Tregenza 1995): habitats are selected in proportion to the amount of resources that are available, and this availability decreases when the

number of competitors increases leading to density-dependent fitness. Habitat quality decreases with increasing competition for common resources, and at a given density, additional individuals will gain more resources and realize a higher fitness by selecting a lower-quality habitat where competition with conspecifics is lower. Individuals should distribute themselves among habitats such that they all have the same fitness expectations, and this process leads to the Ideal Free Distribution (Fretwell & Lucas 1970). According to this theoretical concept, organisms are assumed to be "ideal" in their decision-making (i.e. 'perfect' assessment of habitat quality leading to adaptive habitat selection) and 'free' to move from one site to the other in order to find and select the highest-quality option (i.e. searching costs are assumed to be null). This Ideal Free Distribution framework has led to a variety of applications predicting the behaviour and distribution of animals. Although the ideal free distribution relies on several assumptions, considerable empirical support has been found (Haugen et al. 2006, Morris 2006). Therefore, the theoretical background beyond the Ideal Free Distribution has been suggested to serve as a tool for wildlife conservation and management strategies (Morris 2003).

Individuals may be unable to settle at the best places, as there may be social exclusion by competition. In this respect, dominant individuals have the ability to preempt the highest-quality habitats creating an Ideal Preemptive Distribution (Pulliam & Danielson 1991). This development of the Ideal Free Distribution led to the source-sink dynamics model (Pulliam 1988), which also was inspired by the metapopulation (Levins 1969) and the core-satellite models (Boorman & Levitt 1973). The source-sink model is one of the most important concepts in landscape ecology for the understanding of habitat-dependent population dynamics (Wiens et al. 1993). In such a system, a population source is defined as a habitat in which the reproductive rate is higher than the level necessary to counterbalance mortality rate (i.e. population growth rate, $\lambda > 1$), in contrast to sinks ($\lambda < 1$). Source habitats produce an excess of individuals, which may disperse into sink habitats. This emigration-immigration process maintains individuals in low-quality habitats and generates a dynamic source-sink system. Two mechanisms might generate source-sink dynamics in heterogeneous environments (Dias 1996). The first mechanism involves active decision-making by the organisms; intra-specific competition for high-quality habitats favours immigration into sinks because individuals in source habitats force subdominant individuals to occupy sinks. Blue Tit (*Cyanistes caeruleus*) populations in southern France provide a well-documented example: deciduous oak forests are source habitats (population growth rate, $\lambda > 1$) with subordinate individuals achieving higher fitness compared to individuals in evergreen forests ($\lambda < 1$), and with evidence of gene flow from sources to sinks (Blondel et al. 1993, 1999, Blondel 2007). The second mechanism is rather passive (e.g. seed dispersal by plants), such as the physical forces of wind or water currents transferring individuals from source habitats to sinks regardless of resource availability. Several other

models of animal populations were developed to predict the spatial distribution of organisms in environments varying in quality (reviewed in Tregenza 1995, Morris 2003). It is important to note that all these models assume the preference for high-quality habitats, and thus assume that individuals are able to correctly evaluate, or at least appropriately respond to habitat quality.

Environmental cues

However, individuals are not always able to directly judge habitat quality in terms of fitness returns as assumed in most of these models. Instead, organisms typically have to rely on environmental cues to guide their settlement decisions (Kristan 2003). Environmental cues represent features of the environment that the organism perceives at the time of settlement and they are informative in terms of habitat quality and associated fitness expectations at some later time (Williams & Nichols 1984, Stamps & Krishnan 2005). This cueing is expected to lead to adaptive habitat selection, and at least two reasons might explain the use of cues. First, environmental conditions change over time and may be unpredictable in the period after habitat selection (e.g. Orians & Wittenberger 1991, Jonzén et al. 2004), such that the use of appropriate cues will efficiently guide the organism into high-quality habitat. Secondly, decision-making during habitat selection may have to operate quickly as most species have a restricted temporal reproductive window. Hence, rapid settlement decisions permit breeding earlier, which is generally advantageous in terms of fitness (Verhulst & Nilsson 2008). These two constraints may complicate judging habitat quality directly during the habitat selection phase, and thus favour the use of cues that predict the future state of the environment (Mönkkönen et al. 1999).

Environmental cues represent proximate factors (i.e. what triggers a decision-making) which stimulate habitat preference, although ultimately (i.e. the reason behind the decision-making), other factors than the environmental cues may determine individual fitness (Hildén 1965). For instance, habitats composed of high foliage density (proximate factor) is an attractive cue stimulating habitat selection in the Red-eyed vireo (*Vireo olivaceus*), because foliage density is associated with caterpillar abundance and hence good feeding conditions (ultimate factor) that affect fitness (Marshall & Cooper 2004). Another well-known example is that of heterospecific attraction during habitat selection; the presence and density of other species is used as an indicator of a high-quality habitat, as their presence reflects food availability or safe breeding sites (Thomson et al. 2003, Mönkkönen et al. 1999, Forsman et al. 2007). Other well-studied types of cues are the presence of conspecifics (Ward & Schlossberg 2004), their reproductive performance ('public information', see Doligez et al. 2002, Danchin et al. 2004), predator abundance (Fontaine & Martin 2006a) and anti-predation

shelters (Thomson et al. 2006). Adaptive habitat selection therefore involves a tight relationship between proximate and ultimate factors, such that the proximate cues to which an individual responds during its habitat selection will ultimately maximize fitness. This evolutionary process makes cue reliable indicators of the future state of the environment (Schlaepfer et al. 2002).

Habitat selection in a changing world: the ecological trap theory

Human-driven environmental changes may induce a mismatch between the attractiveness of the habitats (i.e. the response of the individuals to the cues) and their quality (i.e. the fitness returns for the individuals) (Schlaepfer et al. 2002, Kristan 2003, Battin 2004, Robertson & Hutto 2006). As a consequence, organisms may prefer lower-quality habitats although higher-quality options are available. In the literature, this phenomenon is labelled as **ecological trapping** and may occur when 1) cues for habitat selection become uncoupled from habitat quality (i.e. unchanged habitat attractiveness in combination with decreasing habitat quality), 2) changing (or newly created) habitat selection cues increase the attractiveness of some habitats with no effect on habitat quality, or 3) both conditions co-occur (Robertson & Hutto 2006). In the case of an ecological trap, habitat quality has been expressed in terms of individual reproductive performance (i.e. the number and quality of offspring) and/or reproductive success (i.e. the probability of producing at least one offspring) (Robertson & Hutto 2006), and population-based performance estimates (Delibes et al. 2001, Kristan 2003). Although the ecological trap concept was first introduced in ornithological field studies by Dwernychuck & Boag (1972) and Gates & Gysel (1978), the phenomenon has only recently attracted interest among theoretic and field ecologists as well as among conservation biologists (Schlaepfer et al. 2002, Battin 2004, Robertson & Hutto 2006, Gilroy et al. 2011, Harabiš & Dolný 2012). Ecological traps represent a particular case of evolutionary traps, involving a mismatch between the cues that organisms use to make any behavioural or life-history decision (e.g. mate choice) and fitness expectations associated with that decision (Schlaepfer et al. 2002, Rodewald et al. 2011).

The ecological trap theory deviates from adaptive habitat selection models as there is an individual preference for low-quality habitat. Hence, organisms do not correctly evaluate the (future) state of the environment at the time of habitat selection. Importantly, for ecological trapping there is a clear distinction between habitat preference and habitat quality, whereas both notions are amalgamated in Ideal Free Distribution or source-sink models (Battin 2004). Therefore, testing the ecological trap concept in the field can be challenging, as habitat preference needs to be rigorously quantified during the habitat selection process in order to show the preference for a low-quality habitat compared to higher-quality options. In contrast with the other models, ecological trapping is an individual behavioural process; preference and fitness should therefore be individually quantified

(Robertson & Hutto 2006). Besides the general preference for low-quality habitat, there is the possibility that this trapping occurs for a non-random group of the individuals in a population. In territorial species, the most dominant or higher-quality individuals (i.e., with higher resource holding potential or RHP) might be more attracted by low-quality habitat whereas the high-quality habitat remains less preferred and only occupied by lower quality individuals (Battin 2004, Igual et al. 2007, Porlier et al. 2009, Jessop et al. 2012).

More recently, there has also been interest for the reversed trapping phenomenon in case minor habitat changes decrease attractiveness although the underlying habitat quality remains unchanged, constituting an undervalued resource (Gilroy & Sutherland 2007) or also called a perceptual trap (Patten & Kelly 2010). Here, a high-quality habitat lacks or has lost the appropriate cues to trigger preference, and it has been proposed that the further investigations of undervalued resources in the field will be necessary to encourage settlement in suitable anthropogenic habitats as to counter biodiversity loss due to human activities. Figure 1.1 illustrates the link between habitat preference and habitat quality on the one hand, and different habitat selection conceptual frameworks on the other hand.

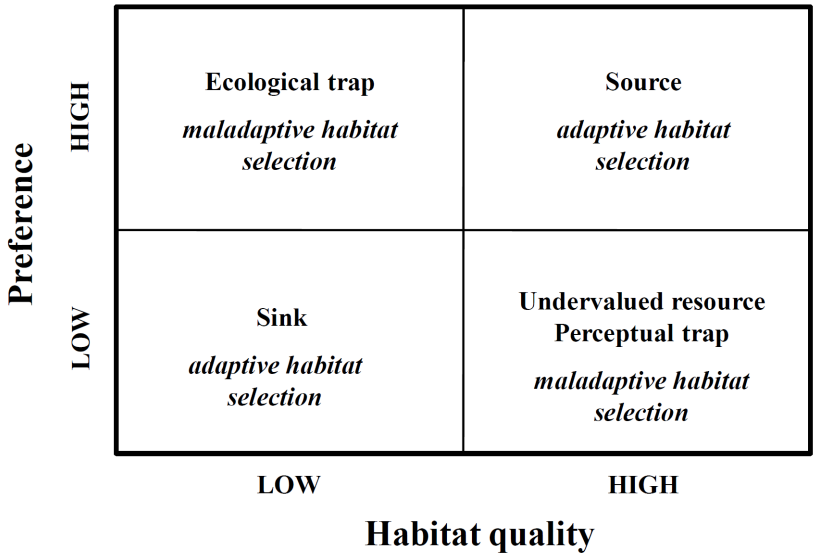


Figure 1.1 – Interpretation of (mal)adaptive habitat selection as a combination of habitat preference and habitat quality resulting in sources, sinks, ecological traps and undervalued resources (or perceptual traps) following Battin (2004), Gilroy & Sutherland (2007) and Patten & Kelly (2010). Note that the ecological trap starts from an individual process but might have consequences for population persistence. This has led to inconsistencies for the definitions of ecological traps (Kristan 2003): individual-level (i.e. preference for lower-quality habitats instead of higher-quality options, Robertson & Hutto 2006) and population-level (i.e. preference for sink habitats associated with negative population growth rate (Delibes et al. 2001, Battin 2004, Fletcher et al. 2012) definitions can be found in the literature. In contrast with the ecological and perceptual traps, preference estimates are not *per se* included in the source-sink models; high- and low quality habitats are *assumed* to be preferred and avoided, respectively.

Evidence of ecological trapping in the field so far…

Two review papers addressed the empirical evidence of ecological traps and concluded that sound evidence was still scarce (Battin 2004, Robertson & Hutto 2006). Only very few studies were found to meet the most important criterion to correspond to the definition of an ecological trap (i.e. preference for lower-quality habitat) (Delibes et al. 2001, Battin 2004, Robertson & Hutto 2006). Studies often fail to use valid individual-level preference measures for habitat preference, with density being the most commonly used although it is a population-level metric and does not reflect an individual decision, as we discussed before (Robertson & Hutto 2006, but see Van Horne 1983). Other studies often lack replicated measures of habitat preference and fitness in space and over time, although this is important to understand whether trapping represents a transient situation or not. Some of the fitness measures used to study ecological traps may also weakly correlate with reproductive performance, such as using artificial nest predation as a surrogate of fitness or relying on a single measure only (e.g. nest success).

Since then, additional studies have, however, been conducted and some of them appear to better meet the conditions of an ecological trap with the use of more robust measures of habitat preference and/or fitness. For instance, some studies compared the properties of microhabitats at nesting sites to that of random and unoccupied sites in order to understand which habitat characteristics are preferred and how it affects fitness (Latif et al. 2011). Radiotracking has been used to study individual habitat preference and fitness estimates in the context of ecological traps (Rantanen et al. 2010, Northrup et al. 2012). Using a migratory bird, Arlt & Pärt (2007) used territory establishment and long-term occupancy time-series to derive territorial preference measures. More recently, Tozer et al. (2012) used the arrival dates of a migratory bird coupled with the distribution of phenotypes between habitats as an index of preference. Other studies used the combination of abundance and reproductive behaviour (e.g. intensity of oviposition in terms of egg number) of several insects on natural substrates such as plants (e.g. Severns 2011) or artificial surfaces (e.g. solar panels, asphalt road, oil surface, car) as measures of habitat preference (Horváth et al. 2009, 2010, see Fig. 1.2). Horváth et al. (2009, 2010) provide one of the strongest cases of the existence of traps to date, as there is evidence of biased individual habitat choice (e.g. choice between an artificial polarized light surfaces and a natural water surface as oviposition site) towards a habitat type associated with negative fitness consequences (e.g. egg survival). Moreover, the mechanisms misleading the insects toward low-quality habitat have been elucidated; artificial polarized light surfaces act as a supernormal optical stimulus cueing the insects, so that they prefer laying eggs on these artificial surfaces over natural water bodies.

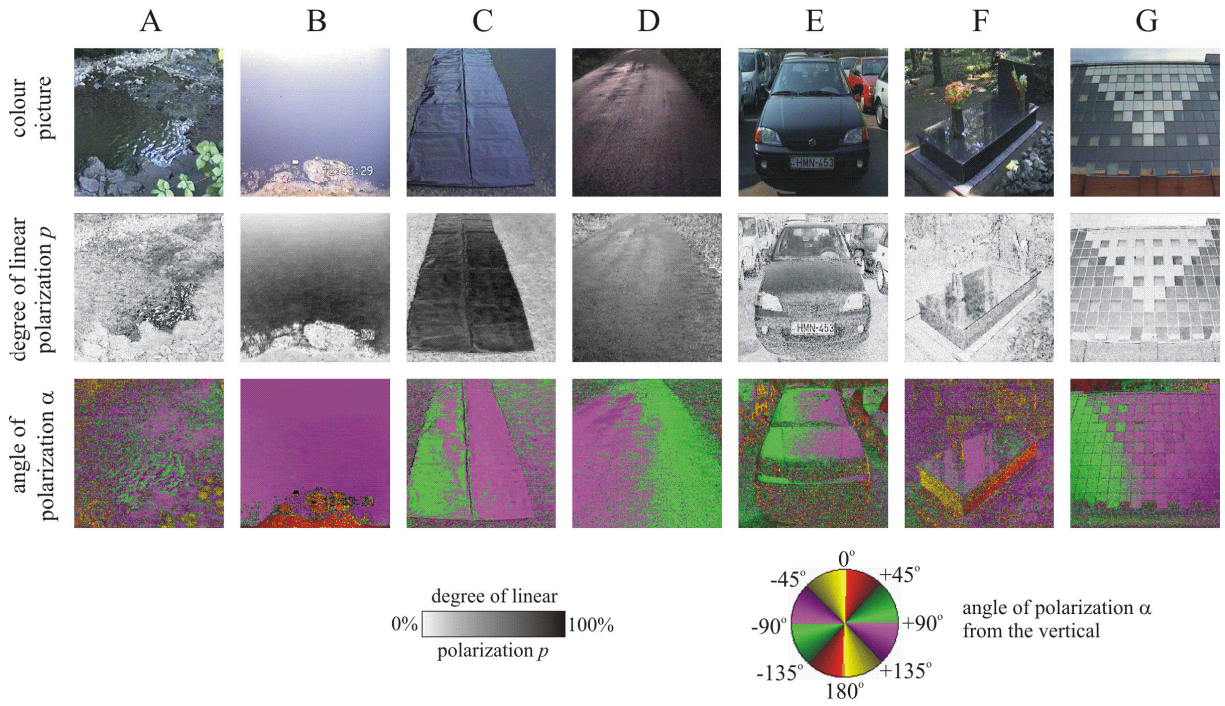


Figure 1.2 – Degree and angle of light polarization for different artificial surfaces known to attract aquatic insects; (A) dark water body, (B) crude oil lake in the desert of Kuwait, (C) black plastic sheet on an asphalt road, (D) dry asphalt road, (E) black car, (F) polished black gravestone, (G) windows with black/gray glass ornamentation. Reproduced with permission from Horváth et al. (2009).

Apart from these few studies, the mechanisms leading to maladaptive decision-making and ecological trapping remain unclear in most studies so far, especially in the wild where choice experiments are not easily conducted. For instance, several bird studies showed that nest success was lower in preferred habitat due to higher nest predation (e.g. Flaspohler at al. 2001, Weldon & Haddad 2005, Gilroy et al. 2011, Latif et al. 2011), but it remains unclear whether predation pressure was misevaluated by the birds during habitat selection, whether the predator community varied between habitats or whether nests were more easily detected by predators in the preferred habitat. The cues leading to maladaptive decision-making have rarely been investigated experimentally in the field. Indeed, experimental alteration of the distribution or quality of cues in order to understand the mechanisms leading to ecological trapping in the field typically remains constrained for logistic reasons. Besides the studies on insects and artificial polarized light surfaces mentioned previously, there are to date no studies – to the best of our knowledge – that were able to identify the behavioural mechanisms leading to an ecological trap, i.e. to identify the proximate factors (cues) that trigger habitat preference and mislead the organisms in low-quality habitats, as well as the ultimate factors that explain lower fitness returns in the preferred habitat type. Finally, little is known on the ability of organisms to escape from an ecological trap; short-term processes could be involved such as through habitat preference changes or learning, but also a long-term process such

as through natural selection, all potentially leading to the colonization of high-quality habitat types. Species adapted to more stable environemnents might be more at risk to become ecologically trapped in case of anthropogenic disturbance, because being contrained from plastic habitat selection (Ekroos et al. 2012).

Where and under which conditions are traps most likely to occur?

Ecological traps are usually associated with novel anthropogenic habitat changes (Schlaepfer et al. 2002, Robertson & Hutto 2006). These recent changes probably involve the alteration of cues which than will then misinform the organism about habitat quality; maladaptive behaviours might evolve from this because the environmental cues organisms used to guide their habitat selection may no longer elicit an adaptive outcome as they did in the past (Levins 1969, Sih et al. 2011). Ecological traps have been shown to occur under different environmental conditions, inlcuding altered habitats like fragmented forests or clearcuts (e.g. Weldon & Haddad 2005, Robertson & Hutto 2007, Tozer et al. 2012), agricultural land (Stallman & Best 1996, Rantanen et al. 2010, Gilroy et al. 2011, Northrup et al. 2012), cities (Boal & Mannan 1999) or other artificial habitats (Horváth et al. 2010, Huang & Pike 2011). Other studies have shown bird species to prefer breeding in exotic vegetations, although some components of fitness were lower compared to breeding in native vegetation (e.g. Remeš 2003, Lloyd & Martin 2005). As most of these habitats are widespread, it opens the question whether ecological trapping might be a common phenomenon, and to what extent it contributes to the decline of previously common species in human-modified environments. Recently, Huang & Pike (2011) suggested that climate change has the potential for turning some anthropogenic habitats into ecological traps. In the lizard *Eutropis longicaudata*, gravid females used to reach a higher fitness in anthropogenic habitat (i.e. concrete walls) compared to natural habitat (i.e. rocks), but ongoing climate change may alter the currently good anthropogenic habitat into a too warm habitat which will result in decrease of fitness expectations compared to the natural habitat.

To conclude, ecological traps occur mostly in human-modified environments in which there is preference for a low-quality environment. However, several studies use weak surrogates of habitat preference and/or habitat quality. New studies have raised additional support for ecological trapping in the wild, but the mechanisms leading to ecological trapping remain poorly explored, and hence, poorly understood.

This thesis focuses on the effect of human-modified environments on habitat preference and quality of a farmland bird species that recently expanded its breeding habitat into artificial open areas in Spruce plantation forests. This system offers the opportunity to test whether or not resources and

conditions in this novel habitat lead to adaptive habitat selection as compared to traditional farmland. In this context, the following sections of the general introduction focus on the origin of farmland-forest landscapes in NW-Europe and the associated open-area wildlife, with a particular focus on birds.

Farmland-forest landscapes in NW-Europe and farmland birds

A historical perspective

Before the Neolithic period, the dominant vegetation type in temperate-zone Europe was closed broad-leaved or evergreen forest with open, early-successional gaps or large open areas (Vera 2000). The open areas were the result of natural disturbances that varied in spatial and temporal intensity (e.g., wildfires, floods, insect outbreaks, grazing by large ungulate groups) and they were attractive to open-area wildlife communities (Pykala 2000, Vera 2000, Svenning 2002, Swanson et al. 2011). Human settlement during the Neolithicum led to large-scale conversions of natural forests to much more open land dedicated to farming and livestock rearing. Since the industrial revolution during the 18th century, shortage of wood supply in many European countries stimulated the development of fast-growing, even-aged, and single-species plantations. This contributed to the reforestation of the open landscape (Heil et al. 2007, Szymanski 2007). However, this reforestation has affected physical properties of the forest including tree diversity or age structure, and with important modifications of the disturbance regime compared to natural forests (Paillet et al. 2010). As a consequence, plantation forests may host lower species diversity compared to natural forests, depending on the level of habitat degradation and ecosystem simplification (Carnus et al. 2006, Brockerhoff et al. 2008, Chazdon 2008). This also opens the question to what extent plantation forests represent a valuable alternative habitat in terms of fitness consequences compared to other habitat types (natural or anthropogenic) selected by a same pool of species.

Open-habitat wildlife of farmland and plantation forests

Since the last few decades, single-species plantations (e.g., Norway Spruce *Picea abies*) are typically managed with large-sized cutblocks in even-aged forest stands (du Bus de Warnaffe & Deconchat 2008). From a forestry viewpoint, post-harvesting, early-successional regeneration areas are considered a transitional, stand initiation phase. Reforestation (i.e. tree planting) or post-disturbance logging may shorten the duration of the early-successional stage, promote structural homogenization, lower plant diversity or eliminate biological processes that are important for the

forest regeneration and the associated communities (Young & Giese 2003, Paillet et al. 2010, Swanson et al. 2011, Brewer et al. 2012). However, young stages in plantation forests have been appreciated worldwide from a conservation viewpoint as they may host open-area wildlife populations (Carnus et al. 2006, Chazdon 2008, Brockerhoff et al. 2008, Paz Acuña & Estades 2011, Swanson et al. 2011). Several disturbance-dependent, farmland bird species have been observed to expand their breeding sites into these regeneration areas of plantation forests (Fuller et al. 2004, Paquet et al. 2006, Loyn et al. 2007). This phenomenon has generated special interest among conservationists given the many environmental problems this group of birds faces in the major breeding sites on agricultural land (Brawn et al. 2001, DeGraaf & Yamasaki 2003, Paquet et al. 2006, Forsman et al. 2010, Swanson et al. 2011). Although this community has been labeled 'farmland' birds (see Fig. 1.3), they essentially are early-successional specialists; they may recognize and realize their ecological niche under different environmental conditions other than farmland *per se*. This raises the questions how farmland and open areas in plantation forests may influence decision-making during habitat selection, and whether early-successional bird species achieve similar or different fitness in each of these human-modified environments.



Figure 1.3 – Examples of early-successional bird species commonly breeding in both farmland and young plantation forests in Belgium (Paquet et al. 2006) and other European countries (e.g. Fuller 2000, Wilson et al. 2006, Söderström & Karlsson 2011, Lislevand 2012, Zmihorski 2012). From left to right: Stonechat (*Saxicola torquata*), Yellowhammer (*Emberiza citrinella*), Common whitethroat (*Sylvia communis*), Willow warbler (*Phylloscopus trochilus*) and Red-backed shrike (*Lanius collurio*). Illustrations from www.rspb.org.uk.

It has been suggested that these species used to live in open areas created by natural disturbances in forests before they shifted to agricultural land (Paquet et al. 2006, Söderström 2009, Söderström & Karlsson 2011). It is difficult to assess which open-habitat species were found in natural forest gaps, because these natural forests have almost entirely disappeared in Europe. Moreover, the conditions and resources in remnants of present-day primeaval forests are probably not fully comparable to past conditions. Habitat requirements of the species may also have changed over time (Fuller 1995). It has, for instance, been argued that several species found in edge habitat (i.e. open ecotone between two transitional habitats) might act as substitutes for the natural forest gaps (Fuller 2012). However, some primeaval forests still provide natural forest gaps due to treefall events. In these natural gaps, bird communities were found to differ significantly from closed forest parts, especially

through the presence of several insectivorous long-distance migrants in gaps (Fuller 2012). Although some of the previously mentionned bird species (Fig. 3) do not seem to select treefall gaps, they were found in nearby large clearcuts in Spruce plantations (Fuller 2000). Probably, the small gaps formed by local treefals do not provide sufficient breeding opportunities and resources. However, larger gaps due to massive wind storms were shown to be benefical for some of these species (Zmihorski 2012). The effect of other disturbances, such as fire or insect outbrakes have been reported to offer a temporary opening of the natural forests where some early-successional, farmland birds may settle (T. Wesełowski, pers. comm.). Although examples of the presence of early-successional bird species in natural forest gaps remain scarce, there are some reasons to believe at least some of these species currently observed in farmland originated from large forest gaps maintained by natural disturbances. In this respect, clearcutting in plantation forests does partly imitate the regime of natural disturbances that used to shape the landscape composition and configuration before the Neolitics.

Modern, and thus recent agricultural activities such as cyclic mowing or intensive grazing of livestock maintain farmland into an early succession stage, providing several bird species with open habitat. On the other hand, early-successional vegetation areas emerge after harvesting activities like clearcut in plantation forests and may therefore constitute a novel environment that is assumed to share some features with the historical habitat of these species, i.e. the habitat they used to occupy before the appearance of farmland during the Neolitics. However, the current forest management practices affect the properties of the early-successional vegetation in several ways and make them probably also different from the post-disturbance ecosystems in natural forests (Sutherland 2002, Johnson et al. 2006b, Swanson et al. 2011, Askins et al. 2012, Brewer et al. 2012). Therefore, although being potentially interesting artificial environments for the conservation of farmland wildlife, plantation forests might have reverse effects on habitat quality compared to traditional farmland habitat.

Although the effects of forestry and agricultural intensification on habitat quality (e.g. Hart et al. 2006, Griesser et al. 2007, Wilson et al. 2012) and biodiversity (e.g. Benton et al. 2003, Chazdon 2008, Foley et al. 2005, Goudie 2006, Flohre et al. 2011, Swanson et al. 2011) have been examined separately in the past, there is a need to understand the global functioning of early-successional ecosystems as habitat for wildlife communities in the relatively recent, human-created open areas in plantation forests as compared to traditional farmland habitat. In landscapes where farmland and open areas in plantation forests create mosaics of two different types of habitats that share similar species assemblages, it is of particular interest to examine whether these two structural habitats have similar, or alternatively, contrasting resources and conditions for early-successional birds (e.g.

food availability, microclimate, predation pressure), and whether they provide similar habitat quality for these organisms. Such a comparative study will improve the knowledge on the process of habitat selection (i.e. habitat preference) for farmland birds in anthropogenic landscapes composed of different human-modified habitats, as well as the associated fitness returns. This will permit testing whether habitat selection is adaptive, or if there is evidence of the existence of ecological trapping in such human-modified environments.

Chapter 2

Research objectives of the thesis

This PhD-thesis compared the habitat preference, habitat use and habitat quality for the Red-backed shrike (*Lanius collurio*) between open areas in farmland and forest habitats in order to test whether habitat selection is adaptive in this study system and to understand the functional mechanism underlying (mal)adaptive habitat selection (Fig. 2.1).

Key environmental conditions and resources for the species (e.g. predation pressure, microclimatic conditions and food availability) were sampled to understand the between-habitat variation in habitat preference, habitat use and habitat quality, and hence, the mechanisms underlying (mal)adaptive habitat selection in human-modified landscapes. This overarching main objective was further splitted into five different questions (and chapters).

Q1) Is habitat selection adaptive in two structurally different early-successional habitats within a mixed farmland-forest landscape?

We used multiple measures of habitat preference (i.e. settlement chronologies after migration and distribution of phenotypes) and fitness components (i.e. reproductive performance as the number of offspring produced and their quality, and reproductive success as the probability of producing at least one fledgling) of the Red-backed shrike in farmland and open areas in forest to test whether habitat selection is based on adaptive decision-making, or alternatively, whether there is support for ecological trapping in a human-modified mixed farmland-forest landscape.

Q2) Do habitat preference measures based on settlement chronologies reflect an individually motivated behaviour?

Using male arrival date (i.e. settlement chronologies after migration) as a surrogate of habitat preference, we tested the assumption that early arriving Red-backed shrikes are more willing to

defend their territorial resource than individuals arriving later, and most importantly, that this valuation is higher in preferred habitat. To do so, a simulated territorial intrusion experiment was conducted to measure the territorial defense in late and early arriving individuals and in farmland and forest habitat.

Q3) Is nest predation an important mechanism to explain variation in nest success between farmland and forest habitat?

We recorded nest success in the Red-backed shrike in farmland and forest habitat and we examined the extent to which brood failures are caused by nest predation. Predator abundance during habitat selection was measured in farmland and forest habitat to understand whether predation pressure is valuated accurately during settlement and influences habitat choice. We also tested how parental behaviour (i.e. nest visiting rates) and nest properties (i.e. nest concealment) affected nest predation rates and, hence, nest success in farmland and forest habitats.

Q4) Do food abundance and quality for early-successional, insectivorous farmland birds differ between farmland and forest?

The abundance (quantity) and size (quality) of ground-dwelling and above-ground invertebrates as prey items for insectivorous, farmland birds was measured with standardized sampling procedures to address to what extent early-successional vegetation in farmland and forest habitats represent similarly valuable breeding sites as regards food availability, and hence whether plantation forests may represent a valuable alternative to the farmland areas.

Q5) How does food availability affect reproductive performance in farmland and forest habitat?

Food availability (invertebrate abundance and size) and the associated food provisioning by the parent birds to the nest were compared between farmland and forest habitats and related to the reproductive performance (i.e. nestling condition) of the shrikes. We also tested how nestling condition varied with the among-nestling competition for food (i.e. number of nestlings competing for food in the same nests) in both habitat types to understand the importance of food limitation for the reproductive performance and habitat use of the shrikes in farmland and forest habitats.

The integration of these five questions will permit to answer the main objective of this thesis and to gain insights into the mechanisms and consequences of habitat selection of a farmland bird species expanding into a novel human-modified habitat.

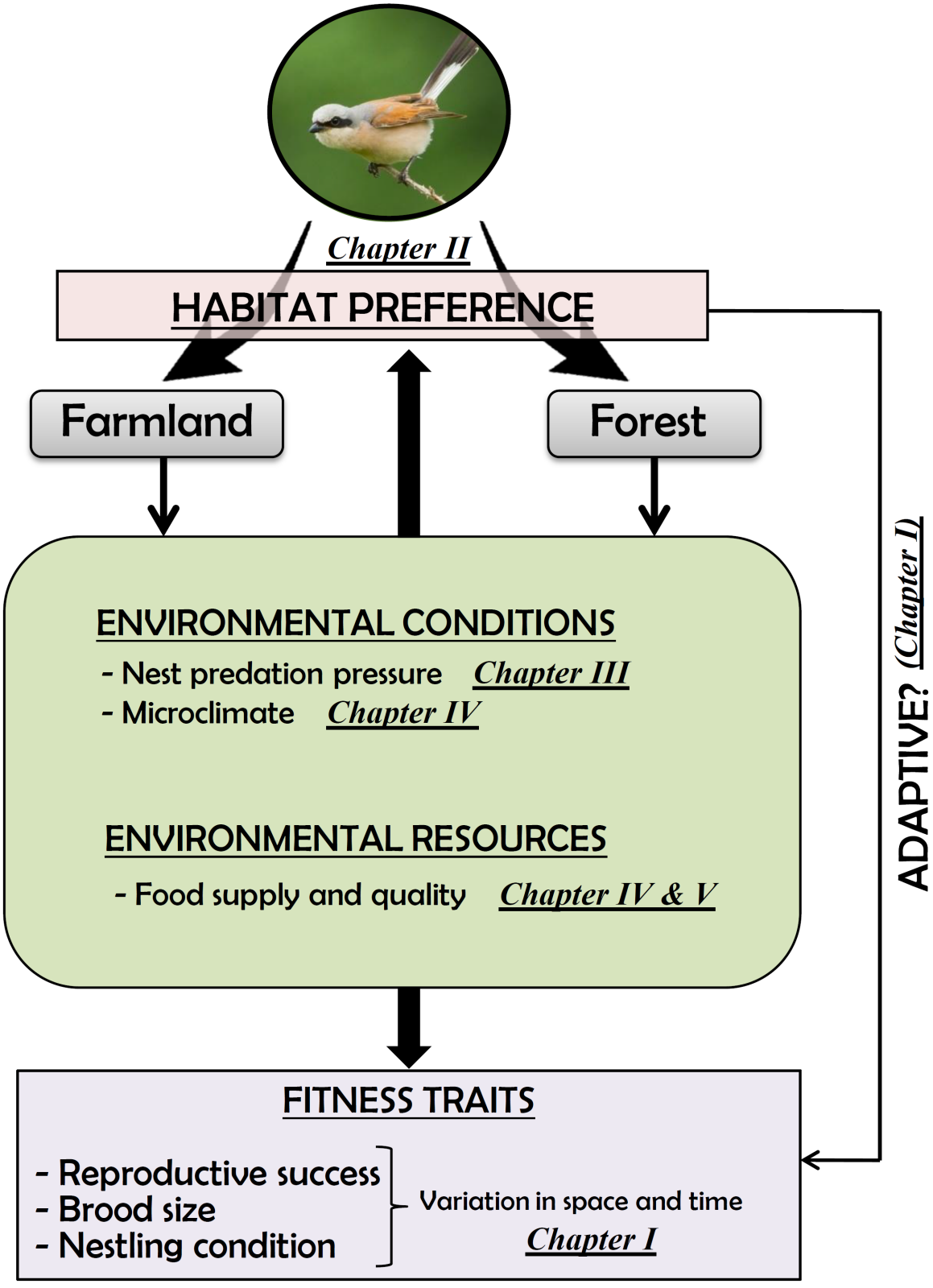


Figure 2.1 – Schematic illustration of the different research questions (and associated chapters) investigated in this thesis, using the Red-backed shrike as a model organism.



Red-backed shrike (juvenile), 17 June 2010, Salvacourt. Picture: F. Hollander

Chapter 3

Materials and methods: an overview

Agriculture and forestry in southern Belgium: a historical perspective

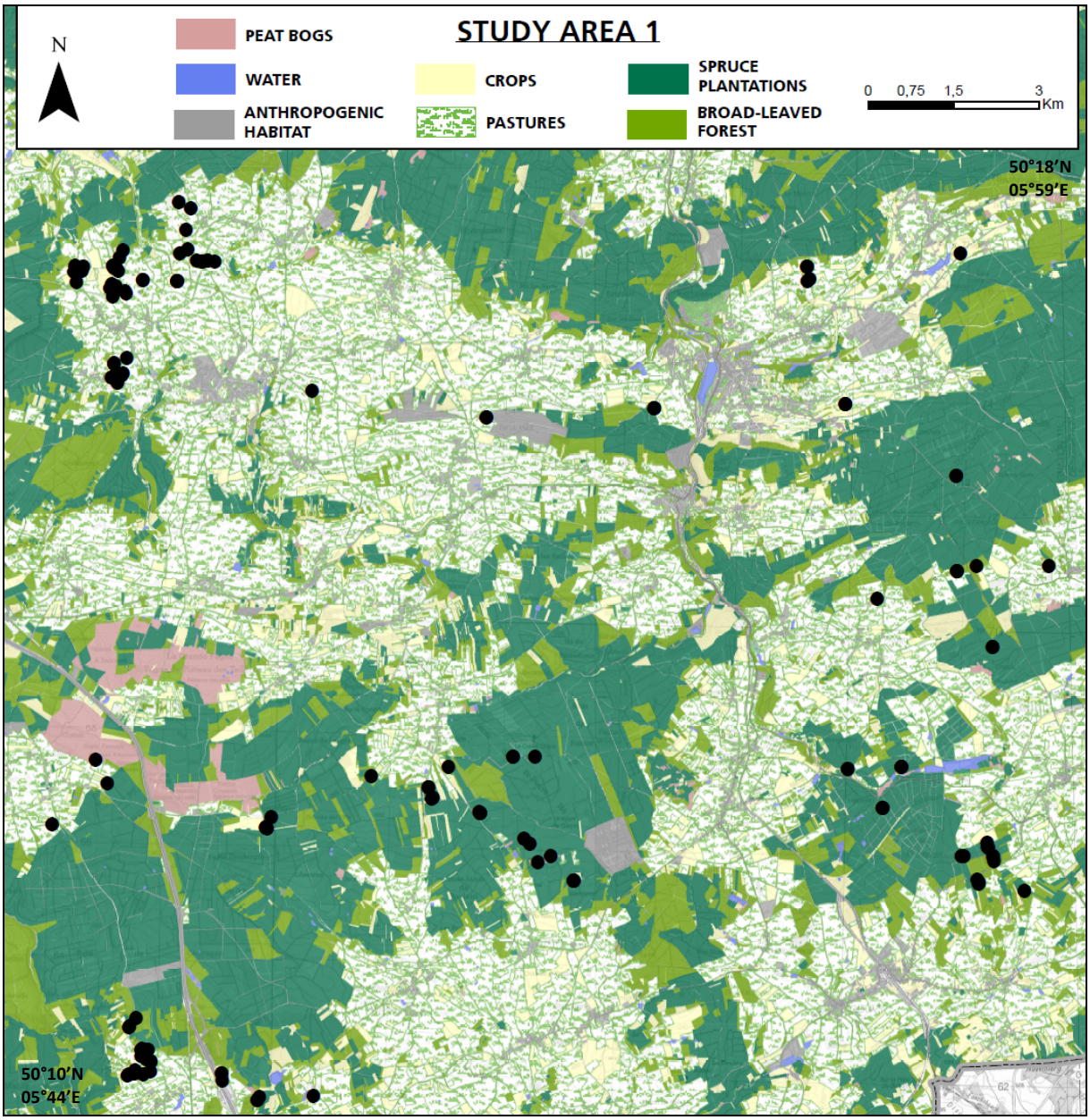
The Ardenne region is the hilliest part of Belgium, where agriculture and forestry are the major forms of land use. Agriculture activities include high-density livestock rearing and timber plantations mainly use Spruce (*Picea abies*) in this region. The landscape structure emerged from historical land-use changes including several cycles of reforestations. Celts and Romans (1st century) massively cut down native forests when wood was needed for constructions. Afterwards, deforestation became less pronounced and uncultivated land was reforested through natural succession (Petit & Lambin 2002). The increase of the human population during the 11th century led to the development of agricultural activities at the cost of forest ecosystems. Agricultural activities were maintained until the 16th century, until the first appearance of wood shortage for fire and heating. Instead of wood, peat bogs were then exploited to extract fuel and the forest remnants were further converted into coppice plantations for the local tanneries. In the 18th and 19th centuries, wood consumption increased even more for the purpose of industrial activities, during which there was a pronounced demographic increase (Petit & Lambin 2002). Despite this industrial revolution, there were some periods of famine. These induced the further extension of agriculture and forestry on uncultivated heathland in order to produce enough food and wood resources for the growing population. Starting from the mid-19th century, Spruce plantations were initiated to avoid the abandonment of uncultivated land, but also to increase timber production for firewood and coalmine activities given the rapid growth of Spruce compared to local tree species (Petit & Lambin 2002). For this reason, the coverage of Spruce plantations increased fourfold during the 20th century (Lecomte et al. 2003). The coverage is currently estimated to be more than 30% of all forested areas in the Walloon region, and 50% in the Ardenne region (Lecomte et al. 2003). In most cases, Spruce forests are now managed with large-sized cutblocks in mature stands (du Bus de Warnaffe & Deconchat 2008).

The major soil type of the Ardenne region is stony and acidic loam soil, which is not ideal for crop agriculture. Therefore, this region is mainly composed of pastures (for cattle breeding) covering more than 90% of the agricultural area (Goidts & van Wesemael 2007), and Spruce forests (Lecomte et al. 2003). An additional reason for this type of farmland-forest landscape is that, at the Belgian level, this region is relatively elevated (600m) and encounters the harshest national climatic conditions with cold winters and high annual rainfall (Petit & Lambin 2002, Goidts & van Wesemael 2007).

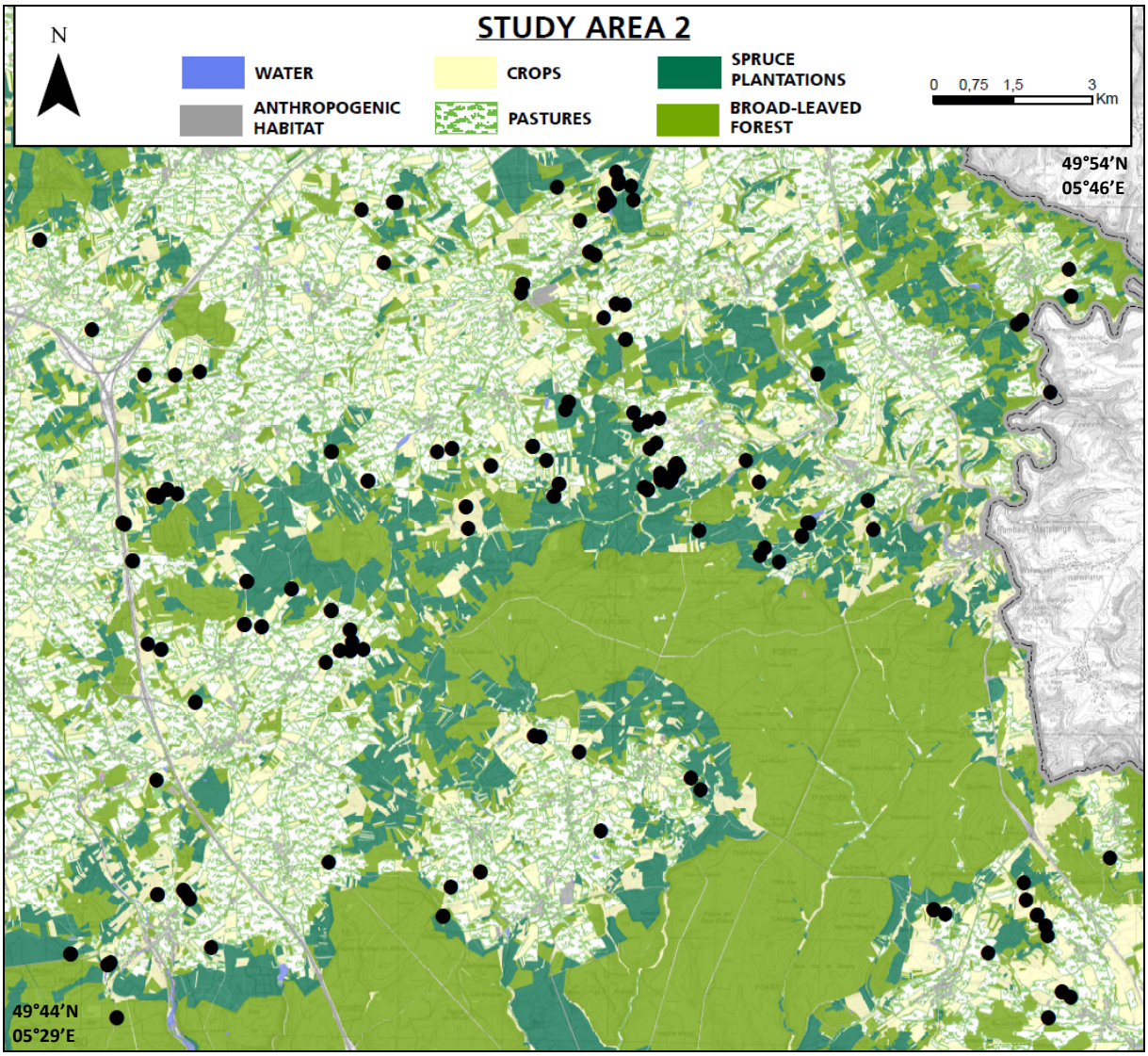
Study areas and study sites

Two study areas of 400km² each were selected in the hilly Ardenne region (southern Belgium), both representing this farmland-forest dominated landscape (Fig. 3.1). The study areas are covered by two distinct land-use types: 1) pastures and hay meadows for intensive livestock rearing, and 2) Spruce plantation forests for timber production, where succession stages range from clear-cut to mature stand. Although the landscape composition is quite similar between both study areas (farmland-forest dominated landscapes), the spatial confirguration of farmland and forest is different between both areas (Fig. 3.1). In particular, there is a large difference in the proportion of Spruce plantations and broad-leaved forests between both study areas.

In 2007, a total of 118 breeding sites ($N_{farmland}$ = 58, N_{forest} = 60) within both study areas were selected to investigate the settlement and reproductive performance of the Red-backed shrikes. A breeding site is defined as an open patch (2-10 ha) in farmland or forest with early-successional and shrubby vegetation. Each breeding site enclosed one or a few shrike territories. These sites were chosen based on the *a priori* distribution of the Red-backed shrike using atlas data (Titeux et al. 2010). Additional breeding sites were also selected based on the expert opinion of local birdwatchers or on the presence of the main habitat requirements for the species as determined during the winter of 2007. The early-successional vegetation concerns grass pastures and hayfields dotted with thorny shrub lines (*Crataegus sp., Prunus sp. and Rosea sp.*) in farmland, and post-harvested natural regenerations (*Sambucus sp.* and *Cytisus sp.*) or young Spruce plantations in forest habitat (Fig. 3.2).


N
STUDY AREA 1
PEAT BOGS
WATER
ANTHROPOGENIC HABITAT
CROPS
PASTURES
SPRUCE PLANTATIONS
BROAD-LEAVED FOREST
0 0,75 1,5 3 Km
50°18'N
05°59'E
50°10'N
05°44'E


BELGIUM
STUDY AREA 1
STUDY AREA 2



	STUDY AREA 1		STUDY AREA 2	
	ha	%	ha	%
Spruce plantations	156554,7	40,6	59862,9	19,6
Broad-leaved forests	3461,7	8,1	83752,5	27,5
Crops	24789,3	7,6	46711,8	15,3
Pastures	124476,3	38,0	108301,5	35,5
Water	899,5	0,3	355,1	0,1
Peat bogs	4804,0	1,4	67,0	0,1
Anthropogenic habitat	12957,8	4,0	5779,4	1,9
TOTAL	327943,3	100,0	304830,3	100,0

Figure 3.1 – Location of breeding sites of the Red-backed shrike in 2008-2010 (black dots) and main land-use types in study areas 1 and 2. Each study area borders partly with Luxemburg in the south-east (study area 1) and east (study area 2). The location of both study areas in Belgium is indicated, as well as the proportion of natural and anthropogenic structural habitat types.

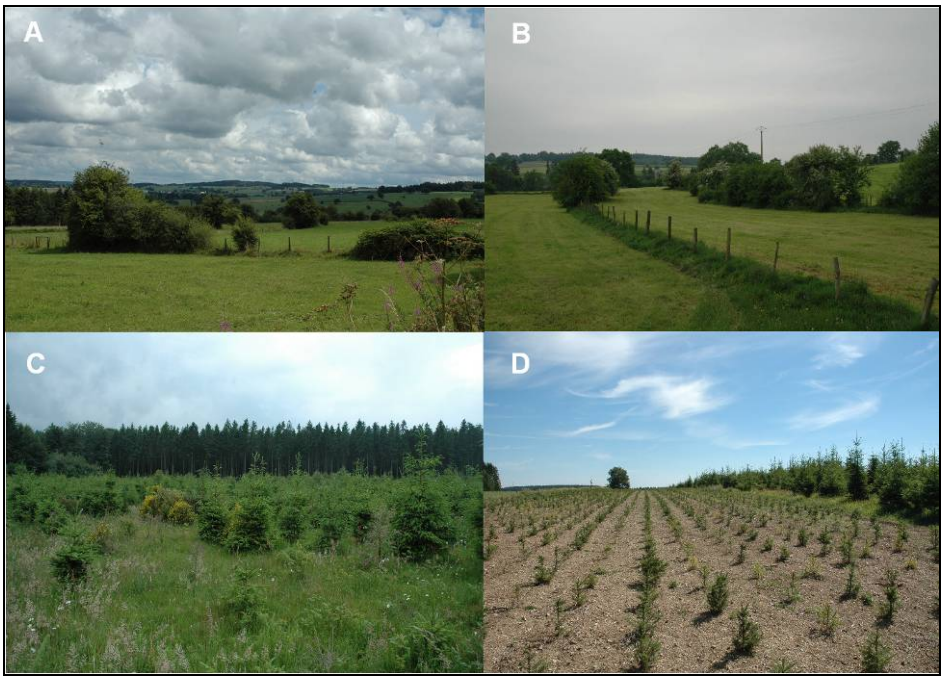


Figure 3.2 – Breeding sites of the Red-backed shrike. A) farmland site, B) farmland site which has just been mown (hayfields), C) young Spruce plantation surrounded by mature forest, D) new plantation adjacent to an older plantation (Pictures: F. Hollander).

The study model

Distribution, migration and ecology of the Red-backed shrike

The Red-backed shrike (*Lanius collurio*) is a small, long-distance migratory passerine staying from May until August on Eurasian breeding grounds, and overwintering in the southern part of Africa (Lefranc & Worfolk 1997). It is a species which has undergone severe population declines in several European countries (BirdLife International 2012), and is of conservation concern in Europe (EU Birds Directive 2010). It is the most common shrike species of Europe; after undergoing large declines during the 1970s, populations have remained stable or have even slightly increased after that period (BirdLife International 2004, 2012). In Belgium, populations have been declining until the mid-1970s, and increased during the 1980s-1990s (Titeux et al. 2010). In spring, it is one of the latest European migratory passerines to arrive on the breeding grounds, but it also departs late from African wintering grounds. Migration speeds have been found to be high compared to other European migrants (Yohannes et al. 2009). Using geolocators, Tøttrup and co-workers (2011) recently showed that: 1) migration transits are achieved about twice as fast during spring than during autumn, 2) males travelled faster than females during successive staging sites *en route* and, 3) schedules could be individually characterized (i.e. individual consistency in the timing of departure along a migration cycle). This reflects the high competition in spring to reach the breeding grounds early, and this

earliness is probably achieved by the best-competing males (Kokko 1999). The annual variation in arrival dates is mostly dependent on spring temperatures (Schaub et al. 2011). Long-term studies have reported that shrikes tend to arrive on breeding grounds and breed significantly earlier compared to several decades ago (Tryjanowski & Sparks 2001, Hušek & Adamík 2008, Hušek et al. 2012). This is probably due to climate change as reported in other migratory bird species (Jonzén et al. 2006).

After one year Red-backed shrikes are able to reproduce. Natal dispersal is typically high in this species, but once settled, adults can be faithful to their breeding sites from year to year although this pattern varies geographically (Geertsma et al. 2000, Müller et al. 2005, Pasinelli et al. 2007, Tryjanowski et al. 2007, Schaub et al. 2011). In our study areas, site faithfulness in adults was estimated to be low (9%) based on the occurrence of colour-ringed individuals (see further). Survival of adults at year t+1 is partly affected by the success of reproduction at year t (Schaub et al. 2011). The longest recorded life-span in the Red-backed shrike is 10 years, but most individuals probably only reach a couple of years (Fransson et al. 2010). We are not aware of any data on the relationship between adult body condition and the probability to survive.

The Red-backed shrike as a model organism

From the set of farmland bird species breeding in Spruce plantations in the Ardenne region (Table 3.1), the Red-backed shrike was used as a model to investigate the different research questions of this study. The reason for this choice was based on several methodological issues. It is a long-distant migrant, giving the opportunity to sample arrival dates as a surrogate for individual habitat preference (see Chapter I and II). Because territorial males exhibit a conspicuous perching behaviour and produce noisy advertising calls (mate attraction) in springtime, they are easy to survey with high detection probability (Lefranc & Worfolk 1997). Nests are relatively easy to detect (Fig. 3.3A, B) and the feeding ecology of the species has been extensively studied (Tryjanowski et al. 2003, Karlsson 2004, Goławski 2006, 2007, Goławski & Meissner 2007, Goławski & Golawska 2008) (Fig. 3.3C). As the species only produces one brood per year, it permits to easily record reproductive success (Antczak et al. 2009). Replacement clutches are initiated after predation events, and in the Ardenne these are always produced by the same parents in the same territory (see Chapter I). This gives the opportunity to control for the effect of clutch sequence (i.e. first or replacement clutch) and study the impact of habitat-dependent brood failures due to the occurrence of nest predation. There is good knowledge about the reproductive ecology of the species, including the determination of the age of nestlings based on feather characteristics (Olsson 1995, Fig. 3.3D). Finally, adults can be efficiently trapped with spring traps using mealworms as lures which facilitates the recording of adult

body condition (Fig 3.3E, F). Trapped adults were colour-ringed with a unique colour combination in order to facilitate individual recognition in the field by means of binoculars. The IRScNB-KBIN (Brussels) provided us with a national license for *Lanius collurio* trapping.

Table 3.1 – Open-habitat or disturbance-dependent farmland bird species breeding in Spruce plantations in the study area (see chapter IV for further details). 1 = scarce, 2 = fairly common, 3 = very common.

Species	Farmland	Forest	Migratory
Common whitethroat (*Sylvia communis*)	3	3	Yes
Red-backed shrike (*Lanius collurio*)	2	2	Yes
Stonechat (*Saxicola torquata*)	1	2	Yes
Tree Pipit (*Anthus trivialis*)	1	3	Yes
White wagtail (*Motacilla alba*)	2	2	No
Willow warbler (*Phylloscopus trochilus*)	2	3	Yes
Yellowhammer (*Emberiza citrinella*)	3	3	Yes



Figure 3.3 – A) clutch B) female on the nest in a Spruce tree, C) feeding visit of the female with prey (Coleoptera; Carabidae), D) 11-days old nestling, E) male captured in a spring trap, F) colour-ringed male (Pictures: F. Hollander).

Field and experimental methods

Most of the field and experimental methods are explained in details in the following five chapters. The present section only aims to better illustrate certain methods or to give additional relevant information.

Food availability and microclimatic conditions

The diet of the Red-backed shrike is mainly composed of ground-dwelling (i.e. Coleoptera) and flying invertebrates (Lepidoptera, Hymenoptera), but occasionally also small mammals, birds or reptiles (Tryjanowski et al. 2003, Karlsson 2004, Goławski 2006, 2007, Goławski & Meissner 2007, Goławski & Golawska 2008). To study the food availability in farmland and forest habitat, we therefore used pitfall traps to capture ground-dwelling arthropods and yellow-pan traps (Fig. 3.4A) to capture flying arthropods. Microclimatic conditions around pitfall traps were recorded by means of thermo-probes with dataloggers (Hobo® UA-002-08) (Fig. 3.4B).

All arthropod specimens were conserved in 96% ethanol. In the laboratory, we identified the specimens to the order or family level for documenting the spectrum of prey availability in both habitats. Typical captured invertebrates known to be consumed by the Red-backed shrikes are illustrated in Fig. 3.5.



Figure 3.4 – A) yellow-pan trap B) thermo-probe with data logger (Pictures: F. Hollander).

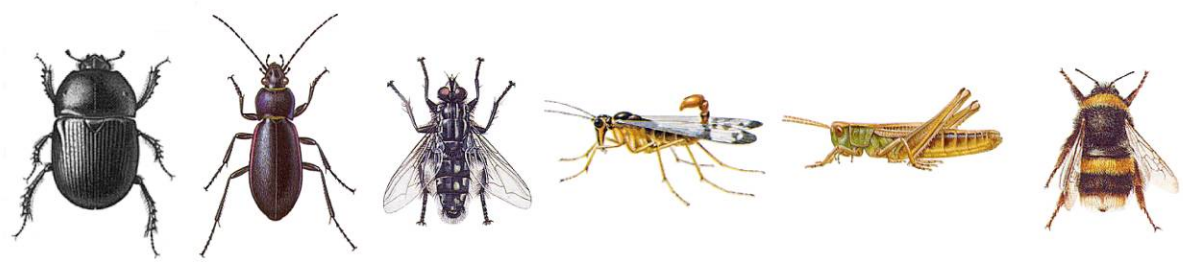


Figure 3.5 – Examples of captured invertebrates by means of pitfall or yellow-pan traps and commonly consumed by the Red-backed shrike. From left to right: *Geotrupes stercorarius* (Coleoptera), *Carabus violaceus* (Coleoptera), *Sarcophaga carnaria* (Diptera), *Panorpa communis* (Mecoptera), *Chorthippus parallelus* (Orthoptera), *Bombus terrestris* (Hymenoptera) (Drawing source: Chinery 2002).

Food provisioning

During the breeding season, some nests were video recorded to compare prey delivered to the nest between farmland and forest habitats. We used a digital video camera with internal memory and with long-life batteries (camera-model: JVC Everio 40Go), and a tripod to fix the camera. This system was placed about 1 to 2 m in front of the nest (Fig. 3.6) and permitted to record parental feeding trips for approximately 3 hours.



Figure 3.6 – Video recording of a Red-backed shrike nest. The nest site is indicated (red circle) (Picture: F. Hollander).

Nest predation

Most common breeding corvid species in the study areas and which are documented as the natural nest predators of the Red-backed shrike are the Eurasian Jay (*Garrulus glandarius*), the Carrion Crow (*Corvus corone*) and the Magpie (*Pica pica*) (Jacob et al. 2010) (Fig. 3.7).



Figure 3.7 – Main nest predators of the Red-backed shrike. From left to right: Magpie, Carrion Crow and Eurasian Jay (Drawing source: www.unapaf.com).

These species are visual predators and they cause nest losses only for open-cup nesting birds, but nest contents (including eggs and nestlings) do not represent a major part of their feeding regime (Snow & Perrins 1998). It has been shown that their abundance is an important factor to explain the prevalence of nest predation in the Red-backed shrike, at least in farmland habitat (Roos 2006). These three corvid species start to be territorial early in the season and eggs are laid most often during the end of March or April (Joys & Crick 2004). This means they start feeding their offspring when the Red-backed shrikes lay their first clutches. These nest predators are known to detect nests by following the feeding visits of parents, or to search actively for nests by using marks or trails leading to the nest sites of their prey (Picozzi 1975) (Fig. 3.8).



Figure 3.8 – Two Carrion Crows in a breeding habitat of the Red-backed shrike and perched on young Spruce trees (Picture: F. Hollander).

We conducted an artificial nest experiment to estimate the difference in predation rate between farmland and forest habitats when there is no parental effect (i.e. parental nest visits). Artificial nests (Fig. 3.9A) were constructed with dried weeds and concealed in a similar way as for natural nests. Each nest contained two Japanese quail eggs (*Coturnix japonica*). Some nests were also provided with plasticine eggs in order to identify predators through their bill marks (Fig. 3.9B).



Figure 3.9 – A) hand-made artificial nest in Spruce tree with two Quail eggs B) hand-made artificial nest in Spruce tree with three plasticine eggs (Picture: F. Hollander).

Table 3.2 summarizes the sample sizes for the different measurements taken in farmland and forest during this thesis.

Table 3.2 – Number of breeding sites, shrike territories, nests, nestlings, insect traps and thermoprobes examined during the 3-year long fieldwork. Several measurements can be taken in the same breeding site (e.g. in different shrike territories or during successive years). Hence, the numbers between brackets refer to the total number of breeding sites where mesurements were taken.

N =	FARMLAND	FOREST
Breeding sites	58	60
Shrike territories	104 (58)	109 (60)
Shrike nests	200 (58)	238 (60)
Nestlings	476 (58)	525 (60)
Artificial nests	235 (26)	260 (25)
Video-recorded nests	29 (29)	32 (32)
Insect traps - pitfalls	307 (36)	288 (31)
- yellow-pan traps	77 (36)	84 (31)
Thermo-probes	32 (8)	36 (9)



Red-backed shrike (female), 19 June 2010, Heinstert. Picture: F. Hollander

Chapter 4

Maladaptive habitat selection of a migratory passerine bird in a human-modified landscape

The content of this chapter has been published:*
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* text in the thesis has marginally been modified compared to the published version

ABSTRACT

In human-modified environments, organisms may preferentially settle in poor-quality habitats where fitness returns are lower relative to available higher-quality habitats. Such ecological trapping is due to a mismatch between the cues used during habitat selection and the habitat quality. Maladaptive settlement decisions may occur when organisms are time-constrained and have to rapidly evaluate habitat quality based on incomplete knowledge of the resources and conditions that will be available later in the season. During a three-year study, we examined settlement decision-making in the long-distance migratory, open-habitat bird, the Red-backed shrike (*Lanius collurio*), as a response to recent land-use changes. In Northwest Europe, the shrikes typically breed in open areas under a management regime of extensive farming. In recent decades, Spruce forests have been increasingly managed with large-sized cutblocks in even-aged plantations, thereby producing early-successional vegetation areas that are also colonised by the species. Farmland and open areas in forest create mosaics of two different types of habitats that are now occupied by the shrikes. We examined different measures of habitat preference (order of settlement after migration and distribution of phenotypes) and several reproductive performance parameters in both habitat types to investigate whether habitat preference is in line with habitat quality. Territorial males exhibited a clear preference for the recently created open areas in forest with higher-quality males settling in this habitat type earlier. Reproductive performance was, however, higher in farmland, with higher nest success, offspring quantity and quality compared to open areas in forest. The results showed strong among-year consistency and we can therefore exclude a transient situation. This study demonstrates a case of maladaptive habitat selection in a farmland bird expanding its breeding range to human-created open habitats in plantations. We discuss the reasons that could explain this decision-making and the possible consequences for the population dynamics and persistence.

INTRODUCTION

Habitat selection theory generally assumes that individuals are able to make optimal settlement decisions, thereby selecting the highest-quality habitats that are available in a heterogeneous landscape to maximize their fitness returns (Morris 2003). Such adaptive habitat choices are expected to produce an ideal free distribution (Fretwell & Lucas 1970) or similar patterns (Nocera et al. 2009). In this vein, the source-sink models of animal populations (Pulliam & Danielson 1991) are based on the assumption that individuals accurately evaluate habitat quality. Many studies have found strong empirical support so far (e.g. Pulliam 1996, Blondel et al. 1999, Hels 2002), however, individuals are not always able to directly judge habitat quality in terms of fitness returns and, instead have to rely on environmental cues to guide their settlement decisions (Storch & Frynta 1999). These environmental characteristics need to be reliable at the time of habitat choice, but should also reflect habitat quality at some later time (e.g. Kokko & Sutherland 2001, Stamps 2001). For instance, migratory birds are often time-constrained in the selection of their breeding sites and have to use indirect cues to determine local habitat quality. The use of environmental cues allows the migratory animal a fast assessment of habitat quality. It has been shown that these organisms may rely upon a host of proximate cues reflecting the environmental conditions that will ultimately affect fitness, such as the vegetation structure and phenology (e.g. Marshall & Cooper 2004), food availability (e.g. Orians & Wittenberger 1991, Marshall & Cooper 2004, Hromada et al. 2008), anti-predation shelters (e.g. Thomson et al. 2006) or social attraction (e.g. Fletcher 2006).

Human-driven environmental changes may induce a mismatch between the attractiveness of the habitats (i.e. the response of the individuals to the cues) and their quality (i.e. the fitness returns for the individuals) (Schlaepfer et al. 2002, Kristan 2003, Battin 2004, Robertson & Hutto 2006, Gilroy & Sutherland 2007). As a consequence, anthropogenic activities may bring some organisms to prefer lower-quality habitats although higher-quality options are available. Such an ecological trapping may occur when 1) cues for habitat selection become uncoupled from habitat quality (i.e. unchanged habitat attractiveness in combination with decreasing habitat quality), 2) changing (or newly created) habitat selection cues increase the attractiveness of some habitats with no effect on habitat quality, or 3) both conditions are combined (Robertson & Hutto 2006, Pärt et al. 2007). Although ecological trapping is a behavioural, individual process (Robertson & Hutto 2006), this phenomenon may have negative population-level consequences and reduce the likelihood of population persistence (Delibes et al. 2001, Kristan 2003, Fletcher et al. 2012).

Ecological trapping is an extreme situation of non-ideal habitat selection, with a negative relationship between habitat preference and quality (Schlaepfer et al. 2002, Kristan 2003, Battin 2004, Robertson & Hutto 2006, Gilroy & Sutherland 2007, Pärt et al. 2007), therefore field studies need to determine: 1) a quantitative evaluation of habitat preference at the individual level, and 2) the ultimate influence of habitat quality relative to several fitness attributes (Robertson & Hutto 2006, Pärt et al. 2007). Habitat preferences should ideally be estimated with choice experiments, but this often proves to be unachievable in the field for logistical reasons. Hence, Robertson & Hutto (2006) listed some surrogate measures of preference: order of settlement (in migratory organisms), distribution of phenotypes, site fidelity and temporal variation in population size. To date, few studies examining the existence of an ecological trap have investigated the link between habitat characteristics, fitness and individual preferences using multiple measures of habitat preference over a substantial time period.

Here, we examined the link between habitat preference and fitness in the Red-backed shrike (*Lanius collurio*), a migratory passerine that occupies two distinct types of breeding habitats in northwest Europe. The Red-backed shrike is typically considered as a farmland bird inhabiting open areas under a management regime of extensive farming (Lefranc & Worfolk 1997, Titeux et al. 2007). However, during the last few decades, the species has also colonised novel and artificially created open areas in Norway Spruce (*Picea abies*) plantations that result from recent changes in forest harvesting techniques (Olsson 1995, Paquet et al. 2006, Titeux et al. 2010, Söderström & Karlsson 2011). In most cases, Spruce forests are managed with large-sized cutblocks in even-aged plantations (du Bus de Warnaffe & Deconchat 2008). It has been suggested that in an evolutionary past, the shrikes (and other birds of this 'farmland' community) lived in open areas created by natural disturbances in forests (e.g. windfalls or wildfires; Lefranc & Worfolk 1997, Svenning 2002) and that they secondarily shifted to extensively managed, heterogeneous farmland since the Neolithic period (Wilson et al. 2009). So, the early-successional regeneration areas following harvesting activities in Spruce plantations constitute a novel habitat compared to farmland, and this habitat is likely to share some features with the historic natural forest breeding habitat (Hansson 1994). Hence, open areas in Spruce plantations may function as a potentially attractive environment to the species. We used multiple measures of individual habitat preference (i.e. settlement pattern and distribution of phenotypes) and fitness components (i.e. reproductive performance) in both habitat types over several years to test whether habitat selection in the Red-backed shrike is based on adaptive decisions, or alternatively, whether there is support for ecological trapping in a human-modified landscape undergoing quick changes.

MATERIALS & METHODS

Study species

The Red-backed shrike is an insectivorous long-distance migratory bird that has a wide breeding range across the Western Palaearctic and overwinters in southern Africa (Lefranc & Worfolk 1997). Males arrive on the breeding sites from late April to late May, and on average two days before females (Olsson 1995, Söderström 2001, Schaub et al. 2011). The breeding season is typically short (May-July) producing a single clutch, although there can be a replacement clutch in case of breeding failure (Roos 2002, Söderström 2001).

Study areas

Based on prior knowledge of the distribution of shrikes in southern Belgium (Titeux et al. 2010), two study areas of 400-km^2 each were selected (centres of study areas 1 and 2 are 50°14'N 5°50'E and 49°49'N 5°39'E, respectively), representing a mosaic of farmland and forest breeding habitats (i.e. farmland with bushes and early-successional regeneration areas in Spruce plantations). The farmland areas are mainly covered by pastures and hay meadows and, to some extent, by fields. In southern Belgium, Spruce plantations were initiated in 1850 and over the last century their cover has increased fourfold (Lecomte et al. 2003). The current coverage of Spruce plantations is estimated to be 30% of all forested areas (Lecomte et al. 2003).

Habitat preference

Local population density may not necessarily reflect habitat preference (Van Horne 1983, Skagen & Yackel Adams 2010). In migratory birds, one of the closest alternatives to choice experiments is the order of settlement (Robertson & Hutto 2006, Pärt et al. 2007). During the winter of 2007-2008 and in both study areas, all potential sites for the establishment of shrike territories in farmland and forest sites were identified based on the presence of the main habitat requirements for the species (e.g. nest sites and foraging areas; Titeux et al. 2007). During three consecutive breeding seasons (2008, 2009 and 2010), the farmland and forest sites in both study areas (N = 118) were visited on a bi-daily basis from late April to late May. To avoid bias in the occupancy histories, the same proportion of farmland and forest sites was visited each day and the order in which sites were visited was randomized. During a 15-minute survey within each site, we checked the presence of territorial

males using both visual and auditory cues. Males are easy to survey with high detection probability due to their conspicuously territorial signalling behaviour in springtime. Once settled, males attract females by repetitive advertising calls on perches and by typical fluttering flights (Lefranc & Worfolk 1997). Males are highly territorial: they defend their territorial resources against intruders and this may induce escalated conflicts (Jakober & Stauber 1989). As assumed in other (long-term) studies on arrival dates in the Red-backed shrike (Schaub et al. 2011), we considered the date of first detection in a site as a reliable estimate of the arrival date.

The distribution of phenotypes among habitat types is another alternative measure of habitat preference since higher-quality or older individuals are expected to preempt preferred habitat types (Robertson & Hutto 2006). In shrikes, adult wing length has been shown to be positively related to age (Jakober & Stauber 2000) and body size (Tryjanowski et al. 2004), and hence may be used as an indicator of the resource holding potential (RHP) (Kelly 2008). Breeding individuals were captured all along the breeding season with bird traps using mealworms as lures. The outermost primary wing length was measured (precision: ± 0.1 mm). We also examined the size of black eye-stripes (facial mask) in males because in other species it has been shown that this morphological trait is an indicator of male quality (Tarof et al. 2005). The male mask size was measured from digital pictures (digital camera Nikon D70 with Nikkor 50 mm lens) taken at standardized focal distance (20 cm) using ImageJ analysis software.

Reproductive performance

In all farmland and forest habitat where adult presence was recorded in 2008, 2009 and 2010, we searched for nests from mid-May to late July on a regular basis (i.e. every 2-5 days depending on the progress of the reproduction). During these surveys, the male and/or female feeding behaviour provided us with reliable indication of the nest location. Because adults are likely to abandon their brood if disturbed during incubation (Olsson 1995, Söderström 2001), nests were mostly visited during the nestling period (i.e. when feeding visits of both male and female were observed). Nestling age was estimated with a 1-day precision by means of visual comparisons with feather characteristics of age-known broods (Olsson 1995). The number of nestlings and their body condition were mostly measured at the age of 12 days (range: 11-15 days). Measurements included tarsus length and outermost primary wing length (digital callipers; precision: ± 0.01 mm), as well as body mass (laboratory balance; precision: ± 0.1 g). Since these measurements were strongly correlated, the first component of a principal component analysis (PCA) was used as a synthetic measure of nestling body condition (variance explained: 89%).

A double brood is considered as an exceptional event in the Red-backed shrike (Lefranc & Worfolk 1997) and this never occurred in our study. Predation by corvid robbing may, however, be considerable in this passerine species during the incubation or the nestling period, and is the main reason for breeding failure (Roos 2002). During our surveys in the sites every 2-5 days over the course of the breeding season, we recorded the interruption of feeding visits by both the male and female and we attributed this to a breeding failure related to predation or accidental loss due to harsh weather conditions. After a breeding failure, the same parents renested within the same territory site, thereby excluding within-season movements between territories (Betts et al. 2008).

We used the following measures of reproductive performance in first or replacement clutches ('clutch sequence': 1 or 2 respectively) for each breeding pair in each year: nest success (i.e. production of at least one fledgling), brood size (i.e. number of nestlings older than 12 days) and nestling body condition (i.e. combination of tarsus length, wing length and body mass). The use of a series of fitness-related parameters that incorporate several components of reproductive performance (i.e. offspring quantity and quality in first and replacement clutches) is well suited to evaluate habitat quality at the individual level (e.g. Pidgeon et al. 2006).

Weather conditions

Weather conditions may affect nestling body condition because of weather-related insect prey activity (e.g. Gebhardt-Henrich & Richner 1998). A possible general trend in weather conditions over the course of the breeding season may therefore confound the relationship between habitat preference and fitness consequences, as some estimates of preference in our study (arrival date) are related to breeding time. To control for this in our analyses, the following climatic variables were used to reflect regional weather conditions during a 5-day period before the nestling measurements: wind velocity (Bf), precipitation (mm), ambient temperature (°C) and solar radiation (Watt/m²). They were derived from 15-minutes resolution datasets (data sampled between 7h30 am and 7h00 pm) that are freely available from nearby weather stations in Luxembourg (Pfister et al. 2005). The stations Schimpach and Roodt are at 10 km and 21 km from the study areas 1 and 2, respectively.

Statistical analyses

We first examined how the structural characteristics of territories in different habitats (i.e. farmland versus forest) were linked to individual-level measures of habitat preference (arrival date and male

phenotype) and, second, whether there was a link between the habitat and the measures of reproductive performance (nest success, brood size and nestling body condition).

We used generalized linear mixed models (GLMMs, Maximum Likelihood estimations) to relate arrival date of males (N = 300), male wing length (N = 102), male mask size (N = 94), nest success (N = 438), brood size (N = 243) and nestling body condition (N = 1001) to the type of habitat (i.e. farmland versus forest) and some covariates. Sample sizes differed between different models due to missing values and because of the contrasting level of the response variable (male, nest or nestling). We used normal distribution models with identity link, except for the models of nest success where we used binomial distribution models with logit link. Apart from the models of nestling body condition, the breeding site identity was always defined as a random factor because 1) the same site can be occupied in several years, and 2) more than one breeding pair or individual male can occupy the same site. The number of shrike territories enclosed in the breeding sites varied from 1 to 6. In the models of nestling body condition, the nest identity was defined as a random factor because the measures on the nestlings from the same nest are not independent. In all models we included year, study area and their interaction with habitat as independent variables to investigate the consistency of the results over time and in space. Because the settlement of a male may be triggered by social information relative to the presence of other males in the neighbourhood (e.g. Fletcher 2006), we calculated, for each male in each year separately, the total number of males settled within a radius of 500 m and we included this territory aggregation factor ('aggregation') as an independent variable in the models of arrival dates. To reduce the influence of prior occupancy on settlement decisions, colour-ringed males showing site fidelity from year t-1 to year t (N = 8) were excluded from the analysis of arrival dates. The clutch sequence and its interaction with habitat were included in the models of nest success, brood size and nestling body condition to account for possible differences in reproductive performance between first and replacement clutches. In addition, we used nestling age and weather conditions as covariates in the models of nestling body condition to control for their possible effect on the nestling measurements. Complete brood failures due to predation or harsh weather conditions after the replacement clutch (N = 20) were excluded from the models of brood size and nestling body condition.

Model selection procedures were implemented to evaluate the strength of evidence for the relative influence of the different independent variables included in the models (Burnham & Anderson 2002, Bolker et al. 2009). Full models included the whole set of independent variables and covariates separately for arrival date of males, male wing length, male mask size, nest success, brood size and nestling body condition. All possible combinations of variables ('candidate models') were then

derived from the full models. Interactions were only incorporated in a candidate model when both main effects were also included. The covariates were forced in all candidate models.

Information-theoretic multimodel inference was used based on the Akaike's Information Criterion corrected for small sample sizes (AIC_c). ΔAIC_c were calculated for each candidate model to reflect the difference with the best candidate model (i.e., the model with the smallest AIC_c). A ΔAIC_c value < 2 (relative to the best model associated with the smallest AIC_c) was used as a threshold for a model to be considered as having support (Burnham & Anderson 2002). The relative support for the alternative models was obtained by scaling them according to their AIC_c weight (Burnham & Anderson 2002). The relative importance of a variable (w_+) was estimated by summing the AIC_c weights across all candidate models in which the variable occurred. Since the prevalence of the variables in the set of candidate models (v) varied from one variable to the other and because this prevalence restricts the w_+ values associated with the variables (Burnham & Anderson 2002), the v values are reported as a baseline reference along with the w_+ values. The model-averaged parameter estimates (β), the estimate precision (unconditional standard errors) and the w_+ values inform on the strength of importance of each variable (Burnham & Anderson 2002). In order to facilitate the interpretation, these estimates were converted into percentages relative to the average value of the response variables (Δ[difference between two levels of a variable]). All analyses were performed with R 2.13 and SAS 9.1 (MIXED procedure) software.

RESULTS

Table 4.1 summarizes the different sets of supported models ($\Delta AIC_c < 2$) related to habitat preference and reproductive performance derived from the model selection procedures.

Arrival date of males - There was strong support for the effect of year on male arrival date (Table 4.2, w_+ = 100%, Δ[2008-2009] = -20%, Δ[2008-2010] = -36%) and for overall differences in arrival date between habitats (w_+ = 100%, Δ[Farmland-Forest] = 17%). On average, males arrived more than 3 days earlier in forest compared to farmland habitat. A low AIC_c-based weight was found for the territory aggregation variable (w_+ = 31%): the settlement of males was earlier when other males were settled in the neighbourhood, but this influence was only weakly supported. Arrival dates of males were rather similar in both study areas (w_+ = 56%, Δ[1-2] = -3%). The weak support for the interactions (all $w_+ < 14\%$) indicates that the earlier arrival of males in forest habitat was consistent over time and space. Fig. 4.1 shows the cumulative number of males in farmland and forest habitats over the course of the breeding season. In each year, early-arriving males occupied forest habitat

more frequently than farmland habitat at the beginning of the breeding season and this pattern was gradually inverted during the progress of the season. As a consequence, the cumulative curves of male arrival (Fig. 4.1) were found to follow different distributions between both habitat types (Kolmogorov-Smirnov Two-Sample Tests, 2008: p = 0.03, D = 0.34; 2009: p = 0.02, D = 0.35; 2010: p = 0.02, D = 0.27).

Table 4.1 – Set of supported ($\Delta AIC_c < 2$) and best non-supported ($\Delta AIC_c > 2$, between brackets) models for habitat preference (arrival date, wing length and mask size of males) and reproductive performance (nest success, brood size and nestling body condition) measures along with their respective support (AIC_c weight).

Response	Supported and (best non-supported) models	K	Log Likelihood	ΔAIC_c	AIC_c weight
Arrival date of males	- Habitat + Year	6	-973.03	0.00	0.26
	- Habitat + Year + Study area	7	-971.99	0.03	0.25
	- Habitat + Year + Aggregation	7	-972.69	1.43	0.13
	- Habitat + Year + Study area + Aggregation	8	-971.80	1.76	0.11
	- (Habitat + Year + Study area + Habitat x Study area)	(8)	(-971.99)	(2.14)	(0.09)
Male wing length	- Habitat	4	-220.57	0.00	0.41
	- Habitat + Year	6	-219.13	1.59	0.19
	- Habitat + Study area	5	-220.31	1.69	0.18
	- (Habitat + Year + Study area)	(7)	(-218.93)	(3.51)	(0.07)
Male mask size	- Habitat + Year + Habitat x Year	9	-946.23	0.00	0.25
	- Habitat + Year	7	-948.63	0.06	0.24
	- Habitat + Year + Study area	8	-947.62	0.38	0.20
	Habitat + Year + Study area + Habitat x Year	10	-945.66	1.30	0.13
	- (Habitat + Year + Study area + Habitat x Study area)	(9)	(-947.61)	(2.77)	(0.06)
Nest success	- Habitat + Year + Study area + Clutch sequence + Habitat x Study area	8	-246.81	0.00	0.37
	- Habitat + Year + Study area + Clutch sequence	7	-248.57	1.45	0.18
	- Habitat + Year + Study area + Clutch sequence + Habitat x Study area + Habitat x Clutch sequence	9	-246.66	1.79	0.15
	- (Habitat + Year + Study area + Clutch sequence + Habitat x Clutch sequence)	(8)	(-248.57)	(2.92)	(0.09)
Brood size	- Habitat + Clutch sequence + Year + Habitat x Clutch sequence	8	-343.42	0.00	0.34
	- Habitat + Clutch sequence + Year	7	-345.09	1.23	0.19
	- Habitat + Clutch sequence + Year + Study area + Habitat x Clutch sequence	9	-343.30	1.90	0.13
	- (Habitat + Clutch sequence + Year + Study area)	(8)	(-345.05)	(3.26)	(0.07)
Nestling body condition	- Habitat + Clutch sequence	10	-1289.84	0.00	0.48
	- (Habitat)	(9)	(-1292.08)	(2.43)	(0.14)

ΔAIC_c refers to the differences in AIC_c between the model and the best candidate model associated with the smallest AIC_c. The number of parameters (K) is reported for each model.
Response variables: Arrival date of males = arrival dates of males in springtime, Male wing length = outermost primary wing length in males, Male mask size = size of black eye-stripes in males, Nest success = production of at least one fledgling, Brood size = number of nestlings older than 12 days, Nestling body condition = PCA-based combination of nestling tarsus length, wing length and body mass.
Fixed effects: Habitat = farmland versus forest habitat, Clutch sequence = first versus replacement clutches, Year = 2008, 2009 or 2010, Study area = 1 or 2, Aggregation = number of males settled within a radius of 500 metres.
Random effects: territory site identity (for arrival date, male wing length, nest success and brood size) or nest identity (for nestling body conditions).

Male wing length - On average, male wings were longer in forest habitat than in farmland habitat (Table 4.2, w_+ = 100%, Δ[Farmland-Forest] = -16%, Fig. 4.2A), and the influence of year and study area was not supported (all w_+ < 36%). Interestingly, there was also a slight trend for longer wing length in early arriving males (simple linear regression, p = 0.0002, $F_{1,87}$ = 15.4, R^2 = 0.14).

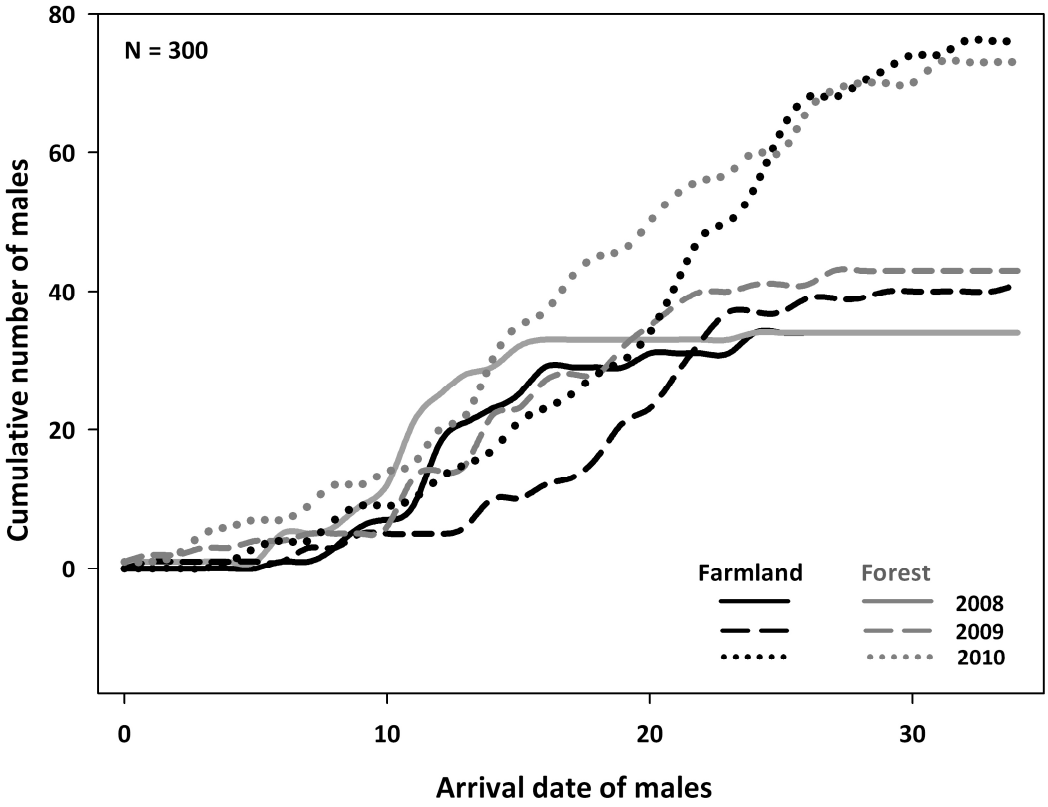


Figure 4.1 – Cumulative number of territories occupied by males along the breeding in farmland and forest sites. The date corresponding to the first arrival within each year is set to 0.

Male mask size - The size of black eye-stripes in males was larger in forest than in farmland habitat (Table 4.2, w_+ = 92%, Δ[Farmland-Forest] = -5%, Fig. 4.2B), although there was more among-year variation in this phenotypic trait (w_+ = 100%, (Δ[2008-2009] = -12% and Δ[2008-2010] = -18%). The larger male mask size in forest habitat was more important in 2009 ('Habitat x Year': w_+ = 41%, Δ[Farmland-Forest] = -12%), than in 2008 (Δ[Farmland-Forest] = -2%) and 2010 (Δ[Farmland-Forest] = -2%).

Table 4.2 – Results of the AIC_c-based multimodel inference procedure examining the variations in habitat preference relative to the independent variables.

	Arrival date of males					Male wing length				Male mask size			
Fixed effect	**v**	w_+	**B**	**S.E.**	**Effect**	w_+	**β**	**S.E.**	**Effect**	w_+	**β**	**S.E.**	**Effect**
(Intercept)	*100*	*100*	*13.89*	*1.12*		*100*	*94.63*	*0.42*		*100*	*43555*	*1532*	
Habitat (Forest)	69	100	-3.58	1.00	Settlement of males earlier in forest sites	100	1.47	0.48	Male wing length longer in forest sites	92	1819	1907	Male mask size is larger in forest sites
Year (2009)	62	100	4.40	1.06	Settlement of males earlier in 2008 and later in 2010	35	-0.14	0.22		100	4658	2165	Male mask size larger in 2010 and smaller in 2008
Year (2010)			6.31	1.00			-0.31	0.27			9429	1756	
Study area (2)	62	56	0.67	0.61		36	0.09	0.18		48	823	793	
Habitat x Year (Forest, 2009)	23	13	-0.07	0.27		7	0.09	0.11		41	2455	1920	Larger male mask size in forest is more pronounced in 2009
(Forest, 2010)			-0.16	0.28			0.05	0.08			441	1278	
Habitat x Study area (Forest, 2)	23	14	0.02	0.24		9	0.04	0.09		10	- 41	272	
Aggregation	50	31	-0.06	0.09		-	-	-		-	-	-	

The AIC_c-weighted relative importance (w_+), the model-averaged estimate (β) and their unconditional standard error (S.E.) are reported for each parameter (main effects and interactions), as well as their respective prevalence in the candidate models (v). The v and w_+ values range between 0 and 100%. The parameter estimates refer to the level indicated between brackets as a baseline. The interpretation of each effect is provided in case of AIC_c-based support.

Response variable: Arrival date of males (days) = arrival dates of males in springtime, Male wing length (mm) = outermost primary wing length in males, Male mask size (mm^2) = size of black eye-stripes in males.

Fixed effects: Habitat = farmland versus forest habitat, Year = 2008, 2009 or 2010 and Study area = 1 or 2, Aggregation = number of males settled within a radius of 500 metres.

Random effects: territory site identity.

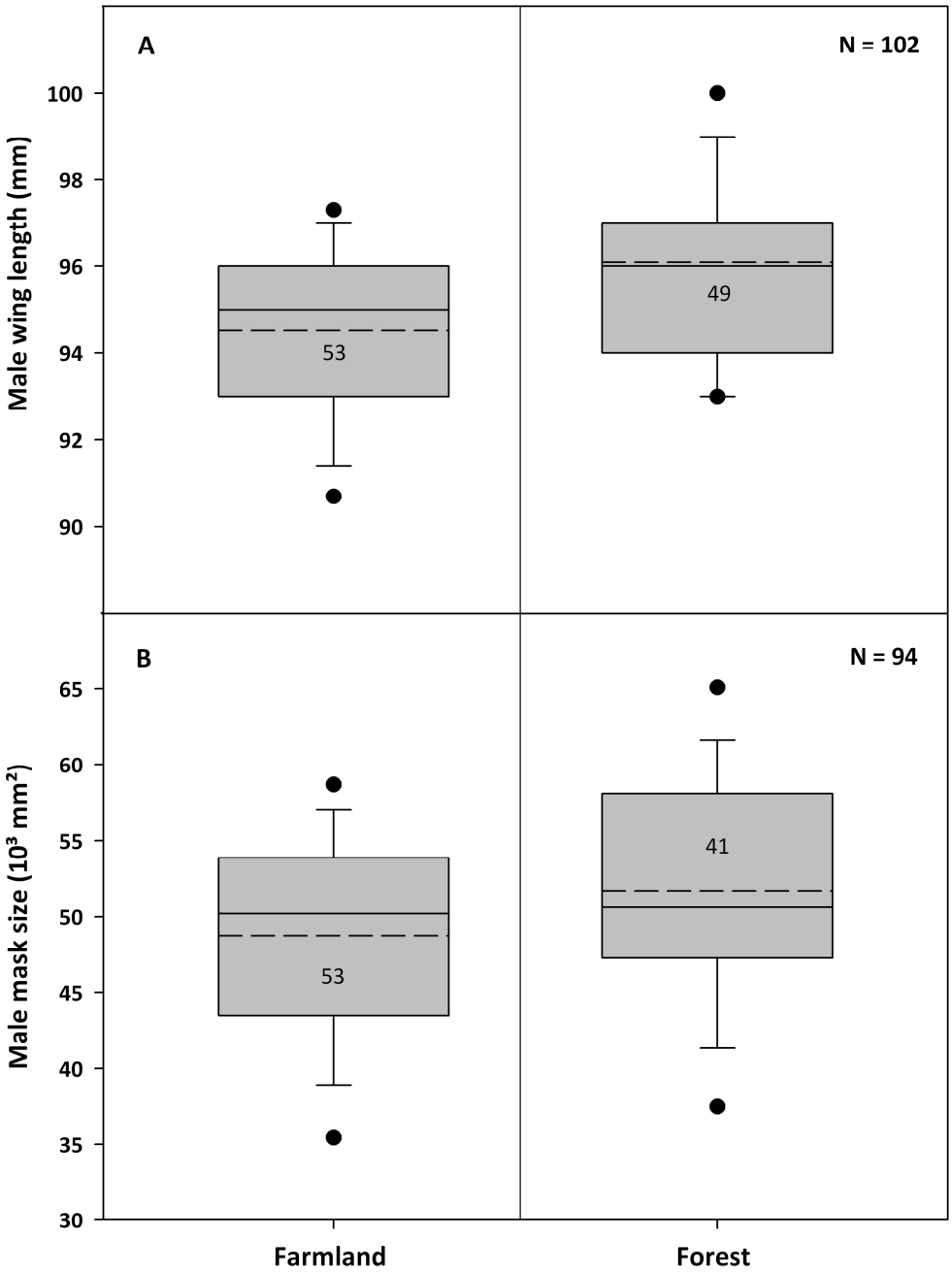


Figure 4.2 – Variation in phenotypic traits of males in farmland and forest sites. Box-and-whisker plots and quartile distributions (5^{th} and 95^{th} percentiles [⊥ and ┬], min-max [•], mean [--] and median [–]) for male wing length (A) and male mask size (B) in farmland and forest sites.

Reproductive performance

Nest success - The nest success of shrikes was markedly higher for a replacement clutch than for a first clutch (Table 4.3, w_+ = 100%, Δ[1-2] = -39%, Fig. 4.3A, B). On average, nest success was also higher in farmland than in forest habitat (w_+ = 97%, Δ[Farmland-Forest] = 8%, Fig. 4.3A, B) and this difference is more pronounced in first clutches (Δ[Farmland-Forest] = 14%) compared to replacement clutches (Δ[Farmland-Forest] = 1%) ('Habitat x Clutch sequence', w_+ = 30%, Fig. 4.3A, B). There is also support for a difference in nest success among years (w_+ = 95%, Δ[2008-2009] = -12%, Δ[2008-2010] = -9%) and study areas (w_+ = 95%, Δ[1-2] = -8%). Importantly, the higher nest success in farmland sites was consistent over time ('Habitat x Year', w_+ = 10%). The difference between farmland and forest habitats was more markedly pronounced in study area 2 compared to study area 1 ('Habitat x Study area', w_+ = 61%).

Brood size - The AIC_c-based model selection procedure provided strong evidence for an effect of clutch sequence on brood size (Table 4.1): an overall difference of almost one nestling per nest was found between first and replacement clutches (Δ[1-2] = 14%) (Table 4.3, w_+ = 100%, Fig. 4.3C, D). Clear evidence was also found for a difference in brood size between farmland and forest habitats, with on average half a nestling increase in nests located in farmland habitat (w_+ = 100%, Δ[Farmland-Forest] = 9%). Furthermore, there was an interaction between habitat type and clutch sequence (w_+ = 64%) suggesting that the difference in brood size is particularly marked in first clutches (Δ[Farmland-Forest] = 19%) and less pronounced in replacement clutches (Δ[Farmland-Forest] = 5%). There was some support for a year effect on brood size (w_+ = 97%, Δ[2008-2009] = -7%, Δ[2008-2010] = -12%), but the number of nestlings was similar is both study areas (w_+ = 34%). A higher brood size in farmland sites was consistently found over time and space ('Habitat x Year' and 'Habitat x Study area', all w_+ < 17%).

Nestling body condition - One single best model indicated strong support for a difference in nestling body condition between farmland and forest habitats and, to a lesser extent, for an effect of clutch sequence (Tables 4.1 and 4.3, Fig. 4.3E, F). Better nestling body condition was observed in farmland habitat (Table 4.3, w_+ = 100%, Δ[Farmland-Forest] = 6%) and for first clutches (w_+ = 74%, Δ[1-2] = 3%). The effects of habitat type and clutch sequence on nestling body condition were additive as there was no support for an interaction between both variables (w_+ = 10%). In addition, the influence of year and study area on nestling body condition was not supported.

Table 4.3 – Results of the AIC_c-based multimodel inference procedure examining the variations in reproductive performance relative to the independent variables.

	Nest success					Brood size				Nestling body condition			
Fixed effect	**v**	w_+	**β**	**S.E.**	**Effect**	w_+	**β**	**S.E.**	**Effect**	w_+	**β**	**S.E.**	**Effect**
(Intercept)	*100*	*100*	*-0.85*	*0.38*		*100*	*4.80*	*0.22*		*100*	*0.25*	*0.68*	
Habitat (Forest)	77	97	-0.32	0.37	Nest success higher in farmland sites	100	-0.55	0.24	Brood size higher in farmland sites	100	-0.41	0.09	Nestling body conditions higher in farmland sites
Clutch sequence (2)	63	100	2.11	0.34	Nest success higher in replacement clutches	100	-0.83	0.21	Brood size higher in first clutches	74	-0.19	0.09	Nestling body conditions higher in first clutches
Year (2009)	63	95	0.93	0.32	Nest success higher in 2009 and lower in 2008	97	0.36	0.21	Brood size higher in 2010 and lower in 2008	12	0.014	0.02	
Year (2010)			0.65	0.30			0.57	0.19			0.055	0.06	
Study area (2)	63	95	0.79	0.35	Nest success higher in study area 2	34	-0.01	0.05		20	0.027	0.03	
Habitat x Clutch sequence (Forest, 2)	26	30	0.11	0.18		64	0.30	0.20		10	0.003	0.02	
Habitat x Year (Forest, 2009)	26	10	0.01	0.07		17	-0.05	0.08		1	-0.003	0.004	
(Forest, 2010)			0.01	0.06			-0.002	0.06			-0.001	0.003	
Habitat x Study area (Forest, 2)	26	61	-0.50	0.33	Higher nest success in farmland is more pronounced in study area 2	9	-0.009	0.03		3	0.001	0.005	

The AIC_c-weighted relative importance (w_+), the model-averaged estimate (β) and their unconditional standard error (S.E.) are reported for each parameter (main effects and interactions), as well as their respective prevalence in the candidate models (v). The v and w_+ values range between 0 and 100%. The parameter estimates refer to the level indicated between brackets as a baseline. The interpretation of each effect is provided in case of AIC_c-based support.

Response variables: Nest success = production of at least one fledgling, Brood size = number of nestlings older than 12 days, Nestling body condition = PCA-based combination of nestling tarsus length, wing length and body mass.

Fixed effects: Habitat = farmland versus forest habitat, Clutch sequence = first versus replacement clutches, Year = 2008, 2009 or 2010, Study area = 1 or 2.

Random effects: territory site identity (for nest success and brood size) or nest identity (for nestling body condition).

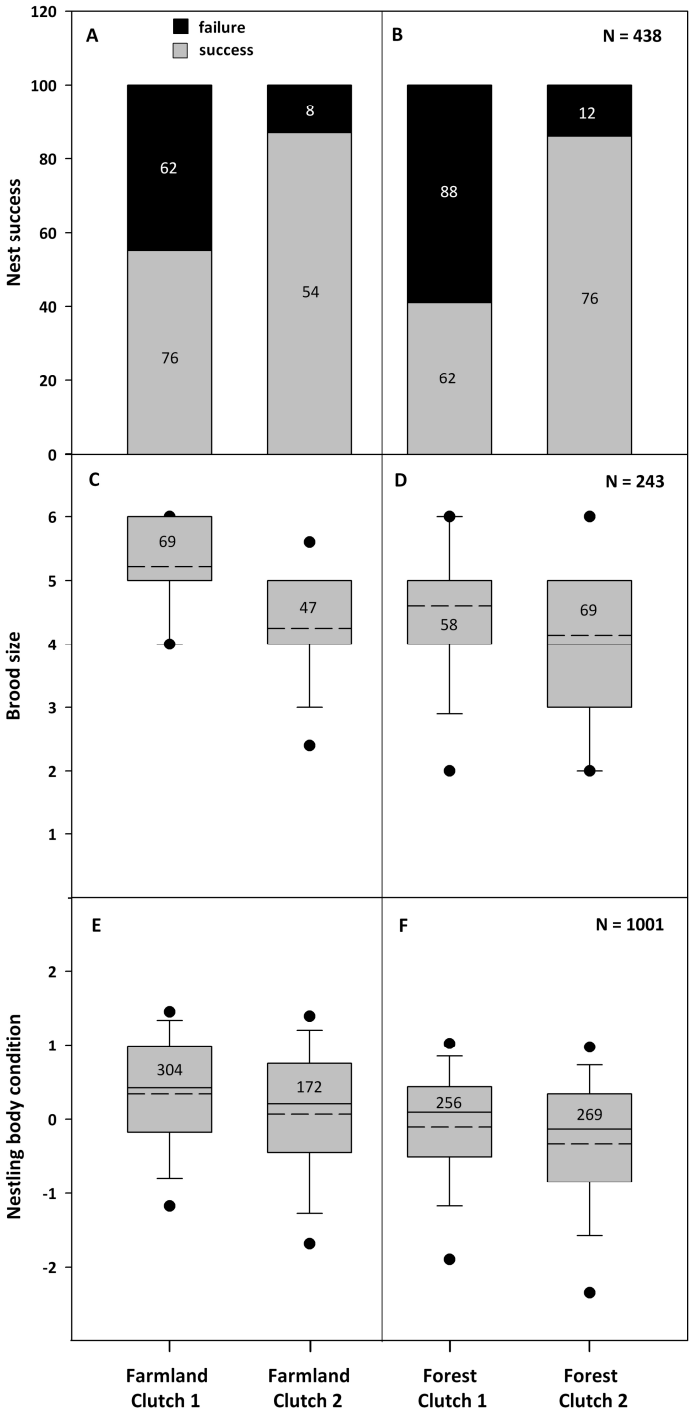


Figure 4.3 – Reproductive performance in farmland and forest sites. Proportion of breeding attempts associated with success (grey) and failure (black) in farmland (A) and forest (B) sites for the first (1) and replacement (2) clutches. Box-and-whisker plots and quartile distributions (5^{th} and 95^{th} percentiles [⊥ and ┬], min-max [•], mean [--] and median [–]) for brood size (C, D) and nestling body condition (E, F) in farmland and forest sites for the first and replacement clutches. The nestling body condition data used in the plots are the residuals resulting from a linear regression against nestling age and weather conditions to remove the effect of the covariates included in the analysis. The number of nests (for nest success and brood size) or nestlings (for nestling body condition) is indicated in the boxes.

DISCUSSION

Over recent decades, changes in forest harvesting techniques have created rotation systems of large, open areas in plantation forests (Lecomte et al. 2003, du Bus de Warnaffe & Deconchat 2008). Interestingly, some similar bird assemblages (and other wildlife populations; Paz Acuña & Estades 2011, Swanson et al. 2011) are found in farmland sites and in early-successional vegetation following the harvesting activities (Paquet et al. 2006). Using the Red-backed shrike as a model organism that occupies both habitat types in a mosaic of farmland and forest sites, we demonstrate a preference for Spruce plantations over farmland sites, even though reproductive performance was higher in farmland.

On average, territorial males occupied the forest sites before the farmland sites and males with longer wing length and, to a lesser extent, larger mask size were found more often in forest sites. As habitat-dependent order of settlement and distribution of phenotypes are considered as individual-level measures of habitat preference (Robertson & Hutto 2006), these results indicate a preference for the novel forest environment rather than for the traditionally used farmland. Early arrival has been shown to be beneficial for territory acquisition and reproductive performance in territorial, migratory birds (Smith & Moore 2005), but the costs for arriving early should be considerable (Kokko 1999) and the individuals with the best condition arrive earliest at the breeding sites (e.g. Becker et al. 2008, Choi et al. 2010). Such a cost-benefit issue is likely to explain the between-habitat differences in arrival date and phenotype distribution in the Red-backed shrike, but further research is clearly needed. It is also warranted to test whether early-arriving males show a higher motivation to defend their territorial resource in forest compared to males arriving later in farmland.

Unlike most studies (see Schmidt & Whelan 2010), reproductive performance was examined according to a hierarchical approach combining nest success, fecundity (brood size) and offspring quality (nestling body condition) in first and replacement clutches. First, the proportion of successful first clutches was considerably higher in farmland sites, whereas a higher amount of replacement clutches was recorded in forest sites. This is of great importance as replacement clutches produced, on average, one nestling less compared to first clutches. Replacement clutches are known to be costly in additional energy use, thereby explaining the reduced brood size (e.g. Antczak et al. 2009, Travers et al. 2010). Second, fecundity in first clutches was higher in farmland sites than in forest sites. Third, individual nestling body condition was better in farmland sites and this pattern was

consistent for first and replacement clutches. Hence, both offspring quantity and offspring quality were higher in farmland than in forest.

The observed mismatch between habitat preference and fitness-related parameters is in agreement with the Robertson & Hutto's definition of an ecological trap (Robertson & Hutto 2006): our results on the Red-backed shrike indicate the existence of maladaptive habitat selection in mixed farmland-forest landscape under intense human use where the species has recently colonised open areas in Spruce plantations. Importantly, this study shows that the behaviour of the shrike is maladaptive over several years and so demonstrates that the identified ecological trap does not simply represent transient and exceptional conditions. Ecological trapping has recently attracted much attention in anthropogenic environments, but few studies have provided empirical evidence so far (Robertson & Hutto 2006). We suggest here that the novel environment in a human-modified farmland-forest landscape may induce the preference for lower-quality habitats in the Red-backed shrike and possibly in other birds. However, important points need further study. First, reproductive performance is only one component of fitness and estimation of survival rates is important for a complete capture of habitat quality (e.g. Pidgeon et al. 2006). Second, population growth rates need to be evaluated separately for farmland and forest before we can argue that forest sites constitute an attractive sink. Third, the behavioural processes operating during habitat selection and the cues used by individuals to select their breeding habitat remain unknown.

Use of reproductive performance to estimate habitat quality may receive criticism because there could be a possible trade-off between reproduction and survival (e.g. Scheirs et al. 2000). Arlt and colleagues (2008) have recently shown that the Northern Wheatear (*Oenanthe oenanthe*) occupies structurally different habitat types in central Sweden and, although habitats differ with respect to reproductive performance, differences in habitat-specific population growth are largely due to differences in adult and first-year survival rates. Although nestling body condition correlates strongly with first-year survival rates in passerine species (Lindén et al. 1992, Naef-Daenzer et al. 2001), this reproductive performance measure was not considered in the extensive work of Arlt and colleagues. With our hierarchical examination of reproductive performance nestling body conditions in shrikes were found to be higher in farmland and so, we can reasonably assume that poorer reproductive performance in forest sites may not be compensated for by higher first-year survival rates. We acknowledge, however, that a more complete estimation of fitness based on long-term reproduction and survival data (also on adults, see Sillett & Holmes 2002) is needed to determine local recruitment, lifetime reproductive performance and population growth rates. Such a complete estimate of individual fitness would better determine whether shrikes exhibit a preference for habitats associated with negative consequences for population dynamics or prefer the lower-quality

of two source habitats. So far, population declines induced by individual, maladaptive habitat choices have been validated only on a theoretical basis (Delibes et al. 2001, Kokko & Sutherland 2001, Kristan 2003, Fletcher et al. 2012), and empirical evidence is lacking. Arlt and colleagues showed that wheatears in Sweden display non-ideal habitat selection because individuals fail to discriminate between source and sink habitats, but their results were not in agreement with an ecological trapping situation where lower-quality habitats are preferred over higher-quality ones (Arlt et al. 2008, Arlt & Pärt 2007). An estimation of survival rates based on long-term data is clearly lacking in our study system to support the existence of an attractive sink, even if we demonstrated a mismatch between habitat preference and some important fitness components.

A possible explanation for the observed decision-making pattern in the Red-backed shrike is that early-successional vegetation in Spruce plantations shares some features with the open areas created by natural disturbance regimes in forest (e.g. Hansson 1994, Brawn et al. 2001, Svenning 2002, Robertson & Hutto 2007) and shrikes (and other bird species) probably used these features in the past to guide their settlement decisions (i.e. genetically inherited cues; see Jaenike & Holt 1991, Kokko & Sutherland 2001). Although they can imitate ancestrally used habitats, current forest management practices may also influence important resources and conditions in such a way that habitat quality for the species is much lower in artificial early-successional regeneration areas than in the naturally disturbed areas. In particular, reforestation (i.e. tree planting) or post-disturbance logging may shorten the duration of the system, influence microclimate conditions, modify vegetation structure or eliminate some biological legacies such as woody debris or other organically derived structures (Swanson et al. 2011). Weldon and Haddad (2005) showed, for instance, that a disturbance-dependent bird species, the Indigo Bunting (*Passerina cyanea*), is attracted by habitat edges associated with increased predation pressure, which results in decreased fitness along edgy environments. The authors suggested that, even though current forest management might create vegetation structures that share some similarities from the bunting's perspective with the historically used habitats, this attraction is detrimental in terms of fitness. Similarly, nest failures for the shrikes were more prevalent in the habitat associated with a higher preference. As the vegetation surrounding the farmland and forest sites is structurally different, with a higher amount of forest edges close to the forest sites, this may induce a contrasting level of on-nest predation pressure (Chalfoun et al. 2002). Alternatively but not exclusively, nests are located in different vegetation structures in farmland sites (i.e. thorny shrubs) compared to forest sites (i.e. young trees of Spruce or Black Elder), which may be significant for differences in nest concealment and anti-predation sheltering.

Other candidate habitat selection cues in the case of the Red-backed shrike may relate to food availability. Hromada and colleagues (2008) have recently shown that larders (i.e. storing of prey items) of the Great-grey shrike (*Lanius excubitor*) are used as cues by males of Red-backed shrike to evaluate habitat quality and to rapidly trigger the territory establishment after migration arrival in springtime. Future work in our study system should, therefore, also analyse potential differences in the availability, use and nutritional quality of food resources between the habitat types during the whole breeding season. This may contribute to the proximate factors explaining the differences in habitat preference and reproductive performance between farmland and forest sites.

In summary, this study on a long-distance migrant and territorial bird in a mosaic of farmland and forest habitats indicates that the newly colonised forest environment may be a less favourable habitat in contrast to what has been assumed previously based on presence/absence and abundance data only (Paquet et al. 2006, Paz Acuña & Estades 2011). A compound estimate of fitness based on long-term reproduction and survival data is, however, needed if we are to evaluate the significance of maladaptive individual decisions for the population dynamics in the landscape. Our study illustrates the need for a proximate understanding of the processes of habitat selection in farmland bird species that expand their breeding sites to other human-created habitats like early-successional vegetation following harvesting activities in Spruce plantations. It more generally demonstrates the significance of integrating knowledge on landscape-level behavioural processes with conservation and landscape management in dynamic environments under intense human use (e.g. Jose & Gordon 2008).

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Chapter 5

Territorial resource valuation deviates from habitat quality in an ecologically-trapped, long-distance migratory bird

Individual-based habitat preference is a crucial component for testing the existence of an ecological trap. In this chapter, we will use the resource-valuation theory in animal contests to test whether arrival dates are functional proxies of habitat preference in the Red-backed shrike.

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* text in the thesis has marginally been modified compared to the published version

ABSTRACT

Preference measures are widely used in habitat selection studies to test an animal's choice relative to particular habitat features, but most measures are subject to criticism as they fail to indicate the underlying behavioural motivation. Order of settlement on breeding grounds has been proposed as an effective measure in migratory organisms, as it conceptually approaches a choice experiment. We tested the assumption that early Red-backed shrikes (*Lanius collurio*) are more willing to defend their territorial resource than individuals arriving later. We earlier showed that shrikes arriving first settled in forest plantations that resulted in lower reproductive performance compared to territories on farmland, suggesting an ecological trap. Therefore, individuals are expected to valuate to a higher degree the lower-quality sites in forests. Within the context of resource-valuation theory in animal contests, we used a simulated territorial intrusion experiment to measure territorial defense to assess the perceived value of the territory during the settlement phase in both habitat types. Males arriving early were much more motivated to defend their territory than late birds. After correction for the disparity in the timing of arrival between habitat types, shrikes also more vigorously defended their territories in the forest habitat associated with the lowest reproductive returns. Although the precise mechanisms for the resource-valuation during habitat selection remain unclear, our results show that early and late arriving individuals strongly differ in behavioural motivation to hold their territorial resources. This study also demonstrates for the first time that organisms may exhibit a higher degree of territorial aggressiveness in a lower-quality habitat.

INTRODUCTION

In human-modified landscapes, organisms may preferentially settle in low-quality habitats although higher-quality habitats are available, a concept known as ecological trapping (reviewed in Schlaepfer et al. 2002, Battin 2004, Robertson & Hutto 2006). In contrast with the ideal free distribution or source-sink theory, the concept of ecological trapping considers habitat preference and habitat quality separately. Habitat preference is, however, not always easy to test under field conditions, and so far most studies have relied on assumed habitat preference measures (Robertson & Hutto 2006). A frequently used surrogate of habitat preference is population density, but its use can be problematic for several reasons (Van Horne 1983, Skagen & Yackel Adams 2010). Dominant individuals may, for example, pre-empt high-quality habitats, forcing subdominant individuals to aggregate at higher densities in lower-quality habitats (Holmes et al. 1996). Other habitat preference measures more closely connected to habitat selection include, for example, settlement chronology and distribution of high-quality individuals among habitats that differ in quality (Robertson & Hutto 2006). However, such measures lack a behavioural underpinning and fail to reflect the underlying processes that relate to individual motivation. The best evidence would, therefore, come from field experiments that show differences in the individual, motivation-related behaviour of the studied animals relative to the observed pattern of assumed habitat preference in the field.

Migratory birds are interesting study organisms to address the issue of habitat selection because the arrival sequence and settlement on the breeding sites in this group of birds offers the possibility to sample habitat preference at the individual level in the field (Robertson & Hutto 2006, Dingle & Drake 2007). Conceptually, it approaches a choice experiment: the individuals are confronted with local or regional habitat heterogeneity with those arriving earlier assumed to select higher-quality habitats (e.g. Smith & Moore 2005, Becker et al. 2008). Based on this assumption, we have shown in Chapter 4 evidence for maladaptive habitat selection in line with ecological trapping in the Red-backed shrike (*Lanius collurio*) in agroforestry landscapes in NW Europe (Hollander et al. 2011). In such a landscape, this territorial migratory passerine may either breed on farmland sites (with hedgerows and bushes) or on clear-cuts in spruce plantations. Early arriving males prefer to settle in the clear-cut forest sites, but reproductive performance is lower than in the farmland sites occupied by later arriving individuals (Hollander et al. 2011).

This provides the opportunity to test whether the preferred territorial resources (i.e. breeding sites selected earlier in forest plantations) where reproductive performance is lower (i.e., low-quality habitat) are more vigorously defended by the shrikes than the less preferred territories (i.e. breeding

sites selected later in farmland) where reproductive performance is higher (i.e., high-quality habitat). Here, we report on a field experiment conducted during the territory settlement phase of *L. collurio* that allows testing if territorial resource valuation differed between lower- and higher-quality habitats in early and late arriving males. We evaluated the extent of territorial defense in male shrikes through a simulated territorial intrusion experiment. In agreement with the theory on animal contests, the variation in territorial defense was assumed to indicate the perceived value of the territorial resources (e.g. Fort & Otter 2004, Camfield 2006, Arnott & Elwood 2008) as the cost and energy invested in confrontation should be proportional to the perception individuals have of the defended resource (reviewed by Arnott & Elwood 2008). In the case of an ecological trap, we therefore expect individuals to valuate higher and to defend more intensively the lower-quality breeding territories associated with higher preference in the forest habitat. Because early arrival on the breeding sites is energy demanding (Kokko 1999), we also expect that early arrival will be associated with a high motivation to hold and defend a territory. In turn, this should be translated into an increased motivation to fight during a territorial contest and we corrected for this important issue in the analyses. This study provides a novel, direct behavioural test of the link between habitat preference, habitat quality and territorial defense in a migratory organism faced with habitat heterogeneity in human-modified landscapes.

MATERIALS & METHODS

Study species and study area

The Red-backed shrike (*Lanius collurio*) is a territorial migratory passerine bird visiting European breeding sites from the end of April to mid-August. Males arrive on average 2 days before females to select a breeding territory (Schaub et al. 2011). Once settled, males attract females by repetitive advertising calls on shrubs or other perches and by typical fluttering flights. Males are highly territorial and readily chase male conspecifics out of the territory by directed attack bouts. Male-male conflicts occur by physical attacks and not by song contests or plumage-specific status signaling (Lefranc & Worfolk 1997).

In NW Europe, *L. collurio* typically occurs in farmland with meadows, pastures, hedgerows and shrubs (Titeux et al. 2007). Recent changes in forest harvesting techniques include large-sized cutblocks in even-aged spruce forest plantations (du Bus de Warnaffe & Deconchat 2008) and produce patches of early-successional vegetation. This man-made habitat type is now also occupied by *L. collurio* populations (Hollander et al. 2011, Söderström & Karlsson 2011) and other wildlife (e.g. Paquet et al.

2006, Paz Acuña & Estades 2011). The study area is located in southern Belgium where farmland and open areas in forest plantations create mosaics of two different types of habitats that are occupied by *L. collurio*.

Arrival date in different habitat types

All potential sites for the establishment of shrike territories in farmland and forest were identified during the period 2007-2009 (Hollander et al. 2011, Chapter 4) based on the presence of the main habitat requirements for the species (e.g. nest sites and foraging areas, see Titeux et al. 2007). From the end of April to the end of May 2010, all potential territory sites were visited every two days (15 min survey of each site) to document the chronology of male settlement. The same proportion of sites in farmland and in forest was visited each day. The order that sites were visited was randomized to avoid any temporal bias in shrike detection. As assumed in other long-term studies on arrival dates of *L. collurio* (Schaub et al. 2011), we considered the date of first detection on a site as a reliable estimate of the arrival date. In addition, we included in this study only the males showing a strong territorial behaviour (i.e. female-attractive advertising calls and singing). After the first detection of a male on a territory site, the site was visited on a daily basis to confirm the territorial ownership and the date of pair formation. Once a territory has been selected, shrikes barely switch to other territories (Jakober & Stauber 1983) or disperse to other locations (Tøttrup et al. 2011), therefore, we can be confident that the individuals observed upon arrival were indeed the same individuals that were tested some time later.

Experimental setup

The territorial defense behaviour of 35 males was tested in May 2010 by means of a simulated territorial intrusion experiment measuring their motivation to defend the territory against an intruder. This was done between 2 to 4 days after pair formation. In this nest-building period, courtship behaviour is the most intense and, consequently, males are highly aggressive in mate guarding (Jakober & Stauber 1994). Males were observed when foraging and displaying during 30 min and at a distance of 200 m in order to determine the territorial boundaries and the frequently used vantage points. Then, we used a mounted Red-backed shrike model that was introduced on an artificial perch (height: 2 m) in the centre of each territory (farmland: N=20; forest: N=15) and within ca. 3 m of a vantage point used by the males for territory defense. This simulated territorial intrusion triggered flight attacks of the males, allowing the number of attacks to the model to be recorded from a distance (50 m) with binoculars. The number of attacks within a short time-span has been

previously shown to reflect an accurate measure of fight intensity in birds during simulated territorial intrusion experiments (Duckworth 2006, Hof & Hazlett 2010). We sampled the number of attacks within 3 min after the first attack as a measure of fight intensity. One attack bout was defined as a close flight of the male from a perch to the shrike model followed by a return flight to a perch, even when this occurred without any physical contact between the male and the mount.

We used one shrike model since it has been shown that inter-individual variation among mounted specimens may result in different responses (Scriba & Goymann 2008). However, particular features (e.g. dominance-related traits) of the unique shrike model may cause differences in fight intensity between habitat types or between early and late arriving males (see Mays & Hopper 2004, Petrusková et al. 2007 for a discussion). As an alternative to the use of several shrike models in both habitat types and over the course of the experiment, we also provided an acoustic signal by playing-back a random suite of Red-backed shrike songs at the same sound level during each simulated intrusion. Although forest and farmland habitats consist of a different vegetation structure, it is unlikely that this altered the acoustic nature of the soundtracks as we always placed the loudspeakers in a similar fashion (i.e. on the ground below the shrike model in open areas and at a distance of at least 30 m from any mature forest stand). As bird song is known to vary among individuals and to reflect differences in male quality or condition (e.g. de Kort et al. 2009), a combination of several songs from a variety of sources is likely to alleviate the perceived signals of the physical state and social status of the shrike model. In this way, we measured a generalized response to the shrike model, and hence not different responses based on variation in phenotypic traits or artificial stimuli. These sounds were compiled from several commercially available digital song recordings of *L. collurio*. All experiments were conducted in the morning between 8 and 11 am by the same investigator (F.A.H.) and each male was tested only once.

Body size and age of males

Fight intensity and ability in birds may depend on the difference in body size or experience (i.e. age) between the contestants (Hyman et al. 2004, Logue et al. 2011). In the Red-backed shrike, male wing length has been shown to indicate body size and age (Jakober & Stauber 2000), and this trait was therefore used to control for the influence of age and size on the variation in fight intensity. All males were therefore trapped after the experiment using spring traps with mealworms (*Tenebrio molitor*) as lures. The spring traps consisted of a small 25x25 cm double polyamide net kept open with a trigger, and which closed and trapped the bird once the trigger with the mealworm was removed. Each male was individually marked with a unique color-ring combination, and the outermost primary

right wing length was measured (precision: ± 0.1 mm). Males were trapped after the experiments, and not before, as to minimize trapping and handling-related disturbance of the behaviour of the tested males.

Weather conditions

Food resource supply is important for mate acquisition in shrikes because males offer prey items to the females as an indication of male and local habitat quality during the pre-laying courtship-feeding period (Tryjanowski & Hromada 2005). Weather conditions may, therefore, affect the territorial behaviour of shrikes due to weather-related insect prey activity during this period. For this reason, we conducted the simulated intrusion experiments under the following weather conditions: wind force lower than 10 km h^{-1}, cloud cover lower than 70% and temperature higher than 18°C.

Statistical analyses

We used general linear mixed models (identity link function, Kenward-Roger adjustments of the degrees of freedom) (Kenward & Roger 1997) to test how fight intensity (number of attacks) depended on the habitat type (forest or farmland), the arrival date of the male, and the interaction between both factors. For the arrival date, we calculated the residual variation within habitat types to create independence between both factors. Hence, we removed the effect of among-habitat variation in the settlement chronology and we related fight intensity to a habitat-independent arrival date measure. This standardisation did not enforce differences in fight instensity between habitat types, as the same model but with non-standardised arrival dates gave similar results (details not shown). We also added the difference in male wing length between the territorial male and the mounted specimen as a covariate to control for the difference in RHP (resource holding potential, i.e. the physical or physiological state of the contestants) between the contestants. Song combination was set as a random factor to account for the dependence of males exposed to similar tracks. We always checked for normality of the response variable and of the residuals.

RESULTS

The mean arrival date of the tested males was May 11 (range: April 28 – May 23), and arrival was on average 2.4 ± 1.5 days earlier in forest compared to farmland sites (Table 5.1).

Pairs were formed on average 2.6 ± 0.9 days after the arrival of the male and 2.1 ± 1.1 days earlier in forests (Table 5.1). There was a strong link between the arrival date of males and the date of pair formation (GLM: $F_{1,31}$ = 33.5, β = 1.01 ± 0.03, P < 0.0001, Fig. 5.1) and the time span between arrival and pair formation was similar in both habitats ('Arrival date x Habitat': $F_{1,31}$ = 0.5, β = -0.02 ± 0.04, P = 0.60, Fig. 5.1). Once the model shrike was placed in a territory, the males responded fast (on average 1.5 min) by attack flights. Males attacked the shrike model but never the loudspeakers, suggesting that the mounted specimen was correctly perceived as the intruder. Males never responded by singing or displaying their plumage features, but always by aggressive attacks. During the tests, all shrikes spent 100% of their time budget on reacting towards the mount, and not by preening or scoping the sky for predators, suggesting that the allocated energy was dedicated to territory defense. All tested shrikes responded with attack bouts, with the number of attacks within 3 min after the first attack ranging from 6 to 45. There was a strong effect of habitat type on the fight intensity ($F_{1,28.2}$ = 16.9, β = - 3.16 ± 0.77, with roughly 20% more attacks in forest compared to farmland, P = 0.0003, Fig. 5.2) and a strong support for the negative relationship between the arrival date of males and the fight intensity ($F_{1,29.0}$ = 89.6, β = -1.11 ± 0.11, P < 0.0001, Fig. 5.2). There was no evidence of a link between fight intensity and wing length ($F_{1,24.3}$ = 0.003, β = -0.02 ± 0.40, P = 0.96) or of an interaction effect between arrival date and habitat type ($F_{1,26.3}$ = 0.25, β = 0.06 ± 0.13, P = 0.62).

Table 5.1 – Descriptive data documenting the timing of male arrival, pair formation and field experiment, and the results of the behavioural tests, relative to the habitat type (farmland vs forests).

	Farmland	Forest
Mean arrival date	May 14, 2010	May 12, 2010
Mean pair formation date	May 16, 2010	May 14, 2010
Mean date of behavioural tests	May 18, 2010	May 17, 2010
Number of attacks (± S.D.)	19.5 ± 8.0	26.2 ± 9.2

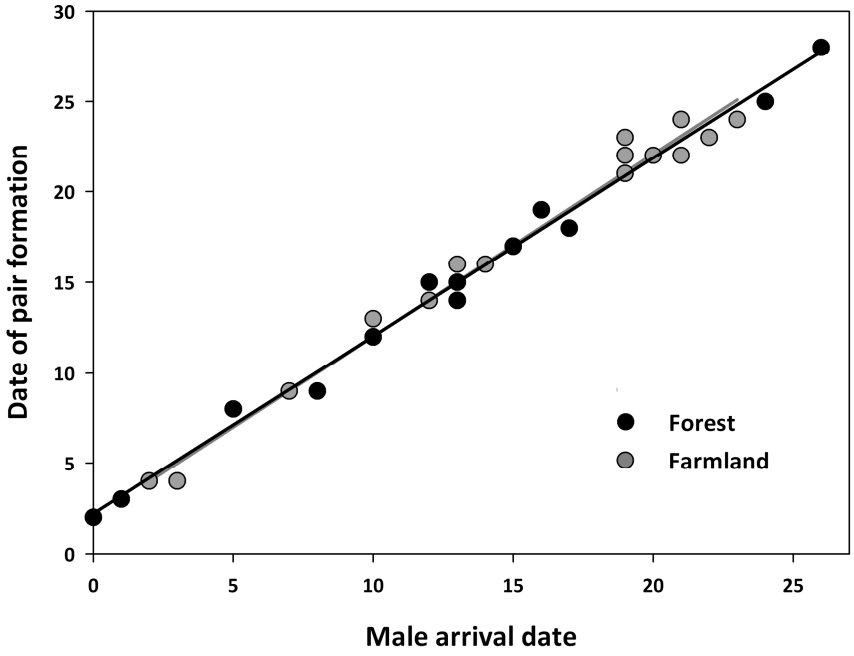


Figure 5.1 – Relationship between male arrival date and date of pair formation in forest and farmland sites. The zero value indicates the date of the earliest arriving male, i.e. April 30, 2010.

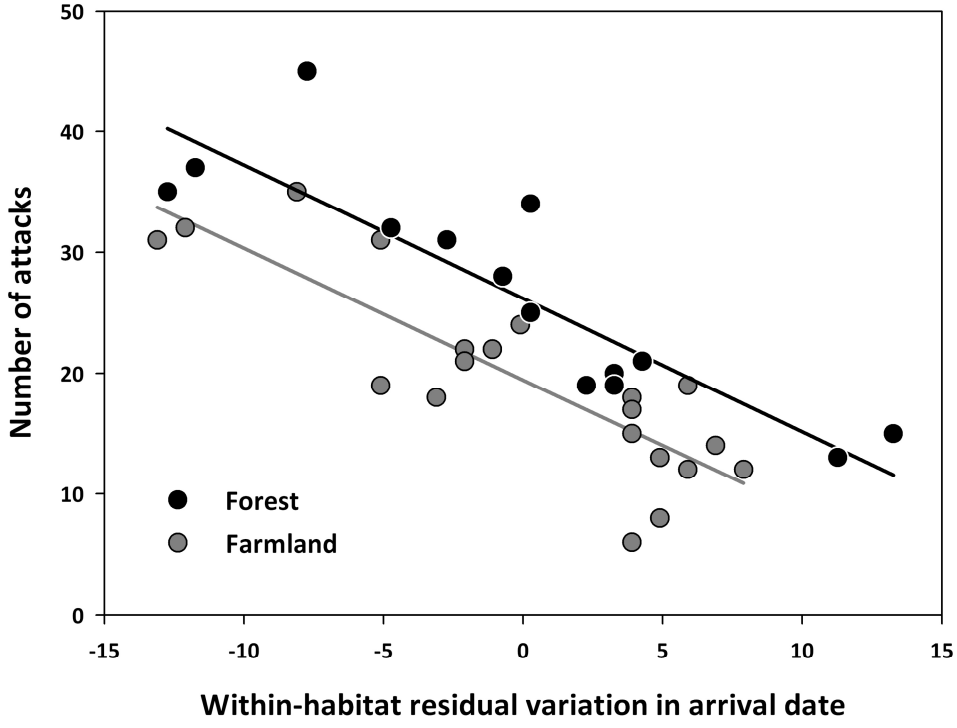


Figure 5.2 – Relationship between the habitat-independent order of settlement of males (= within-habitat residual variation of arrival dates in days) and their fight intensity (= number of attacks within 3 min after the first attack) in forest and farmland sites. The zero value along the residual variation in arrival date of males indicates the mean arrival date within each habitat type, separately.

DISCUSSION

The motivation to defend a territorial resource during territory settlement in males of the Red-backed shrike depends on the habitat type, with males showing a higher motivation to defend territories in plantation forests than in farmland. Moreover, we found evidence for a strong link with arrival date after spring migration and the overall decrease in fight intensity over the course of the settlement phase was similar in each habitat type, even though the settlement of males was, on average, earlier in forest than in farmland sites (Hollander et al. 2011, Chapter 4). Since the arrival date and habitat type were independent of each other in the analysis, the results suggest first, that territories in forest plantations where reproductive performance is lower are defended more intensively by the shrikes than territories in farmland, and second, that the motivation to defend a selected territory is stronger in early arriving males than in those arriving later. Hence, the effects of arrival date and habitat type on fight intensity were found to be additive: higher aggressiveness in forest habitat was, therefore, not confounded by males arriving earlier in this habitat compared to farmland.

In a context of territorial conflict, fight intensity may depend upon 1) the time span between territory acquisition and the territorial contest (i.e. prior ownership), 2) the physical or physiological state of the contestants (i.e. resource holding potential or RHP), and/or 3) the intrinsic value of the territory or elements therein which are perceived as resources (i.e. resource valuation) (Arnott & Elwood 2008), and this territorial quality might be higher for early than for late occupants (Verhulst & Nilsson 2008). Related to this, early arrival might increase the chance to find a high-quality mate and/or increase reproductive performance (Kokko 1999). In the following, we discuss the relevance of such factors on the variation in fight intensity in our simulated territorial intrusion experiment.

Interestingly, we controlled for the impact of prior territorial ownership on fight intensity (e.g. Kokko et al. 2006, Kvingedal & Einum 2011), because all males were tested at a comparable stage of their breeding cycle (i.e. pre-laying courtship period before the egg-laying stage), but at different times over the course of the season depending on their arrival and pair formation date. With this experimental setup, we can be sure, unlike previous studies in migratory birds (e.g. Cristol 1995, Dale & Slagsvold 1995, Snell-Rood & Cristol 2005), that variation in fight intensity is not related to the amount of time since the males acquired the territory.

With regards to the resource holding potential of the males, it is likely that date-dependent variation in fight intensity was related to particular traits underlying fighting ability (Kelly 2008), and that are

also important for the migration performance (Marra et al. 1998, Kokko 1999, Smith & Moore 2005). As in other studies on migratory birds (Cristol 1995, Dale & Slagsvold 1995, Snell-Rood & Cristol 2005, Duckworth 2006), however, we failed to show a link between fight intensity and physical features of the contestants such as body size and age. Alternative traits to consider may be differences in physiological or internal state between contestants (Arnott & Elwood 2008). According to the "Challenge Hypothesis", males are able to increase testosterone levels relative to the territorial challenge to facilitate aggressive behaviour during the breeding season (Wingfield et al. 1990). For instance, Lobato et al. (2010) recently found that early-arriving male Pied flycatchers (*Ficedula hypoleuca*) displayed stronger territoriality and had higher corticosterone metabolite levels compared to late arriving males. However, the aggressive behaviour of males is not always associated with high testosterone levels, and the reasons for this are still under debate (reviewed by Goymann 2009). Studies on behavioural syndromes have recently shown that territorial aggressiveness may be related to personality traits that are independent of body condition (Amy et al. 2010). We have ignored other possible RHP-related traits that may help explain variation in arrival date and subsequent fight intensity. Despite this lack of mechanistic understanding, our results showed that early arriving male shrikes exhibit a higher motivation to chase an intruder away in order to maintain territorial ownership.

Female quality may be a factor that confuses the link between fight intensity, habitat type and arrival date, in the case where high-quality females settle preferentially in forest or arrive earlier than lower-quality females. If female quality regulates fight intensity in males, this may have induced an apparent habitat-dependent or time-dependent territorial defense intensity in males that is possibly independent of habitat quality or arrival date *per se*. However, Müller et al. (2005) showed that reproductive performance in *L. collurio* is mostly affected by environmental conditions (e.g. vegetation structure, nest predation pressure) and is not related to female quality. Hence, we can reasonably assume that variation in female quality should not be the most important factor governing the motivation of a male in a contest. Alternatively, we suggest that the level of fight intensity in males relates to the perceived value of the territory sites and the motivation to monopolize this resource, and we showed that this valuation is higher in the preferred habitat type. This result strongly converges with lab-controlled experiments indicating that a preferred habitat can trigger a higher level of territorial defense (Johnsson et al. 2000).

We conducted the behavioural experiment in the particular case of an ecological trap and showed that the shrikes were more aggressive in the preferred, albeit lower-quality forest habitat as compared to the higher-quality farmland habitat. With respect to the resource-value theory in animal contests (Arnott & Elwood 2008), this suggests that during habitat selection, individuals

valuate plantation forests to a higher degree, thereby misleading them to select habitats with lower reproductive returns. Migratory organisms are often time-constrained in the selection of the breeding sites and are forced to rely on indirect cues (e.g. vegetation structure and phenology, food availability and anti-predation shelters) to determine local habitat quality (e.g. Marshall & Cooper 2004, Thomson et al. 2006, Hromada et al. 2008). A possible explanation for the observed maladaptive habitat selection in *L. collurio* are the shared features that early-successional vegetation in spruce plantations has with the open areas created by natural forest disturbance regimes (Brawn et al. 2001, Svenning 2002). In the past, shrikes may have relied on these features to guide settlement decisions (i.e. genetically inherited cues, see Kokko & Sutherland 2001). It has been suggested that shrikes lived in open areas in forests created by natural disturbances (e.g. windfalls or wildfires) and have since shifted to farmland following the Neolithic period (Lefranc & Worfolk 1997). Although they can imitate ancestrally used habitats, modern forest management practices may also influence important resources and conditions in such a way that habitat quality for the species is lower in artificial early-successional regeneration areas than in the naturally disturbed areas (Hollander et al. 2011, Chapter 4). As a result, there is still a relationship between early settlement and the perceived value of the habitat, as measured by fight intensity in our experiment, but no longer a link with high fitness returns. Although it remains unclear which ultimate factors cause lower reproductive performance in preferred habitat, it is more likely these are to be found in the between-habitat variation of environmental conditions than in that of its occupants. Hollander et al. (2011) showed that higher-quality phenotypes are found in preferred habitat but have lower reproductive performance (Chapter 4). Future work in our study system should, therefore, analyse potential differences in the availability of important resources for the reproduction of shrikes in both farmland and forest sites. It is also warranted to analyze the proximate mechanisms that may explain the observed pattern of maladaptive habitat selection.

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ETHICAL STANDARDS

Permission for the use of the mounted specimen was granted by the Walloon Region, Service Public de Wallonie (DNF/DGARNE). The Royal Institute for Natural Sciences of Belgium (IRScNB-KBIN) provided us with a national license for *Lanius collurio* trapping.

Chapter 6

When predation rate deviates from predator abundance: the role of nest predation in causing an ecological trap in a bird of conservation concern

In Chapter 4, we showed that the Red-backed shrike prefers to breed in a habitat supporting a higher amount of brood failures compared to the alternative habitat type. In this chapter, we explored the cause and mechanism leading to lower nest success in preferred habitat.

Unpublished manuscript, to be submitted

ABSTRACT

In human-modified environments, there is accumulating evidence of the occurrence of ecological trapping induced by a higher preference for low-quality habitat. Causal mechanisms for fitness loss in preferred habitat remain poorly explored, but it is often suggested that preferred habitats host a higher abundance of predators. Although this idea remains largely untested, this issue is of concern for the conservation of several organisms breeding in human-modified environments. We recently showed evidence of ecological trapping in a farmland bird, the Red-backed shrike (*Lanius collurio*), expanding its breeding habitat into clearcuts of Spruce plantations. This long-distance migratory species exhibits a clear preference for this novel habitat but has a higher reproductive success in the traditionally used farmland habitat. Here, we explored the influence of nest predation on reproductive success and we combined different field experiments and observations to explain the occurrence of ecological trapping in this species. Our results showed that shrikes preferred to settle in the plantation forests where nest predator abundance during the settlement period was 50% lower than in farmland habitat. More than 90% of brood failures were caused by nest predation and nest predation rate was 14% higher in the preferred habitat with less nest predators. Based on the comparison of nest predation on natural nests (with parental effect) and artificial nests (without parental effect), our results suggest that parent shrikes enhance the probability of nest detection by predators in the forest habitat. Moreover, nest concealment was considerably lower and explained higher nest predation rates in forest habitat. Differences in nest predation rates between forest and farmland may, therefore, only weakly correlate with differences in predator abundance. This mismatch may underlie the existence of ecological traps in the wild. This is an important message for biodiversity conservation, as managers often propose to reduce the abundance of predators for species under conservation concern. Understanding the ecological significance of predator abundance on habitat preference and fitness of the organisms in human-modified environments is needed to guide effective management actions.

INTRODUCTION

In human-modified environments, there is growing evidence of cases where organisms prefer to reproduce in habitats associated with higher predation rates over other available habitats (e.g. Weldon & Haddad 2005, Gilroy et al. 2011, Hollander et al. 2011, Latif et al. 2011), thereby leading to an ecological trap (Schlaepfer et al. 2002, Robertson & Hutto 2006). It has been suggested that ecological traps may be caused by a higher number of predators in preferred habitat. Only few studies give support to this idea (i.e., Shochat et al. 2005, Robertson & Hutto 2007). Irrespective of the phenomenon of ecological trapping, predator abundance has attracted much attention for the conservation of organisms undergoing high nest predation rates (e.g. Côté & Sutherland 1997, Smith et al. 2010). Some experimental studies have manipulated nest predator abundance, but these studies showed that a decrease in predator abundance may not always result in an increased reproductive success of the prey (e.g. Sargeant et al. 1995, Côté & Sutherland 1997, Marzluff & Neatherlin 2006, Smith et al. 2010, Ellis-Felege et al. 2012). One might therefore question whether there is a clear link between predator abundance and nest predation rates, especially in the case of ecological traps where the mechanisms leading to fitness loss in preferred habitat remain unexplored in many studies. For this reason, it is important to understand how predator abundance influences habitat preference and fitness consequences in ecologically trapped organisms that may experience significant population declines (Delibes et al. 2002, Kristan 2003, Fletcher et al. 2012).

Lower reproductive success in preferred habitat may emerge when the environmental cues that trigger habitat preference become decoupled from the underlying habitat quality (Schlaepfer et al. 2002, Robertson & Hutto 2006). In birds, nest predator abundance has been experimentally shown to be used as a cue during habitat or territory settlement (e.g. Fontaine & Martin 2006a,b), as well as nest predator calls and scents indirectly cueing on predator presence and abundance (e.g. Eggers et al. 2006, Mönkkönen et al. 2009, Emmering & Schmidt 2011, Forsman et al. 2013). Hence, the preference for a habitat with lower predator abundance but also lower reproductive success compared to alternative habitats would provide evidence of such an ecological trap. Rapid changes in the environment due to anthropogenic habitat modifications have the potential to alter the significance of predator abundance into an unreliable indicator of reproductive success. In the case of an ecological trap, it is therefore warranted to test the importance of predator abundance as a cue for habitat preference and its link with the reproductive success of organisms confronted with nest predation.

We have recently shown evidence of ecological trapping in the Red-backed shrike (*Lanius collurio*) (Hollander et al. 2011, Chapter 4), a migratory bird species of conservation concern in Europe (BirdLife International 2012). In Belgium and elsewhere in Europe, this species occupies different types of anthropogenic habitats in mixed farmland-forest landscapes (Karlsson 2004, Hollander et al. 2011, Söderström & Karlsson 2011, BirdLife International 2012). Large-sized clearcut patches in plantation forests resulting from modern forest management practices have recently created a novel habitat type for the species compared to its traditional farmland habitat. Based on habitat preference measures (Chapter 4) and a territorial resource-valuation experiment during spring arrival (Chapter 5), we showed that shrikes consistently prefer breeding in clearcuts of Spruce plantations (*Picea abies*) over adjacent farmland habitat (Hollander et al. 2011, 2012). In this preferred habitat type, the shrikes experience a higher rate of brood failure and therefore, they have lower reproductive success than in traditional farmland habitat (Hollander et al. 2011).

The aim of this paper is to test if nest predation-related mechanisms explain lower reproductive success of the shrikes in their preferred habitat type. First, we examined whether decision-making of shrikes during habitat selection is related to the abundance of their nest predators (i.e., corvids). Second, the probability of nest detection by visually-oriented nest predators may be affected by vegetation structure and by the behavioural response (e.g. parental prudence during nest visits) of the parent shrikes (e.g. Flaspohler et al. 2000, Eggers et al. 2008). Due to important differences in the vegetation structure between both habitat types, higher reproductive success in farmland could be explained by better-concealed nests or higher prudence of the parent birds when they deliver food to the nest. We tested these issues by 1) comparing nest predation rates on artificial nests (without parental effects) and on real nests (with parental effects) to determine the influence of parent birds on nest predation, 2) conducting a predator intrusion experiment to manipulate the perceived risk of nest predation and measure the associated prudence of the parents during nest visits, 3) evaluating the influence of nest concealment on reproductive success. From a conservational viewpoint, this study will provide new insights into the nest predation-related processes that may underlie observed maladaptive habitat selection patterns and into the relevance of predator abundance as an indicator of nest predation rates as often suggested in the literature.

MATERIALS & METHODS

Study species and study areas

The Red-backed shrike is an insectivorous migratory bird with a wide breeding range across the Western Palaearctic (Lefranc & Worfolk 1997). It is a species showing population declines in several European countries (BirdLife International 2012), and is of conservation concern in Europe (EU Birds Directive 2010). Breeding territories have a size of *c*. 1 to 2 ha and this is similar in forest and farmland (Karlsson 2004). The breeding season is short (May-July) with a single clutch, but there is typically a replacement clutch in case of brood failure (Söderström 2001, Roos 2002). Shrike clutches suffer from high predation rates caused by visual-oriented predators like corvid birds (Roos 2002). Both reproductive success and offspring quality are considerably lower in replacement clutches and these ones occur 14% more often in the forest clearcuts than in farmland habitat (Hollander et al. 2011, Chapter 4).

Two 400-km^2 study areas were selected in southern Belgium (centers of study areas: 50°14'N 5°50'E and 49°49'N 5°39'E). Both areas represent a farmland-forest landscape, where the shrikes breed in the two distinct habitat types: 1) farmland covered by pastures and hayfields with hedgerows and shrubs, and 2) large-sized clearcuts (2-10 ha) in Spruce forests composed of young spruce trees (< 10 years old) or natural early-successional vegetation after clearcutting (Hollander et al. 2011). Breeding sites (N = 58 in farmland and N = 60 in forest) were defined as open patches in farmland or forest with early-successional and shrubby vegetation. Each breeding site enclosed one or a few shrike territories (N = 104 in farmland and N = 109 in forest).

In Belgium, Spruce plantations started from 1850 and their cover increased fourfold over the last century (Lecomte et al. 2003). Vegetation composition and structure strongly differ between forest and farmland breeding sites. In farmland, thorny and dense shrubs such as *Rosea sp., Prunus sp. and Crataegus sp.* are used as nest sites, whereas in forests, Spruce trees *Picea abies* and *Sambucus sp.* shrubs are used. Nest sites in forest have a markedly less dense structure compared to those found in farmland.

Field methods

Predator abundance

In the spring of 2009 and 2010, we assessed the abundance of three corvid species in the shrikes' territories ($N_{farmland}$ = 43, N_{forest} = 38): the Magpie (*Pica pica*), the Eurasian Jay (*Garrulus glandarius*) and the Carrion Crow (*Corvus corone*). They are known to be the main nest predators of *L. collurio* (Roos 2002). Small mammals such as Red Squirrels (*Sciurus vulgaris*), Weasel (*Mustela nivalis*) and Mice (*Apodemus sp.*) are only occasional predators (Roos & Pärt 2004). We used corvid count techniques consisting of 1) a 10-min count, 2) a 2-min count with a randomized corvid playback (mix of the three corvid species), and 3) a final 10-min count without playback (Luginbuhl et al. 2001). Only corvids that were present (flying over or calling) in the shrike territories were taken into account. Territorial boundaries of shrikes were known from the seasonal-long mapping of their territories the years before (2008, 2009) the corvid counts. Counts were conducted from early to late April, just before the arrival of the shrikes on the breeding grounds. In this way, we recorded a surrogate of predation pressure during the stage of habitat selection of the shrikes. We replicated between 2 and 6 corvid counts in each site and each year. Within each count, we summed the abundance of the three corvid species as a synthetic measure of predator abundance in the shrike breeding sites (Shochat et al. 2005).

Nest predation rate on shrike nests

During three successive breeding seasons (2008-2010), we evaluated the nest predation rate on shrike nests in farmland (N = 58) and forest (N = 60) breeding sites (Hollander et al. 2011, Chapter 4). Breeding sites were visited every two days, during which the reproductive activities of the parents (i.e. nest building, male courtship feeding of the incubating female, parental feeding visits) were observed with binoculars. This permitted localizing the nest and recording reproductive success. Human nest visitation might increase the probability of corvids to detect nests (Major 1990), but we assumed this effect is not likely to differ between the habitat types. The presence of corvids was always checked visually and auditively before examining shrike nests. The disappearance of a complete clutch or the disappearance of less than 12-day old nestlings was used as a reliable indicator of nest predation (Roos 2002, Söderström 2001). Nest abandonment was recorded when cold eggs were left in the nest. Food limitation was suggested as the cause of brood failure when nestlings were found dead in the nest.

Nest predation rate on artificial nests

We conducted an artificial nest experiment in 2009 and 2010 to estimate the difference in predation rate between farmland and forest when there is no parental effect. As artificial nests were not visited or defended by parent birds, a comparison of predation rates with shrike nests allows assessing the relative effect of the parents on nest predation between habitat types (e.g. Weidinger 2002, Fontaine et al. 2007). However, care is to be paid to the study design for claiming this assumption, particularly that artificial nests have to mimick as much as possible natural nests (Fontaine et al. 2007). We placed three artificial nests (made of dried weeds) containing each two Japanese quail eggs (*Coturnix japonica*) per shrike territory ($N_{farmland}$ = 26, N_{forest} = 25). Nests were located and concealed in a similar way as the natural shrike nests in each habitat type, i.e. placed at 2-3 m height and at a comparable position in shrubs known to be used as nest sites by the shrikes. We placed artificial nests during two consecutive periods (i.e. from early to mid June and from mid to late June). During the second period, all nests were redistributed with new quail eggs in each site. Nest building and egg placement was always done with latex gloves to avoid human odour traces (Amo et al. 2008). Nest predation was recorded when quail eggs disappeared or were broken. In 2010, an additional set of artificial nests (N = 313) were baited with four plasticine eggs: teeth and beak prints on these eggs offered the opportunity to identify the predator(s) (Roos 2002).

Nest concealment

The degree of nest concealment was measured for successful and unsuccessful nests in both habitat types during the three breeding seasons 2008-2010 for first and replacement clutches (i.e. clutch sequence). Nest concealment was estimated in one shrike territory per breeding site by scanning the nest visually at a 1 m distance in the four cardinal directions (Holway 1991). Each nest was attributed a global score: 1 = low nest concealment (≥ 2/3 is visible), 2 = moderate nest concealment (1/3 to 2/3 is visible), and 3 = high nest concealment (≤ 1/3 is visible). All the scores were attributed by the same observer (F.A.H.) to avoid between-observer variation. For successful nests, concealment was evaluated at the time of fledging (nestlings between 12 and 15 days old); for unsuccessful nests this was done within the week after brood failure.

Nest visiting rate under simulated predator intrusion

We measured changes in nest visiting rate by parent shrikes before and after a simulated predator intrusion in their territory. An increase in their level of prudence was assumed to lead to a decrease

of the nest visiting rate compared to nest visiting rates without predator intrusion. In 2010, nests with nestlings of 12 days old (range 11-15 days) were video-recorded during 3 h from 8-9 am to 11-12 am in farmland (N = 26) and in forest (N = 29). A stuffed predator (Jay, Magpie or Crow) was then randomly selected and perched about 2 m above the ground surface at 15 m from the nest. During this first 3 h recording period, the stuffed predator was covered with a plastic bag and usual nest visits were recorded. We then removed the bag and exposed the predator during 30 min. The change in visiting rate was calculated as the ratio between the mean time for parents to visit ten times the nest after and before corvid exposure and was interpreted as a measure of parental prudence level.

Statistical analyses

The central aim of the study is to examine whether between-habitat differences in predator abundance, nest predation rates, nest concealment and parental prudence during nest visits by the shrikes contributed to explaining the pattern of ecological trap in our study system.

First we describe to what extent the higher rate of brood failures is related to a higher nest predation rate in the preferred habitat and we compare the proportion of nest-predated broods between forest and farmland and between first and replacement clutches. Second, we test how predator abundance during shrike settlement varied between preferred and alternative habitat (Table 6.1A). Third, parental influence on nest predation is evaluated via a comparison of predation rates between artificial (without parental effect) and shrike (with parental effect) nests in forest and farmland (Table 6.1B). Fourth, we test whether nest concealment was lower in forest than in farmland (Table 6.1C) and if nests with low concealment are predated more frequently (Table 6.1D). Fifth, we test whether the prudence of parent shrikes during nest visits is lower in forest than in farmland (Table 6.1E).

Table 6.1 – GLM and GLMM model structure with fixed and random effects for the analysis of predator abundance, predation rates, nest concealment and the parental prudence during nest visits.

	N	Response	Fixed effects										Random effects	Response distribution
			Habitat	Clutch sequence	Year	Study area	Nest concealment	Habitat x Clutch sequence	Habitat x Year	Habitat x Study area	Habitat x Nest concealment	Covariate		
A	253	**Predator abundance**	X		X	X			X	X		Date	Territory	Poisson
B	495	**Predation rate on artificial nests**	X		X	X			X	X			Site	Binomial
C	261	**Nest concealment**	X	X	X	X		X	X	X			-	Multinomial
D	261	**Predation rate on shrike nests†**	X				X				X		Site	Binomial
E	55	**Parental prudence**	X				X				X	Age, Brood size	-	Normal

N = sample size = number of count sessions for predator abundance, and number of nests investigated for all other responses.

† As only a subsample of predated nests had been scored for nest concealment (60 out of 261 nests or 23%), and because differences in reproductive success between farmland and forest habitat are treated in detail by Hollander et al. (2011) with larger sample sizes (Chapter 4), we used a simple model to interpret nest concealment and 'Habitat x Nest concealment' interaction effects, being the scope of interest here. Details on the sampling of brood sizes and nestling age can also be found in Hollander et al. (2011) and Chapter 4.

Table 6.1 synthesizes the generalized linear (mixed) models (GLM or GLMM) used in the analyses to test the between-habitat differences in predator abundance, nest predation rates, nest concealment and parental prudence during nest visits by the shrikes. In addition to the factor 'Habitat' included in all models, analyses also accounted for the variation of the response variables over time (between-year variation 'Year' and within-year variation 'Clutch sequence') and in space (Study area). It was also tested whether between-habitat differences in the response variables were consistent over time or in space (interactions: 'Habitat x Year', 'Habitat x Clutch sequence', 'Habitat x Study area') (Table 6.1). Covariates (i.e. recording date, nestling age, brood size) were included to control for their effect on the response variables (Table 6.1).

We used GLMs (Restricted Maximum Likelihood estimations) when a single observation was made in each shrike breeding site (Table 6.1, models C and E) and GLMMs (Maximum Likelihood estimations) with site or territory as random effect when several observations were made in each breeding site or territory (Table 6.1, models A, B and D) (Zuur et al. 2009). All analyses were performed using the R 2.13. and SAS 9.2. software.

Information-theoretic multimodel inference was used based on the Akaike's Information Criterion corrected for small sample sizes (AIC_c). ΔAIC_c were calculated for each candidate model to reflect the difference with the best candidate model (i.e., the model with the smallest AIC_c). A ΔAIC_c value < 2 was used as a threshold for a model to be considered as having support, Burnham & Anderson 2002). The relative support for the alternative models was obtained by scaling them according to their AIC_c weight (Burnham & Anderson 2002). The relative importance of a variable (w_+) was estimated by summing the AIC_c weights across all candidate models in which the variable occurred. Since the prevalence of the variables in the set of candidate models (v) varied from one variable to the other and because this prevalence restricts the w_+ values associated with the variables (Burnham & Anderson 2002), the v values are reported as a baseline reference along with the w_+ values. The model-averaged parameter estimates (β), the estimate precision (unconditional standard errors, S.E.) and the w_+ values inform on the importance of each variable (Burnham & Anderson 2002). In order to facilitate the interpretation, the estimates were converted into percentages relative to the average value of the response variables (Δ[difference between two levels of a variable]).

RESULTS

Table 6.2 summarizes the sets of supported models ($\Delta AIC_c < 2$) derived from the model selection procedures for the analyses of predator abundance, predation rates on shrike and artificial nests, nest concealment and parental prudence during nest visits.

Table 6.2 – Set of supported ($\Delta AIC_c < 2$) and the best non-supported ($\Delta AIC_c > 2$, between brackets) candidate models along with their respective support (AIC_c weight) according to the model selection procedures. ΔAIC_c refers to the differences in AIC_c between the model and the best candidate model associated with the smallest AIC_c. The number of parameters (K) is reported for each model. Corresponding models of Table 6.1 are indicated with a capital letter (A-E).

	Response	Supported and (best non-supported) models	K	Log Likelihood	Δ AIC_c	AIC_c weight
A	**Predator abundance**	Habitat + Year + Study area + Habitat x Study area	7	-209.73	0.00	0.61
		Habitat + Year + Study area + Habitat x Year + Habitat x Study area	8	-209.57	1.82	0.25
		(Habitat + Year)	(5)	(-213.97)	(4.28)	(0.07)
B	**Predation rate**	Habitat + Year + Study area	5	-274.24	0.00	0.23
	on artificial nests	Habitat + Year + Study area + Habitat x Year	6	-273.40	0.36	0.19
		Year + Study area	4	-275.54	0.56	0.18
		Habitat + Year + Study area + Habitat x Study area	6	-274.08	1.73	0.10
		(Habitat + Year)	(4)	(-276.29)	(2.05)	(0.08)
C	**Nest concealment**	Habitat + Clutch sequence + Habitat x Clutch sequence	5	-254.60	0.00	0.24
		Habitat + Clutch sequence	4	-255.66	0.05	0.24
		Habitat + Study area + Clutch sequence	5	-255.59	1.98	0.09
		(Habitat + Study area + Clutch sequence + Habitat x Clutch sequence)	(6)	(-254.56)	(2.03)	(0.09)
D	**Predation rate**	Nest concealment	4	-138.34	0.00	0.44
	on shrike nests	Habitat + Nest concealment	5	-137.48	0.36	0.37
		(Intercept)	(2)	-141.91	3.03	0.10
E	**Parental prudence**	Nest concealment	4	-28.11	0.00	0.47
		Habitat + Nest concealment	5	-27.60	1.41	0.23
		Intercept	2	-31.19	1.59	0.21
		(Habitat)	(3)	(-31.18)	(3.80)	(0.07)

Descriptive statistics on brood failures and nest predation

Out of 183 brood failures in 2008-2010, 170 (93%) were caused by nest predation, 11 nests (6%) were abandoned and 2 nests (1%) were found with dead nestlings, probably because of food limitation. From the 170 cases of nest predation, 88% occurred in first clutches (proportion of first clutches represents 66% of all the breeding attempts) and 12% in replacement clutches (34%): the proportion of nest-predated broods was higher in first than in replacement clutches ($\chi 2 = 50.01$, df = 1, $p < 0.001$). In first clutches, the proportion of nest-predated broods was 14% more frequent in the preferred forest sites than in farmland ($\chi 2 = 4.54$, df = 1, $p = 0.03$). In contrast, this proportion was similar in replacement clutches between farmland and forest habitats ($\chi 2 = 0.04$, df = 1, $p = 0.84$).

Predator abundance

The number of predator count sessions per breeding site was similar in both habitat types (ANOVA: $F_{1,85} = 0.04$, $p = 0.84$, $N_{Farmland} = 3.20 \pm 1.69$, $N_{Forest} = 3.28 \pm 1.64$), and counts before and after corvid sound playback were highly correlated ($r_s = 0.85$, $p < 0.0001$). Therefore, we only used counts during the first 10 min (before playback) in the analyses as a measure of predation pressure.

We observed twice the number of corvids per count session in shrike territories established farmland than in forest (Table 6.3, habitat: $w_+ = 100\%$, Δ[Farmland-Forest] = 53%). Predator abundance was also strongly affected by the factors 'Year' ($w_+ = 100\%$, Δ[2009-2010] = 49%) and 'Study area' ($w_+ = 90\%$, Δ[Study area 1-Study area 2] = -13%). Although predator abundance was higher in farmland than in forest for each study area, the between-habitat difference was larger in study area 1 than in study area 2 (interaction effect 'Habitat x Study area': $w_+ = 86\%$). The higher predator abundance in farmland was consistent among years ('Habitat x Year': $w_+ = 29\%$).

Predation rate on artificial nests

From all the artificial nests with plasticine eggs, 48% showed at least one egg with beak marks, but never mammal teeth marks. This suggests nest predation was almost exclusively attributed to corvids, even though species identity remained undetermined.

In contrast with predation rate on shrike nests, predation rate on artificial nests was higher in farmland than in forest sites (Table 6.3, 'Habitat': $w_+ = 76\%$, Δ[Farmland-Forest] = 13%). This result might to some extent indicate that parent shrikes enhance the probability of nest detection by predators in the forest habitat. Predation rate on artificial nests varied substantially between years ($w_+ = 100\%$, Δ[2009-2010] = -38%) and study areas ($w_+ = 77\%$, Δ[Study area 1-Study area 2] = -12%). The higher predation rate on artificial nests in farmland was consistent between years and study areas (interaction effects 'Habitat x Year' and 'Habitat x Study area': all $w_+ < 35\%$).

Nest concealment

Moderately and highly concealed nests (scores 2 and 3) occurred less frequently in forest than in farmland (Table 6.3, 'Habitat': $w_+ = 100\%$) and in replacement than in first clutches ('Clutch sequence': $w_+ = 98\%$ and Fig. 6.1). Moderate and high nest concealment scores were particularly rare in replacement clutches in forest sites compared to farmland, explaining the significant interaction effect (interaction effect 'Habitat x Clutch sequence': $w_+ = 89\%$ and Fig. 6.1). Nest concealment

remained the same between years and study areas. The difference in nest concealment between habitat types was consistent between years and study areas (interaction effects 'Habitat x Study area' and 'Habitat x Year': all $w_+ \leq 9\%$). Nest predation rate on shrike nests varied with nest concealment: nests with a moderate and high concealment (scores 2 and 3) were less frequently predated than those with a low concealment (score 1) ('Nest concealment': $w_+ = 86\%$). This result was similar in both habitat types (interaction effect 'Habitat x Nest concealment': $w_+ = 5\%$).

Table 6.3 - Results of the AIC_c-weighted GLMM (A, B, D) and GLM (C, E) model selection procedures for the analysis of predator abundance, predation rates, nest concealment and the parental prudence during nest visits.

	Response					
A	**Predator abundance**					
	Fixed effect	**ν**	w_+	**β**	**S.E.**	**Effect**
	(Intercept)	*100*	*100*	*1.56*	*0.17*	
	Habitat (Forest)	69	100	-1.10	0.28	Farmland > Forest
	Year (2010)	62	100	-0.67	0.10	2009 > 2010
	Study area (2)	62	90	-0.23	0.17	1 > 2
	Habitat x Year (Forest, 2010)	23	29	- 0.03	0.06	
	Habitat x Study area (Forest, 2)	23	86	0.71	0.26	Farmland 1 > Farmland 2 > Forest 2 > Forest 1
B	**Predation rate on artificial nests**					
	Fixed effect	**ν**	w_+	**β**	**S.E.**	**Effect**
	(Intercept)	*100*	*100*	*-0.71*	*0.38*	
	Habitat (Forest)	77	76	-0.34	0.36	Farmland > Forest
	Year (2010)	63	100	2.14	0.34	2010 > 2009
	Study area (2)	63	77	0.52	0.33	2 > 1
	Habitat x Year (Forest, 2010)	26	35	-0.23	0.23	
	Habitat x Study area (Forest, 2)	26	18	0.07	0.14	
C	**Nest concealment**					
	Fixed effect	**ν**	w_+	**β**	**S.E.**	**Effect**
	(Intercept NC=2)	*100*	*100*	*0.74*	*0.27*	
	(Intercept NC=3)	*100*	*100*	*-0.92*	*0.27*	
	Habitat (Forest)	77	100	-0.79	0.31	Farmland > Forest
	Year (2009)	63	45	-0.08	0.11	
	(2010)	63	45	-0.01	0.08	
	Study area (2)	63	33	-0.02	0.09	
	Clutch sequence (2)	63	98	-0.44	0.35	1 > 2
	Habitat x Year (Forest, 2009)	26	6	-0.002	0.18	
	(Forest, 2010)	26	6	-0.005	0.02	
	Habitat x Study area (Forest, 2)	26	9	-0.01	0.05	
	Habitat x Clutch sequence (Forest, 2)	26	89	-0.35	0.31	Farmland 1 > Farmland 2 > Forest 1 > Forest 2
D	**Predation rate on shrike nests**					
	Fixed effect	**ν**	w_+	**β**	**S.E.**	**Effect**
	(Intercept)	*100*	*100*	*0.71*	*0.29*	
	Habitat (Forest)	60	46	0.18	0.18	
	Nest concealment (2)	60	86	-0.71	0.33	1 > (2 = 3)
	(3)	60	86	-0.71	0.40	
	Habitat x Nest concealment (Forest, 2)	20	5	-0.01	0.04	
	(Forest, 3)	20	5	0.01	0.05	
E	**Parental prudence**					
	Fixed effect	**ν**	w_+	**β**	**S.E.**	**Effect**
	(Intercept)	*100*	*100*	*0.32*	*0.10*	
	Habitat (Forest)	60	33	-0.03	0.05	
	Nest concealment (2)	60	72	-0.03	0.09	1 > 2 > 3
	(3)	60	72	-0.29	0.14	
	Habitat x Nest concealment (Forest, 2)	20	3	0.004	0.008	
	(Forest, 3)	20	3	0.009	0.02	

Nest visiting rate under simulated predator intrusion

In the presence of the stuffed predator, it took the shrikes on average three times longer to visit their nest 10 times compared to natural visits in the absence of an introduced predator (mean prudence level = 3.1 ± 0.6), but this effect was similar in both habitat types (Table 6.3, 'Habitat': w_+ = 32%, β = -0.03 ± 0.05). There was also some support for higher nest visiting rates, and hence lower parental prudence, associated with better-concealed nests ('Nest concealment': w_+ = 72%, moderate nest concealment; β = -0.03 ± 0.09, high nest concealment; β = -0.29 ± 0.14, Δ[high nest concealment - low nest concealment] = 72%) (Table 6.3).

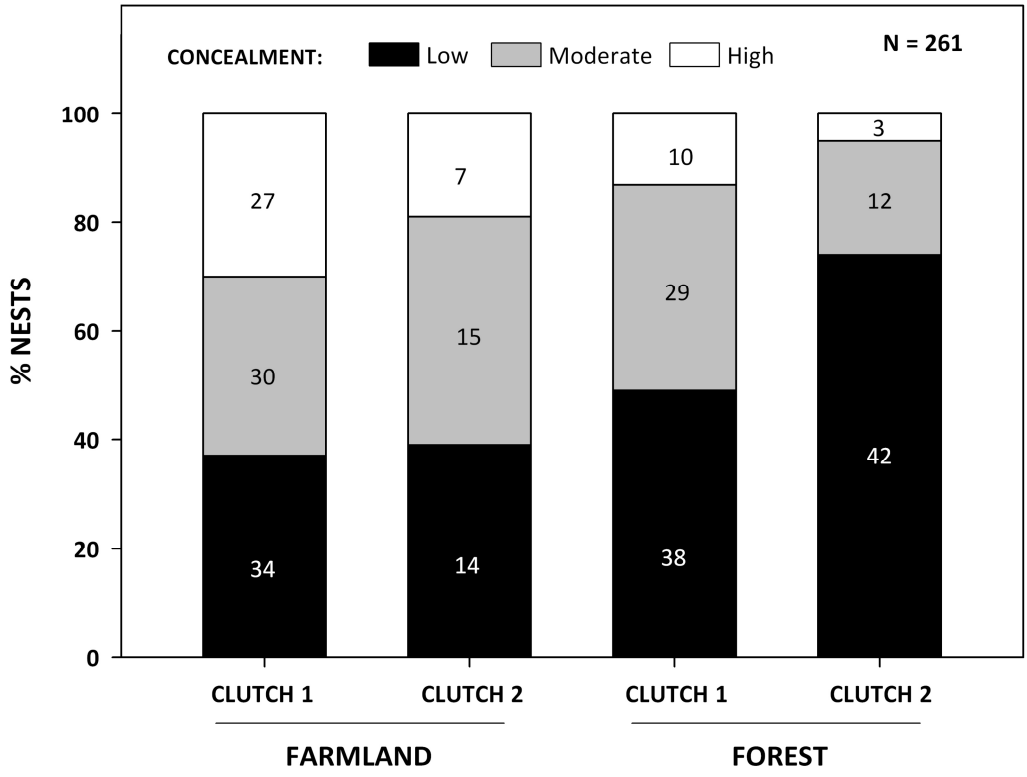


Figure 6.1 – Proportion of nest concealment scores in farmland and forest habitats and in first (CLUCH 1) and replacement (CLUTCH 2) clutches. Sample sizes refer to the number of investigated nests.

DISCUSSION

Over recent decades, changes in forest harvesting techniques have created rotation systems of large, open areas in plantation forests attracting open wildlife populations (Swanson et al. 2011). Interestingly, some farmland birds have recently extended their habitat use into post-harvesting, early-successional areas in Spruce plantations (Paquet et al. 2006, Swanson et al. 2011). In southern Belgium, the Red-backed shrike prefers breeding in such areas, even if the rate of brood failures is higher compared to the traditionally used sites in farmland (Hollander et al. 2011, 2012, Chapter 4). In the present study, we observed that the higher rate of brood failures in the preferred habitat resulted from a higher rate of nest predation by corvids, even if these predators were considerably less abundant. Hence, some processes other than predator abundance *per se* are likely to explain the observed difference in nest predation rate between forest and farmland habitat types. We suggest that if low predator abundance in forest may trigger the preferential settlement of shrikes, it is clear from our study that such habitat attractiveness deviates from habitat quality relative to nest predation. Interestingly, our results draw attention to the importance of nest concealment as a novel functional explanation for the variations in nest predation rate between habitat types in the case of an ecological trap. Hence, this study provides new insights into the mechanisms underlying an ecological trap in nest-predated organisms and shows that predator abundance should not solely be considered by managers to protect and conserve highly predated species. Further work is needed to better grasp the effect of predator species on the shrike's habitat preference and reproductive success, and also on the environmental conditions and resources (e.g. vegetation structure, food) other than predator abundance that influence nest predation.

It has been suggested that most nest predators find nests by chance (e.g. Wilson & Cooper 1998). However, nest predators have also been shown to learn locating the nests of their prey and to make use of cues guiding them to nest sites (e.g. Pelech et al. 2010). The foraging strategies and movements of the predators may also affect the likelihood of finding nests and so, the rate of nest predation for the prey, irrespective of predator abundance (e.g. Söderström et al. 1998, Storch et al. 2005, Sperry et al. 2008). In addition, the visits of the parents to the nest to feed their offspring may themselves attract predators and this attraction mostly results from the interaction between parental prudence of the prey, alertness of the nest predator and vegetation structure. Our study compared nest predation rate in shrike and artificial nests and so, examined indirectly the effect of the parental prudence on nest predation. Nest predation rate was higher in farmland on artificial nests (without parental effect) and higher in forest on natural nests (with parental effect). We argue

that this result may at least indicate that parent shrikes make nest detection by predators easier in forest than in farmland (e.g. Fontaine et al. 2007). More field experiments are now warranted to confirm this and to identify the mechanisms explaining the habitat-dependent parental effects on nest predation. Nest detection by predators surely is a complex interaction between the behaviour of parents, local environmental conditions (i.e. vegetation structure, distance to forest edges) and the behaviour of the predators.

Avoiding nest predation through anti-predation strategies is costly in terms of energy and time. Hence, parent birds are expected to invest less in anti-predation in environments where the perceived predation pressure is low (Forstmeier & Weiss 2004, Lima 2009). The between-habitat difference in nest concealment matches with such expectations, because nests are better concealed in the farmland habitat associated with higher predator abundance during the settlement of the shrikes. This pattern could be explained in terms of the associated costs of nest concealment, as better concealed nests might hinder the view of the surroundings for birds on the nest (Götmark et al. 1995). Another explanation could be found in the potential prey-site hypothesis (Chalfoun & Martin 2009): nest concealment could be lower in habitats where nest site availability is higher because predators have to spend much time to search more potential nest sites compared to habitats where nest site availability is lower. In the present case, Spruce plantations are often composed of numerous tree lines, whereas breeding sites in farmland enclose fewer nest site opportunities (e.g. hedgerows, isolated shrubs). Alternatively, shrikes in forests may not have the opportunity to conceal their nests to a similar level as in farmland due to the differences in available vegetation structures and composition between both habitat types (i.e. dense and spiny shrubby species in farmland versus sparse trees or shrubs in forest). In contrast with predator abundance, the variation in nest concealment was shown to contribute to the pattern of lower reproductive success in the preferred habitat type. We suggest that poor nest concealment in preferred habitat explains, at least partly, the observed ecological trapping scenario.

As in Belgium, Red-backed shrikes in Sweden prefer to breed in forest plantations with lower predator abundance compared to traditional farmland (Söderström & Karlsson 2011). However, nest predation rates are more than twice lower in Sweden (first clutches: 20%) than in Belgium (first clutches: 52%) and, interestingly, higher in farmland than in forest. What could explain such geographical differences? There is increasing evidence that food availability affects the investment in anti-predation strategies (Duncan Rastogi et al. 2006), and that food availability for the diet of the nestlings might differ considerably between populations and regions (e.g. Both et al. 2006). Moreover, nest detection by predators may also be influenced by the hunger state of the nestlings through the effect of increased begging calls (e.g. Maurer et al. 2003). The starvation level of

predators might also determine their foraging activities (Preston & Rotenberry 2006). It is therefore also warranted to determine how food availability in differenet habitat types may modulate anti-predation strategies of parents and the likelihood of nest predation. This again stresses that mechanisms other than predation-related ones might influence the between-habitat variation in nest predation rate.

Farmland hosts several generalist predators in high numbers such as corvids and this induces high nest predation in open-cup nesting birds (Andrén 1992, Söderström et al. 1998, Roos 2002). It has already been shown that modern forestry management practices in plantations forests increase the rate of nest predation in open-cup nesting species compared to open areas in natural forests (e.g. Griesser et al. 2007, Powell et al. 2010). However, to the best of our knowledge, only Rodewald (2002) compared the effect of both forestry and farmland management on avian reproductive success, and she observed that the reproductive success of several songbirds was lower in forest than in farmland as a result of between-habitat differences in nest predation rate. In line with Rodewald (2002), our results indicate that post-harvested, early-successional areas in Spruce plantation forests may constitute less valuable breeding sites for farmland birds than it was previously suggested based on bird presence data only (e.g. Paquet et al. 2006). Hence our results draw attention to the potential of forestry practices to create ecological traps for early-successional bird species from farmland via increased nest predation rates in habitat types that are preferred by the organisms. Conservation management of organisms experiencing high nest predation rates should therefore not only consider predator abundance alone, but also determine the mechanisms behind the variation in reproductive success at the habitat or landscape level.

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Chapter 7

Do early-successional areas in plantation forests provide valuable habitat to insectivorous farmland birds?

We will explore now how farmland and forestry activities affect the availability of food resources for open-area, insectivorous farmland birds expanding their breeding areas into Spruce plantations.

Unpublished manuscript, to be submitted

ABSTRACT

The impact of human settlement and activities on the landscape has resulted in the massive conversion of natural forests into open farmland landscape. During the last centuries, there has been frequent reforestation with fast-growing, even-aged, and single-species plantations. Some of these plantation forests are now managed with large-sized clearcut patches with early-successional vegetation. These areas have been partly colonized by early-successional wildlife. Interestingly, some farmland areas and the open patches in plantation forests now share some similar early-successional, insectivorous bird species. Here, we addressed to what extent open areas in plantation forests represent a valuable alternative to the farmland habitat. As invertebrate supply is one of the most important resources determining bird habitat quality, we compared the quantity and quality of food resources (i.e. ground-dwelling and above-ground invertebrates) between both habitat types. Our results show that invertebrate abundance was substantially higher in farmland sites. This was related to the higher ground-level temperature on farmland sites compared to forest sites. In addition, slightly larger invertebrates were found in the forest sites, probably because large-sized forest-specialist species were inherited from the pre-harvesting forest ecosystem or the surrounding mature forests. Although both habitat types were associated with the same spectrum of invertebrate assemblages, forest and farmland management induce different habitat conditions relative to food quantity and, to some extent, also food quality for early-successional bird species. This must be taken into consideration for conservation strategies because it has previously been suggested that modern forest harvesting techniques may generate valuable habitat conditions for certain farmland birds expanding their habitat use into early-successional vegetation in plantation forests. In this context, we discuss the impacts of differences in food availability between farmland and forest habitats on the fitness consequences of a well-studied bird species.

INTRODUCTION

Before the Neolithic age, the vegetation of temperate-zone Europe was dominated by closed broad-leaved forest alternated with scattered open, early-successional areas (Svenning 2002). These areas were the result of natural disturbances, including wildfires, floods, insect outbreaks, and dense grazing. Early-successional vegetation types provided different sets of resources and conditions compared to the mature forest, and therefore attractive to open-area wildlife communities (Pykala 2000, Vera 2000, Svenning 2002, Swanson et al. 2011, Fuller 2012). Starting at the Neolithic age, human settlement and activity have resulted in massive conversion of natural forest to open land dedicated to farming and livestock rearing (and other land uses). Then, the low timber availability in many European countries as a consequence of forest conversion triggered the establishment of fast-growing, even-aged, and single-species plantations. This action contributed to the reforestation of the open landscape (Heil et al. 2007, Szymanski 2007). Hence, present-day farmland-forest landscapes are the result of a mixture of historic land use and strong current impacts from both farmland and forestry activities (McAdam et al. 2009).

Since the last few decades, single-species plantations (e.g. Norway Spruce *Picea abies*) are usually managed with large-sized clearcut patches in even-aged stands (du Bus de Warnaffe & Deconchat 2008). From a forestry viewpoint, the post-harvesting, early-successional patches are considered a transitional, stand initiation phase. However, these temporary open areas in plantations are also appreciated from a conservation viewpoint as they may host open-area wildlife (Brawn et al. 2001, Brockerhoff et al. 2008, Paz Acuña & Estades 2011, Swanson et al. 2011). Different disturbance-dependent, insectivorous birds typically recorded in heath- and moorland habitats, but also in farmland, have been observed to expand their habitat use into these regeneration areas within plantation forests (Paquet et al. 2006). Given the many environmental problems some of these birds face on farmland (e.g. Brickle et al. 2000, Vickery et al. 2001, Britschgi et al. 2006, Hart et al. 2006), this phenomenon has generated special interest among conservationists as it may offer alternative or complementary conservation strategies. For instance, farmland intensification has been shown to alter food availability, and consequently fitness, in several bird species (e.g. Brickle et al. 2000, Vickery et al. 2001, Atkinson et al. 2004, Britschgi et al. 2006).

Farmland birds may realize their ecological niche under environmental conditions other than farmland *per se*. It has been suggested that they used to live in the open areas (e.g. heath- and moorland) created by natural disturbances in forests before they shifted to farmland (Paquet et al. 2006, Söderström 2009, Söderström & Karlsson 2011, Forsman 2012). Early-successional vegetation

areas in forest plantations may therefore constitute a novel environment that is likely to share some features with the historic natural habitat of these species. However, the current forest management affects the properties of the early-successional communities in several ways and probably makes them also different in several respects from the post-disturbance ecosystems in natural forests (Swanson et al. 2011). For instance, tree planting and post-disturbance logging are known to considerably shorten the duration of the early-successional stage (Christensen & Emborg 1996).

In this paper, we addressed the question whether clearcuts in plantation forests offer valuable habitat for some early-successional, farmland bird species. We focused on food availability as a major component of habitat quality in birds (Martin 1987, Johnson 2007). The distribution of invertebrates in the landscape is known to be influenced by vegetation composition and structure and by microclimatic conditions (e.g. Perner et al. 2005, Bennie et al. 2008, Randlkofer et al. 2010). We studied this issue in landscapes of southern Belgium with a mixture of farmland for livestock rearing and Norway Spruce plantation forests for timber production. In such landscapes, several species of the early-successional, insectivorous bird assemblage that breed in traditional farmland have recently colonized the clearcut habitat created by forest management (Paquet et al. 2006). We compared the abundance and size of a range of ground-dwelling and above-ground invertebrates between farmland and forest breeding habitats for these birds. We also discuss how differences in food availability for early-successional birds may influence optimal foraging (Pyke et al. 1977), and ultimately, fitness consequences in both human-modified habitat types.

MATERIALS & METHODS

Study areas

Two 400-km^2 study areas were selected in the farmland-forest landscape of the Ardenne region in southern Belgium (centres of study areas: 50°14'N 5°50'E and 49°49'N 5°39'E). The study areas are mainly composed of a mixture of two land-use types: 1) a combination of pastures and hay meadows for livestock rearing, and 2) Spruce plantation forests for timber production with succession stages ranging from clearcut to mature stand. The landscape structure emerged from the massive forest conversion to farmland, starting with the Celts in 700 BC (Petit & Lambin 2002). Farmland management has gradually intensified, with the strongest impacts over the last 50 years or so (Petit & Lambin 2002). Reforestations of uncultivated land (e.g. wetland and heathland) with Spruce plantations were initiated in 1850 to avoid the abandonment of land ownership, but also to increase timber production for firewood and coalmine activities. During the 20th century, the coverage of Spruce plantations increased fourfold in the Ardenne (Lecomte et al. 2003) and is currently estimated

to more than 50% of all forested areas in this region (Lecomte et al. 2003). Spruce forests are now usually managed according to a rotational clearcut system in mature stands (du Bus de Warnaffe & Deconchat 2008).

Study sites

In the two study areas, a total of 67 sites were selected in open areas resulting from farmland (N = 36) or forestry (N = 31) management. Farmland sites consisted of a mixture of extensive pastures and hay meadows with hedgerows and thorny bushes (e.g. *Rosa canina*, *Prunus spinosa* and *Crataegus monogyna*). Forest sites were young Spruce plantations (< 10 years old) or post-harvesting, early-successional areas with shrubby vegetation (e.g. *Sambucus nigra and Cytisus scoparius*). Hence, both habitat types differed in vegetation composition and structure. The following insectivorous, early-successional bird species breed in both habitat types of the study sites: Common whitethroat (*Sylvia communis*), Red-backed shrike (*Lanius collurio*), Stonechat (*Saxicola torquata*), Tree Pipit (*Anthus trivialis*), White wagtail (*Motacilla alba*), Willow warbler (*Phylloscopus trochilus*) and Yellowhammer (*Emberiza citrinella*) (Paquet et al. 2006, F.A. Hollander: pers. obs. based on ca. 20 visits per site in 2008 and 2009).

Invertebrate sampling

The feeding ecology of these early-successional bird species is well documented and prey mainly used during breeding include ground-dwelling invertebrates and invertebrates of herbaceous vegetations (Araneae, Coleoptera, Orthoptera) and flying invertebrates (Diptera, Hymenoptera, Lepidoptera) (Davies 1976, Greig-Smith & Quicke 1983, Meury 1991, Snow & Perrins 1998, Moreby & Stoate 2001, Tryjanowski et al. 2003, Krupa 2004, Hart et al. 2006). In 2008 and 2009, we therefore studied food availability in each site with four pitfall traps per site to sample ground-dwelling invertebrates (Araneae, Coleoptera, Orthoptera) and one yellow-pan trap per site to sample flying invertebrates (Diptera, Hymenoptera, Lepidoptera) (Duelli et al. 1999). Pitfall traps were white plastic cups (diameter = 11 cm, depth = 14 cm) and the yellow pan was a yellow plastic cup (diameter = 22 cm, depth = 9 cm). Hence, there was a comparable trapping surface of 380 cm² between the four pitfall traps and the single yellow pan trap within a territory. Each pitfall trap was dug in the ground and filled for 1/3 with a 50:50 solution of ethylene glycol and ethanol; some detergent was added to minimize surface tension. Yellow-pan traps were placed at a height of 1 m on a stick. They were also filled for 1/3 with the same solution as for the pitfall traps. In each territory, the traps were placed at 15 m from each other to avoid interference (Ward et al. 2001) and in obvious foraging areas used by

early-successional bird species. In each site, foraging areas in farmland and forest were identified by mapping the occurrence of the early-successional bird species during May 2008 and 2009. All traps were placed less than 10 m away from the most commonly used vantage points. In both habitat types, we placed the pitfalls in similar herbaceous, unmown grass vegetations to avoid habitat type related biases for trapability of invertebrates (Melbourne 1999). In forest sites, pitfall traps were always distant from mature forest (> 20 m).

In each year, sampling occurred from June 1 to July 15 corresponding to the time of chick rearing in the investigated bird species (Greig-Smith & Quicke 1983, Snow & Perrins 1998, Moreby & Stoate 2001, Tryjanowski et al. 2003). Traps were emptied at the end of June (1st trapping session) and during mid-July (2nd trapping session). All invertebrates were conserved in 96% ethanol and identified to the order or family level in the laboratory. Invertebrate abundance was calculated as the number of items collected in the traps. Body length of individual invertebrates was measured with digital callipers (CONRAD PRO®, precision: ± 0.01 mm). Appendages such as antennae, legs or wings were excluded from the body length measurements.

Microclimatic conditions

In order to record the ground-level temperature in farmland and forest habitats, we placed thermoprobes with dataloggers (Hobo® UA-002-08) in a subsample of the sites (N = 8 in farmland and N=9 in forest). In each site, one probe was positioned close to each pitfall trap (N=4) during the sampling period in 2008 and 2009. In both habitat types, dataloggers were placed in similar vegetation types as described before. Ambient temperature was recorded every 2 minutes (precision: ± 0.5 °C at 25 °C) during the complete period of invertebrate sampling (47 days per year).

Statistical analyses

We used general linear mixed models (GLMM) with normal distribution and identity link function, Maximum Likelihood estimations, Kenward-Roger adjustments of the degrees of freedom) (Kenward & Roger 1997) to analyse the variation in invertebrate abundance (continuous response, log-transformation) and size (continuous response) relative to habitat type (class variable: farmland and forest sites), year (class variable: 2008 and 2009), and study areas (class variable: 1 and 2). The interactions 'Habitat x Year' and 'Habitat x Study' area were included to test whether the between-habitat differences in invertebrate abundance and size were consistent over time and space. We also included the invertebrate order and the interaction 'Habitat x Order' as additional class variables to investigate how the (between-habitat) differences in invertebrate abundance and size depended on

the nature of the invertebrate items. The unit of analysis was the trap for the analysis of invertebrate abundance (N = 756) and the invertebrate item for the analysis of invertebrate size (N = 95191). We used trap type (pitfall trap and yellow-pan trap) and trapping session (1^{st} or 2^{nd}) as covariates in the analyses of invertebrate abundance and size.

We also tested with GLMM the difference in ground-level temperature between habitat types using average temperatures per probe and per site over the entire period of invertebrate sampling (model variables: 'Habitat', 'Study area', 'Year', 'Habitat x Study area' and 'Habitat x Year').

Finally, we examined with GLMM how invertebrate abundance and size varied with the ground level-temperature (model variables: 'Habitat', 'Study area', 'Year', 'Temperature', 'Habitat x Study area', 'Habitat x Year' and 'Habitat x Temperature').

In all GLMM analyses, the site identity was defined as a random factor to account for the fact that data were collected in the same sites but in different traps and during different years or trapping sessions. Starting from the full models including all explanatory variables, we used backward selection of least significant variables using P = 0.05 as a threshold probability value for variable removal. Covariates were forced in all models and were not subject to the variable selection procedure.

RESULTS

A large number and diversity of invertebrate specimens were sampled in each habitat type (N_{total} = 95919; Table 7.1). Overall, Diptera (flies and syrphids), Coleoptera (beetles), Mecoptera (scorpion flies) and Arachnida (spiders) were the most frequently captured taxa, covering more than 90% of the records in farmland sites and almost 80% in the forest sites. Frequencies of the captured taxa were not similar between farmland and forest sites (χ^2_1= 9.73, P = 0.002).

Invertebrate abundance

On average, invertebrate abundance was 35% higher in farmland sites compared to forest sites (GLMM, Table 7.2, Fig. 7.1A). There was no significant difference in abundance between years and between study areas (Table 7.2), and habitat-dependent differences in abundance showed strong consistency in space ('Habitat x Study area') and over time ('Habitat x Year'). In addition, invertebrate abundance differed between species groups ('Order') and between-habitat differences differed significantly between species groups ('Habitat x Order'): higher abundance in farmland sites was

especially due to high numbers of Arachnida, Coleoptera, Diptera and Mecoptera (Table 7.1). Most of the Coleoptera families were between 50% and 100% more abundant in farmland sites (e.g. Cantharidae, Carabidae, Elateridae, Scarabeoidae, Staphylinidae), except for Geotrupidae and Silphidae that were more prevalent in forest sites. Hymenoptera were twice as abundant in forest sites: this difference was particularly pronounced for Formicidae (Table 7.1). Orthoptera were, in contrast, captured at similar frequencies in both habitat types.

Table 7.1 – Abundance of invertebrate prey taxa important for the diet of early-successional insectivorous birds in farmland and forest sites. N_{TOTAL} = total number of invertebrate items collected in each habitat type, N_{TRAP} = mean number of invertebrate items collected per trap in each habitat type, % = relative frequency of invertebrate items collected in each habitat type, Size = mean size (± S.D.) of invertebrate items collected in each habitat type (in mm). ΔN and ΔSize show the results of the t-tests examining differences in invertebrate abundance and size between habitat types for each order in the GLMM analysis (different combinations of the Habitat x Order interaction, see Table 7.2): *** $p < 0.0001$, ** $p < 0.01$, * $p < 0.05$, NS $p > 0.05$. Invertebrate orders are indicated in grey.

	FARMLAND						FOREST			
ORDER / FAMILY	**N_{TOTAL}**	**N_{TRAP}**	**%**	**Size**	**ΔN**	**ΔSize**	**N_{TOTAL}**	**N_{TRAP}**	**%**	**Size**
ARANEAE	**7243**	**18.8**	**12.7**	**5.9 (0.09)**	*	*	**2718**	**7.3**	**7.0**	**5.8 (0.10)**
COLEOPTERA	**13652**	**36.1**	**24**	**11.6 (0.08)**	**	***	**10293**	**27.7**	**26.4**	**12.6 (0.09)**
BYRRHYDAE	52	0.1	0.1				24	0.1	0.1	
CANTHARIDAE	1024	3	1.8				449	1.2	1.2	
CARABIDAE	7204	19	12.6				3366	9	8.6	
CARABIDAE LARVA	748	2	1.3				454	1	1.2	
CERAMBYCIDAE	110	0.3	0.2				245	0.8	0.6	
CHRYSOMELIDAE	22	0.05	0.0				30	0.1	0.1	
COCCINELLIDAE	24	0.05	0.0				9	0.02	0.0	
CURCULIONIDAE	151	0.4	0.3				120	0.3	0.3	
ELATERIDAE	573	1.5	1.0				249	0.7	0.6	
GEOTRUPIDAE	146	0.4	0.3				1943	5.2	5	
HISTERIDAE	309	0.8	0.5				326	0.9	0.8	
HYDROPHILIDAE	87	0.2	0.2				86	0.3	0.2	
LAGRIIDAE	40	0.1	0.1				22	0.1	0.1	
OEDEMERIDAE	207	0.5	0.4				269	0.7	0.7	
SCARABAEOIDAE	646	1.7	1.1				73	0.2	0.2	
SILPHIDAE	924	2.4	1.6				1628	4.3	4.2	
STAPHYLINIDAE	1385	3.6	2.4				1000	2.6	2.6	
DERMAPTERA	**45**	**0.1**	**0.1**	**11.2 (0.45)**	**NS**	**NS**	**3**	**0.00**	**0.0**	**11.6 (1.73)**
DIPTERA	**18951**	**49.3**	**33.3**	**9.4 (0.08)**	**	**NS**	**13416**	**36**	**34.5**	**9.7 (0.09)**
MUSCIDAE/CALLIPHORIDAE	17127	45	30.1				12220	32.9	31.4	
STRATIOMIIDAE	919	2	1.6				772	2	2	
SYRPHIDAE	813	2	1.4				355	0.9	0.9	
TIPULIDAE	92	0.3	0.2				69	0.2	0.2	
HETEROPTERA	**113**	**0.3**	**0.2**	**7.6 (0.29)**	**NS**	**NS**	**37**	**0.1**	**0.1**	**7.3 (0.51)**
HEMIPTERA	**268**	**0.7**	**0.5**	**8.8 (0.20)**	**NS**	***	**210**	**0.6**	**0.5**	**8.0 (0.22)**
CERCOPOIDAE	220	0.6	0.4				106	0.3	0.3	
CICADELLIDAE	48	0.1	0.1				104	0.3	0.3	
HYMENOPTERA	**2074**	**5.4**	**3.6**	**10.2 (0.10)**	***	***	**3950**	**10.5**	**10.1**	**9.5 (0.10)**
APOIDAE	261	0.7	0.5				304	0.8	0.8	
FORMICIDAE	463	1.2	0.8				1855	5	4.8	
ICHNEUMONIDAE	466	1.2	0.8				342	0.9	0.9	
SPHECIDAE	53	0.1	0.1				77	0.2	0.2	
TENTHREDINIDAE	812	2.1	1.4				1364	3.6	3.5	
VESPIDAE	19	0.1	0.0				8	0.02	0.0	
ISOPODA	**592**	**2**	**1.0**	**7.2 (0.15)**	**NS**	**NS**	**193**	**0.5**	**0.5**	**7.3 (0.23)**
JULIDA	**698**	**1.8**	**1.2**	**10.8 (0.14)**	**NS**	***	**663**	**1.8**	**1.7**	**16.3 (0.09)**
LEPIDOPTERA	**387**	**1**	**0.7**	**15.7 (0.17)**	**NS**	***	**343**	**0.9**	**0.9**	**15.1 (0.18)**
MECOPTERA	**12721**	**33**	**22.3**	**16.1 (0.08)**	**	**NS**	**6854**	**18.4**	**17.6**	**16.3 (0.09)**
PANORPIDAE	12721	33	22.3				6854	18.4	16.0	
NEUROPTERA	**30**	**0.1**	**0.1**	**12.4 (0.55)**	**NS**	**NS**	**23**	**0.06**	**0.0**	**12.0 (0.63)**
ORTHOPTERA	**199**	**0.5**	**0.3**	**12.4 (0.23)**	**NS**	**NS**	**202**	**0.5**	**0.5**	**13.0 (0.23)**
TRICHOPTERA	**20**	**0.05**	**0.0**	**9.0 (0.68)**	**NS**	**NS**	**21**	**0.06**	**0.1**	**7.9 (0.66)**
TOTAL	**56993**	**149**	**100**	**10.6 (0.11)**	**	*	**38926**	**104**	**100**	**11.0 (0.17)**

Invertebrate size

Invertebrates were on average 6% larger in forest sites than in farmland sites, but this difference was only weakly significant (GLMM, Table 7.2, Fig. 7.1B). We also found strong variation in invertebrate size among species groups and over time (Table 7.2). The habitat-dependent size differences showed consistency in space ('Habitat x Study area'), but varied significantly over time ('Habitat x Year') and, interestingly, between species groups ('Habitat x Order'). In particular, invertebrate size was larger in forest sites for Coleoptera and Myriapoda, whereas Lepidoptera, Homoptera and Hymenoptera were larger in the farmland sites (Table 7.1). Figure 7.2 illustrates that small-sized (between 4-10 mm) and large-sized (14-20 mm) invertebrates occurred more frequently in farmland sites, while medium-sized (10-14 mm) invertebrates were more abundant in forest sites.

Table 7.2 – Results of the general linear mixed models (GLMM) examining variations in invertebrate abundance and size relative to habitat type (Farmland and Forest), year (2008 and 2009), study area (1 and 2) and taxonomic group (see Table 7.1). F and p values refer to the effects in the final model after the backward selection procedure (bold lines) or at the time of variable removal. The parameter estimates refer to the level indicated between brackets as a baseline.

	Invertebrate abundance (log N)				**Invertebrate size (mm)**			
Fixed effect	**df**	**F**	**p**	**β (± S.D.)**	**df**	**F**	**p**	**β (± S.D.)**
(Intercept)	*290.1*	*29.9*	*<0.0001*	*1.38 (0.05)*	*557.3*	*106.1*	*<0.0001*	*10.7 (0.10)*
Habitat (Farmland)	**3962**	**53.4**	**0.007**	**0.08 (0.03)**	**568.4**	**3.1**	**0.03**	**-0.18 (0.10)**
Study area (1)	63.4	0.5	0.46	-0.02 (0.03)	63.3	2.9	0.09	-0.11 (0.06)
Year (2008)	1237	0.3	0.58	0.01 (0.02)	**405**	**473.8**	**<0.0001**	**-0.29 (0.01)**
Order	**3925**	**218**	**<0.0001**	**†**	**964**	**566.2**	**<0.0001**	**†**
Habitat x Study area	62.5	0.03	0.98	-0.006 (0.03)	62.4	0.89	0.35	-0.06 (0.06)
Habitat x Year	1244	0.1	0.72	0.008 (0.02)	**415**	**20.4**	**<0.0001**	**-0.06 (0.01)**
Habitat x Order	**3925**	**4.2**	**<0.0001**	**†**	**964**	**136.9**	**<0.0001**	**†**

Abundance is log-transformed to satisfy the normality assumption
df refers to the denominator degrees of freedom
† For table clarity, separate estimates (± S.D.) for each order are not provided (but see Table 7.1)

Microclimatic conditions

The ground-level temperature was on average 1.05 °C higher in farmland sites than in forest sites (GLMM, $F_{1,13.1} = 9.81$, $P = 0.008$, $T_{FARMLAND} = 15.86 \pm 0.02$ °C, $T_{FOREST} = 14.73 \pm 0.02$ °C, Fig. 7.3). This difference was stable over time ('Habitat x Year': $F_{1,46.5} = 0.51$, $P = 0.48$) and in space ('Habitat x Study area': $F_{1,12.9} = 2.45$, $P = 0.14$). The mean ground-level temperatures were similar between years ($F_{1,46.5} = 1.31$, $P = 0.26$) and study areas ($F_{1,12.9} = 4.09$, $P = 0.07$). In addition, invertebrate abundance was positively related to the mean temperature recorded around the pitfall traps (GLMM, $F_{1,110.8} = 74.2$, $P < 0.0001$, Fig. 7.4). The increase in invertebrate abundance with temperature differed between farmland and forest sites (GLMM, 'Habitat x Temperature': $F_{1,110.8} = 15.0$, $P = 0.0002$), as it was

particularly marked in the forest sites (Fig. 7.4). In contrast, invertebrate size differences were not related to ground-level temperature (P = 0.51).

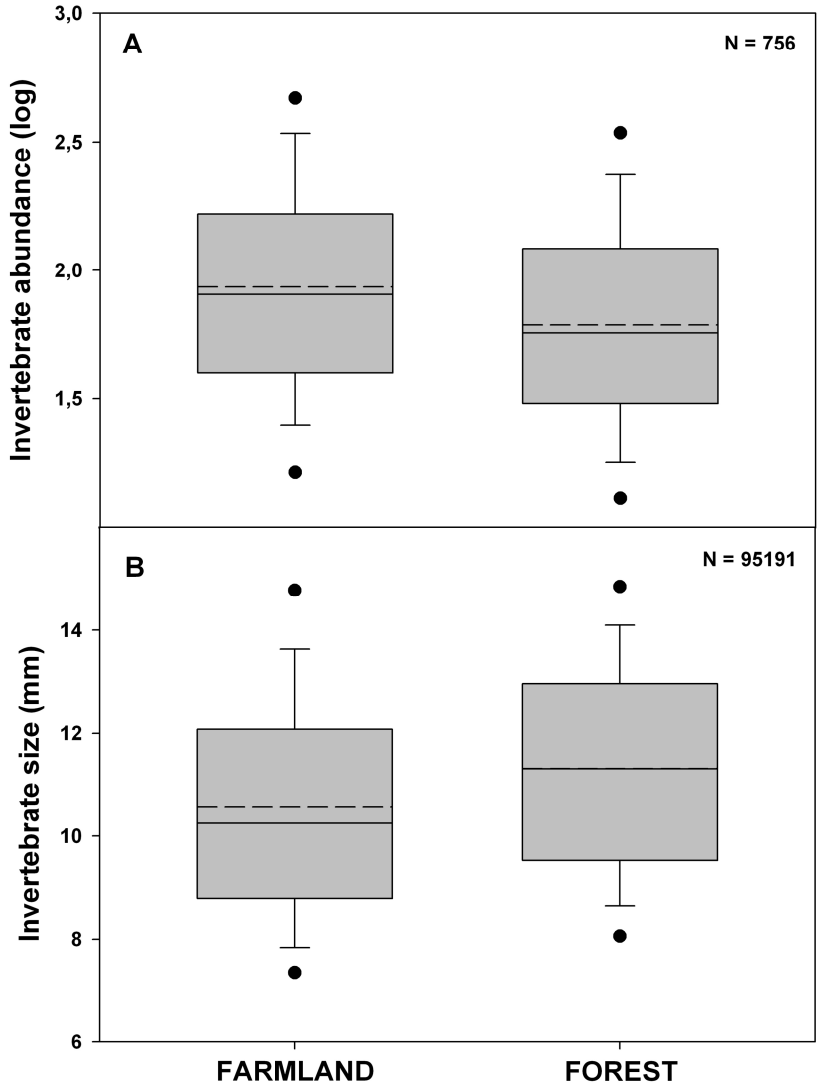


Figure 7.1 – Box-and-whisker plots and quartile distributions (5th and 95th percentiles [⊥ and ┬], min-max [•], mean [--] and median [–]) for invertebrate abundance (A) and invertebrate size (B) per trap in farmland and forest sites. Sample size indicates (a) the total number of pitfall and yellow-pan traps, and (b) the total number of invertebrate items. Habitat-related differences in invertebrate abundance ($F_{1,290.1}$ = 29.9, p<0.0001) and size ($F_{1,557.3}$ = 106.1, p<0.0001) were highly significant.

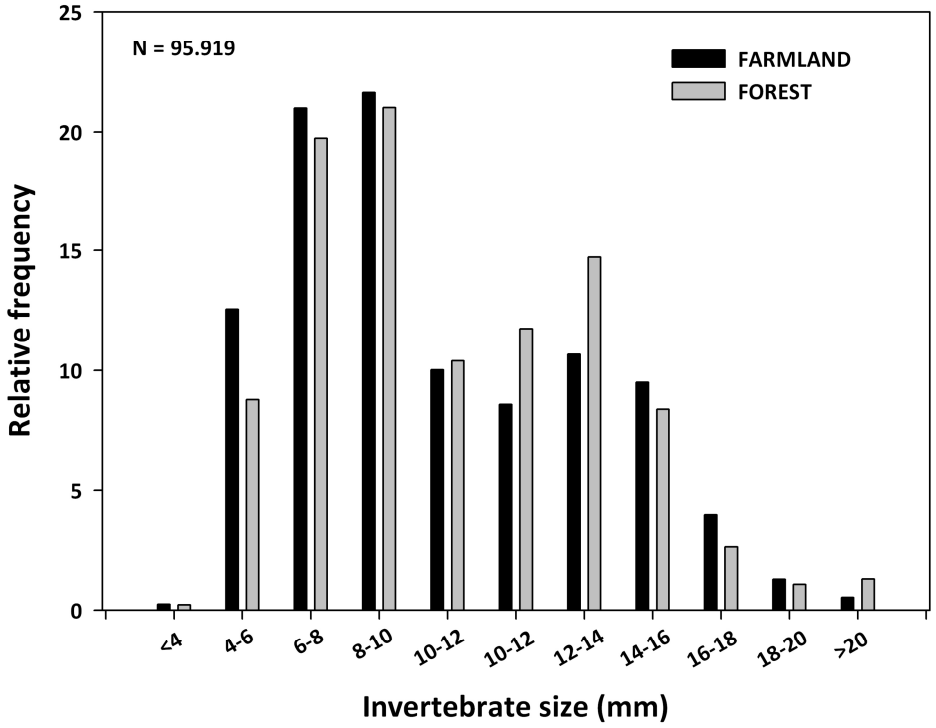


Figure 7.2 – Size distribution of invertebrate items in farmland and forest sites in 2008 and 2009.

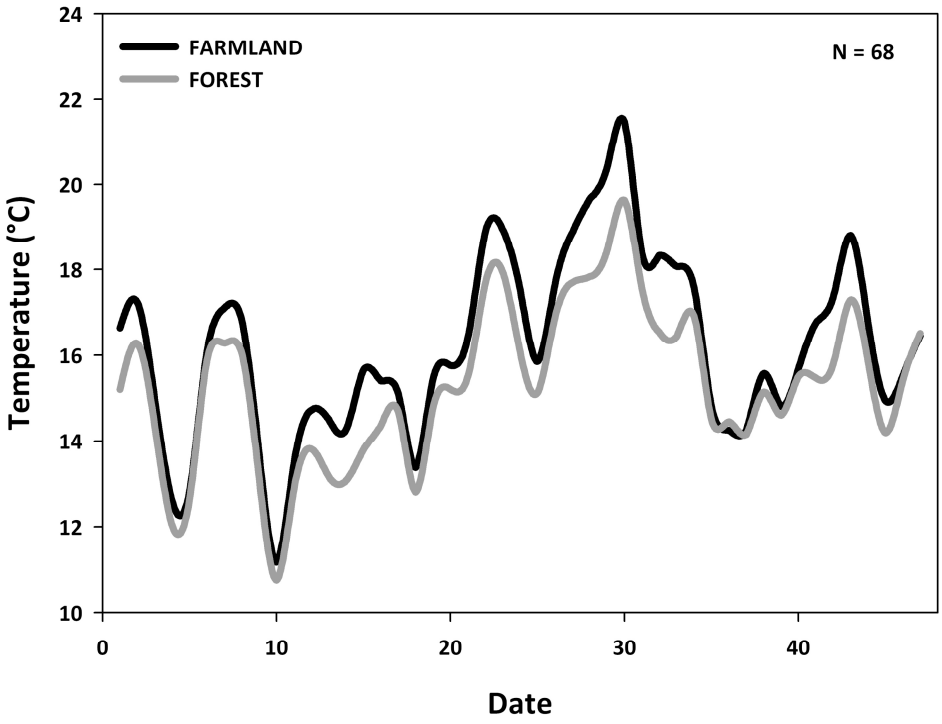


Figure 7.3 – Ground-level temperature curves in farmland and forest sites during the sampling period. Curves are derived from average daily temperatures in 2008 and 2009. Date 0 corresponds to June 1.

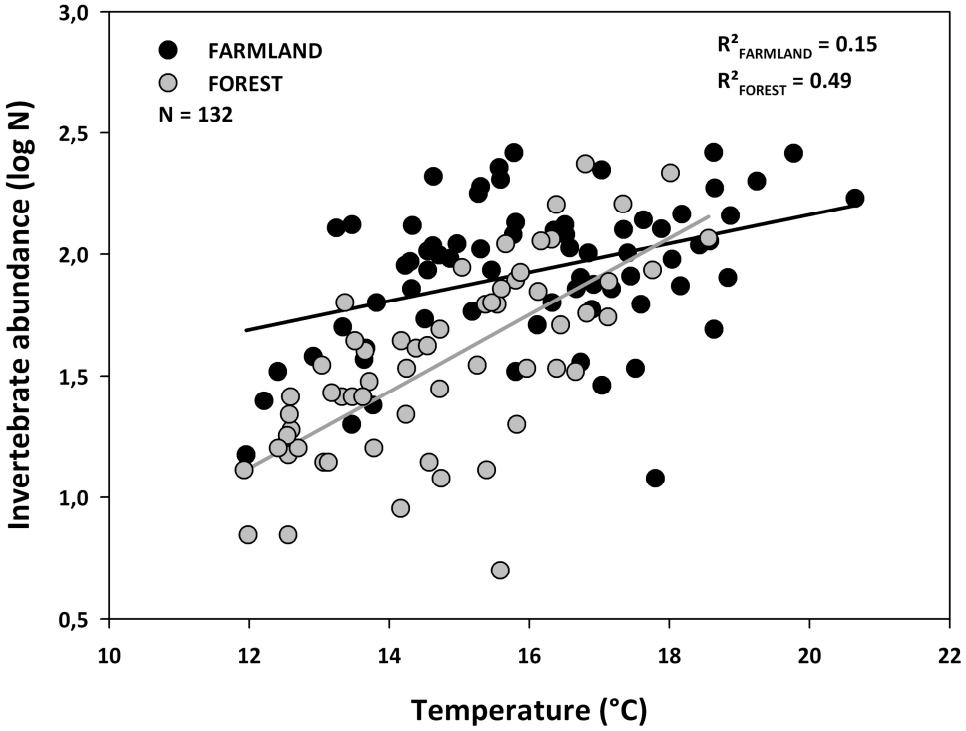


Figure 7.4 – Relationship between invertebrate abundance in pitfall traps and average ground-level temperature in farmland and forest sites during the sampling period in 2008 and 2009.

DISCUSSION

This study compared the distribution of invertebrates in two open habitat types used by a set of early-successional, insectivorous bird species for breeding: farmland (i.e., extensive meadows) and forest plantations (i.e., young Spruce plantations or clearcuts with early-successional vegetation). Trapped items were mostly composed of ground-dwelling and above-ground invertebrates, that is, the most commonly consumed prey during the breeding period of insectivorous bird species. Results show that invertebrates were much more abundant (35%) in farmland sites than in forest sites and that the size of invertebrates was slightly (6%) larger in the forest sites. Higher invertebrate abundance in farmland sites was particularly due to a higher density of spiders, beetles and flies (including scorpion flies), and was also significantly related to higher ground-level temperature in this habitat type. Hence, although early-successional habitats created by farmland and forest land-use were generally associated with the same spectrum of invertebrates, we found considerable differences in invertebrate abundance, and to a lesser extent, invertebrate size, between the two habitat types. Invertebrates are important herbivores and detrivores in terrestrial ecosystems, and variation in plant diversity and productivity may alter their abundances (Perner et al. 2005). In case of bottom-up ecosystem regulation, differences in the abundance of consumers (here invertebrates)

are caused by the underlying dynamics in the plant communities that may in turn differ between the habitat types. Given that the studied farmland and forest sites strongly differed in vegetation composition and structure, this provides scope for differential trophic effects although this would require further testing.

Forest harvesting dramatically modifies the above- and below-ground level resources and abiotic conditions (e.g. Heithecker & Halpern 2006) compared to the post-disturbance ecosystems in natural forests (Marshall 2000, Lindenmayer & McCarthy 2002, Siira-Pietikäinen et al. 2003, Swanson et al. 2011). In large-sized cutblocks of plantation forests, environmental conditions may impact the habitat quality of invertebrates in several ways. In particular, post-disturbance logging or elimination of native plant species may homogenize the vegetation structure or eliminate leaf-litter or woody debris (Swanson et al. 2011). Leaf-litter and woody debris are typically retrieved after clearcutting to promote the plantation of new trees, but have been shown to offer important resources for invertebrates (Abbott & Crossley 1982, Magura et al. 2005). Therefore, clearcutting has been shown to significantly alter the invertebrate communities compared to pre-disturbance conditions (e.g. Duguay et al. 2000, Van Wilgenburg et al. 2001, Pohl et al. 2007) or to alternative semi-natural management practices using burning (e.g. Greenberg & McGrane 1996, Lindenmayer & McCarthy 2002).

After clearcutting, there will be succession by gradual recolonization processes of plants and the associated animal communities. The rate at which recolonization occurs is strongly depending on the distance to source populations and the dispersal capacities of organisms. In our study system, farmland offers food-richer breeding habitat than forest for early-successional, insectivorous birds even if this habitat is under the influence of agricultural activities. We argue that open areas in Spruce plantations provide much lower invertebrate abundance because the recolonization processes after clearcutting is generally slow, especially for ground-dwelling Coleopterans (Koivula et al. 2002, du Bus de Warnaffe & Lebrun 2004, Niemelä et al. 2007, Pohl et al. 2007) and Arachnids (Matveinen-Huju & Koivula 2008). This contrasts with highly-mobile species such as Lepidoptera and Hymenoptera, also found in other studies to quickly colonize post-harvesting areas in forest plantations (Van Wilgenburg et al. 2001, Summerville & Crist 2002, Pengelly & Cartar 2010).

The observed differences in microclimate between farmland and forest sites likely are an important factor explaining, at least partly, the difference in invertebrate abundance. Complex interactions between the amount of vegetated surface, solar radiation, evaporation or soil moisture shape different microclimates between the habitats, which in turn affects the local distribution of the organisms (Chen et al. 1999, Bennie et al. 2008). Fitness (i.e. reproductive performance and/or

survival) and dispersal in ectothermic organisms are negatively affected by low temperatures (Honěk 1988, Coxwell & Bock 1995, Suggitt et al. 2011). In turn, this may also play a role to explain the higher invertebrate abundance in farmland sites. As a consequence of the importance of temperature for the abundance and distribution of invertebrates, fine-scaled differences in vegetation structures can be highly significant for understanding how regional climates are translated in the microclimates.

There is strong evidence of an effect of food abundance on the reproductive performance of insectivorous bird species, including early-successional species such as the Red-backed shrike (*Lanius collurio*) (Goławski & Meissner 2007, Hollander et al. 2011, see Chapter 8), the Stonechat (*Saxicola torquata*) (Greig-Smith & Quicke 1983) or the Yellowhammer (*Emberiza citronella*) (Hart et al. 2006). Therefore, the extent to which the differences in invertebrate abundance and size between farmland and forest sites may affect the reproductive performance of early-successional bird species warrants further research. Using the Red-backed shrike as a model organism that occupies both habitat types, we have recently shown evidence of maladaptive habitat selection in the same farmland-forest landscape as we have studied here: territorial males of this migratory songbird showed a preference for breeding in forest sites, but reproductive performance (e.g. nestling body condition), was on average lower in forest sites compared to the farmland sites (Hollander et al. 2011). In the Red-backed shrike, we also showed that lower abundance of invertebrates in forest sites contributes to the lower offspring quality in this species (see Chapter 8). However, differences in nestling body conditions may also be explained by differences in the use, or in the nutritional quality, of the food resources. Optimal foraging theory indicates that variation in food abundance may be accompanied by changes in the nature, or size, of invertebrate prey items delivered to the nestlings (Pyke et al. 1977).

Many studies have analysed the combined effect of invertebrate abundance and quality on the reproductive performance of insectivorous bird species. Some of them examined how food quantity and quality might be traded off against increased food demand for nestlings during the breeding season, and demonstrated that higher food abundance permits the higher selection for high-quality prey (e.g. Wright et al. 1998, Grieco 2001). It has also been shown that the prey diversity may be even more important than abundance *per se*, such as in Grey Partridge (*Perdrix perdrix*) (Borg & Toft 2000). In Water pipits (*Anthus spinoletta*) however, reproductive performance was to a large extent determined by invertebrate abundance, whereas the nutritional content of invertebrate items did not relate to nestling body condition (Brodmann et al. 1997), even if pipits preferentially selected large-sized invertebrates (Brodmann & Reyer 1999). To date, it remains unclear how habitat-dependent differences in invertebrate abundance and invertebrate size contribute to significant differences in the reproductive performance of early-successional bird species. In this respect,

habitat quality is to be analyzed relative to food resource availability and fitness returns in farmland and forest sites.

Over the last decades, farmland intensification has driven strong population declines in early-successional bird species across Europe (Donald et al. 2001). A number of studies have highlighted the significance of invertebrate food depletion for early-successional bird decline (e.g. Britschgi et al. 2006, Hart et al. 2006). Interestingly, open areas in forest plantations have been suggested to provide a new refuge habitat for some early-successional bird species also breeding in farmland (e.g. Paquet et al. 2006, Paz Acuña & Estades 2011). In this study, we showed that open habitats created by farmland and forest management may share food resources for insectivorous, early-successional birds, but invertebrate abundance is substantially different in both habitat types. This important aspect of the conservation of early-successional wildlife has not been appreciated so far. Therefore, we draw attention to the fact that human-created habitats like early-successional areas following clearcutting in forest plantations may not represent highly favourable habitat as it has been interpreted from presence surveys assuming that the presence of a species reflects suitable habitat. The growing literature on ecological trapping indicates that this assumption may for instance be wrong in recent human-modified environments (Schlaepfer et al. 2002, Hollander et al. 2011).

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Chapter 8

Habitat-dependent prey availability and offspring provisioning explain an ecological trap in a migratory bird

In this chapter, we explore how the variation in food availability between farmland and forets habitats impacts the reproductive performance of the Red-backed shrike, and thus might explain a mechanism for the ecological trapping in this species.

Manuscript resubmitted after revision (Functional Ecology)

ABSTRACT

Ecological trapping implies a preference for low-quality habitats over higher-quality options. Although such a maladaptive decision-making has been shown in a range of organisms, the mechanisms that underlie this habitat selection pattern often remain unidentified. We tested in a human-modified environment whether food availability and food use of a migratory species operate as functional drivers of an ecological trap. The Red-backed shrike (*Lanius collurio*) is a migratory bird that was shown to breed preferentially in forest plantation clearcuts where reproductive performance is however markedly lower than in the traditional farmland habitat. We examined whether differences in food availability between forest and farmland habitats resulted in contrasting food provisioning to the offspring with, in turn, significant impact on the quality of the offspring. Invertebrate prey items for shrikes were 41% more abundant in farmland and prey size was 6% larger in forest habitat. Opposite to the pattern of prey size availability, larger prey items were delivered to the offspring in farmland than in forest habitat. Feeding visits by the parents were 22% more frequent in farmland and evidence of strong among-nestling competition for food was found in forest only. This study demonstrates the existence of food limitation for an organism in a habitat type associated with high preference but low reproductive performance. This result offers a functional explanation for the mismatch between habitat preference and quality, and hence, for an ecological trap in the wild. Beyond the case of migratory birds, this study draws attention to the point that human-modified environments may lead to a biased perception of habitat quality relative to food availability and may induce an ecological trap for organisms that allocate only a limited time budget to habitat selection decision-making.

INTRODUCTION

In human-modified environments, organisms may preferentially settle in low-quality habitats, although high-quality habitats are available; this form of maladaptive behaviour is known as an ecological trap (reviewed in Schlaepfer et al. 2002, Battin 2004, Robertson & Hutto 2006). In different animal taxa, evidence of an ecological trap has been found in the wild (e.g. Horváth & Zeil 1996, Flaspohler et al. 2001, Hawlena et al. 2010, Weldon & Haddad 2005, Gilroy et al. 2011, Latif et al. 2011, Northrup et al. 2012). Many organisms have to rely on environmental cues that allow fast assessment of habitat quality and reduce search costs including the time to find a suitable breeding site (e.g. Stamps 2001, Hromada et al. 2008, Fuller 2012). These environmental cues are expected to be reliable at the time of habitat selection, but their use has been shaped by natural selection to reflect habitat quality and high fitness expectations later in the breeding season (Storch & Frynta 1999, Kokko & Sutherland 2001, Stamps 2001). It has been shown that organisms may successfully use a variety of cues reflecting local environmental conditions, including vegetation structure (Mcnett & Rypstra 2000, Marshall & Cooper 2004), food availability (Marshall & Cooper 2004, Hromada et al. 2008, Mestre & Lubin 2011), anti-predation shelters (Thomson et al. 2006, Mathis & Unger 2012) or presence of conspecifics (Fletsher 2006). Maladaptive habitat selection may, however, occur when there is a mismatch between the environmental cues used by the organisms during habitat selection and the fitness consequences of the individual decision (Schlaepfer et al. 2002, Battin 2004, Robertson & Hutto 2006). It has been proposed that migratory organisms are more likely to misevaluate habitat quality during the habitat selection stage (Battin 2004) and this most probably relates to the limited time budget allocated to settlement decisions (Orians & Wittenberger 1991, Storch & Frynta 1999, Stamps 2001, Hromada et al. 2008, Fuller 2012).

Food availability is a key component of habitat quality in many species because the selection of habitats with sufficient food is a prerequisite for high reproductive success. A shortage of food resources generally results in reduced offspring quantity or quality (i.e. body condition), and hence, lower fitness (Martin 1987, 1995). However, food availability during the breeding period may be difficult to perceive and evaluate correctly during the stage of habitat selection (Orians & Wittenberger 1991, Török et al. 2004, Fuller 2012). A misevaluation of food resources has, therefore, the potential to induce a mismatch between habitat preference and habitat quality (Kloskowski 2012). This issue has been neglected so far and most of the previous studies on maladaptive habitat selection in migratory organisms including birds, restricted the analysis to breeding success (i.e.

offspring production) and associated nest predation (Flaspohler et al. 2001, Weldon & Haddad 2005, Gilroy et al. 2011, Hollander et al. 2011, Latif et al. 2011, see also Chapter 6). There is a lack of studies that examine the link between habitat preference and fitness consequences relative to food availability and how food resources are used by the organisms in different habitat types (Kloskowski 2012).

Here, we deal with the case of an ecological trap for a farmland bird in a mixed farmland-forest landscape of NW-Europe. The landscape is characterized by a mosaic of farmland areas and forest plantations. In the recent decades, rotational clearcutting management in the plantations have created patches of early-successional vegetation attractive to several disturbance-dependent, farmland bird species (Brawn et al. 2001, Paquet et al. 2006, Swanson et al. 2011). For the migratory, insectivorous Red-backed shrike (*Lanius collurio*), we have shown evidence of maladaptive habitat selection: the species prefers to settle in the open areas in forest, where the reproductive performance (i.e. offspring quantity and quality) is lower than in the traditionally used farmland habitat (Hollander et al. 2011, 2012, see Chapters 4 and 5). A variety of mechanisms (e.g. between-habitat differences in nest predation rates, parazitation levels, microclimate suitability, food quantity and/or quality) may induce lower fitness in preferred habitat type (Schlaepfer et al. 2002). In this paper, we test whether food-related differences between habitat types may contribute to a functional understanding of an observed pattern of maladaptive habitat selection. More specifically, we examine if lower food availability may explain the pattern of fitness reduction in the preferred habitat type via an effect on food provisioning to the offspring (i.e. amount of nest visits by the adults and size of the food items delivered to the offspring). We sampled food availability and food provisioning in both habitat types occupied by the species and we analysed these food-related parameters relative to offspring quantity, offspring quality and habitat preference. We explain why our results help identifying part of the mechanisms underlying maladaptive habitat selection in a human-modified environment.

MATERIALS & METHODS

Study species and study area

The Red-backed shrike is a long-distance migratory bird that occupies the breeding sites during a short period only (May-July). The feeding ecology of the species is well-documented and food resources are mainly invertebrates (e.g. Coleoptera and Hymenoptera) (Tryjanowski et al. 2003, Goławski & Meissner 2008). The preference of Red-backed shrikes for open areas in forests over the

farmland habitat type has been reported in different European countries (e.g. Hollander et al. 2011, Söderström & Karlsson 2011). In Europe, it is a species of conservation concern and future negative population trends are expected due to ongoing agriculture intensification (Brambilla et al. 2010). Hence, it becomes of conservation interest to examine the suitability of open areas in forests as an alternative breeding habitat type for shrikes in Europe (Söderström & Karlsson 2011).

Two 400-km^2 study areas were located in the Ardenne region in southern Belgium (centres of study areas: 50°14'N 5°50'E and 49°49'N 5°39'E) where the shrike occupies two distinct habitat types: 1) farmland covered by pastures and hay meadows with hedgerows and shrubs, and 2) large-sized open patches (range of area: 2-10 ha) in Spruce forests composed of young plantations (less than 10 years old) or natural early-successional vegetation after forest harvesting (Hollander et al. 2011). In this landscape, we determined during three consecutive breeding seasons (2008-2010) the habitat preference and the reproductive performance of the shrikes, and we found evidence of maladaptive habitat selection (for details see Hollander et al. 2011, 2012, Chapters 4 and 5). Breeding sites (N = 58 in farmland and N = 60 in forest) were defined as open patches in farmland or forest with early-successional and shrubby vegetation. Each breeding site enclosed one or a few shrike territories (N = 104 in farmland and N = 109 in forest). Shrike density was similar in both habitat types (0.48 and 0.51 shrike territories per km² in farmland and forest, respectively).

Food availability

In 2008 and 2009, we studied food availability in 67 shrike territories (N = 36 in farmland or 35% of all shrike territories, and N = 31 in forest or 28% of all shrike territories). Males and females were observed during foraging activities and nest visits at a distance of 200 m with binoculars in order to determine the territorial boundaries, the frequently used vantage points and the location of the nests. In each shrike territory, we used four pitfall traps (white plastic cups, diameter = 11 cm, depth = 14 cm) to sample ground-dwelling invertebrates and one yellow-pan trap (yellow plastic cup, diameter = 22 cm, depth = 9 cm) to sample flying invertebrates (Duelli et al. 1999). Traps were placed in the shrike territories within the mostly used foraging areas (i.e., within a 50 m buffer around the vantage points), in the vicinity of the nest locations (i.e., within max. 100 m distance) and at a minimum distance of 15 m from each other to avoid interference (Ward et al. 2001). All traps were placed by the same researcher (F.A.H.) to avoid among-researcher variation. There was a comparable trapping surface of 380 cm² between the four pitfall traps and the single yellow-pan trap within a territory. Each pitfall trap was dug in the ground and filled for 1/3 with a 50:50 solution of ethylene glycol and ethanol; some detergent was added to minimize surface tension. Yellow-pan traps were

placed at a height of 1 m on a stick and at 2 m from a shrub or isolated tree. They were also filled for 1/3 with the same solution as for the pitfall traps. In each year, sampling occurred from June 1 to July 15 and traps were emptied twice during this period (end of June and mid of July). All invertebrates were conserved in 96% ethanol and identified to the order or family level in the laboratory. Invertebrate abundance was calculated as the number of items collected in the traps. Body length of individual invertebrates was measured with digital callipers (CONRAD PRO®, precision: ± 0.01 mm) and used as a proxy for invertebrate biomass (Hódar 1996). Appendages such as antennae, legs or wings were excluded from the body length measurements.

Offspring quantity and quality

Shrike nests were located during the three consecutive breeding seasons (2008-2010). Nests were mostly visited during the nestling period since adults are likely to abandon their eggs after disturbance during incubation (Olsson 1995). Nestling age was estimated with a 1-day precision by means of visual comparisons with feather characteristics of age-known nestlings (Olsson 1995). The number of nestlings (i.e. offspring quantity) and their body condition were measured at the age of 12 days (range: 11-15 days). For nestling condition, we measured tarsus length and the outermost primary wing length with digital callipers (precision: ± 0.01 mm), and body weight with a balance (KERN®, precision: ± 0.1 g). Since these size-related measures were strongly correlated, we used a principal component analysis (PCA) to reduce the information to a single variable (PC1) that was used as a synthetic measure of nestling body condition (variance explained: 89%). Offspring quality was calculated for each nest as the average nestling body condition.

Food provisioning

In June and July 2010, shrike nests were video-recorded in 61 territories (N = 29 in farmland and N = 32 in forest) to collect food provisioning data (camera-model: JVC Everio 40Go). Each recording session started in the morning (at 8 am) and lasted for 3 hours. To avoid strong weather-mediated variation in food provisioning, we recorded under suitable conditions only (i.e., no rain, wind velocity < 10 km h^{-1}, cloud cover < 70% and temperature > 18°C). Only nestlings of age between 10 and 15 days were recorded. Food provisioning was the rate of nest visits by the parents and was calculated as the number of times the parent birds delivered prey to their offspring per hour. For each nest visit, we recorded the time elapsed since the previous one, the prey size and the prey type (i.e. order or family). Prey size was estimated relative to the bill length of the parent birds and allocated to one of

the following classes: 1) prey smaller, 2) prey of comparable length and, 3) prey larger than the bill length.

Statistical analyses

The central aim of our paper is testing whether food availability and/or food provisioning is lower in the preferred forest habitat compared to the alternative farmland habitat because food-related mechanisms may contribute to explaining the observed pattern of lower offspring quality in the forest habitat.

We used generalized linear mixed models (GLMM with normal distribution and identity link functions, Maximum Likelihood estimations) with breeding site (class variable) as random factor to analyse the variation in offspring quality between habitat types and with shrike territory (class variable) as a random factor to analyse the variation in food availability between habitat types. GLMM with multinomial distribution, cumulative-logit link functions, Maximum Likelihood estimations and shrike territory as random factor were used to examine the between-habitat differences in the size of prey items delivered to the nestlings. We used Maximum Likelihood estimations in the GLMM analyses (instead of Restricted Maximum Likelihood estimations) to allow a sound comparison of models with a varying number of fixed effects (Pinheiro & Bates 2000, Bolker et al. 2009). Generalized linear models (GLM with normal distribution and identity link function, Restricted Maximum Likelihood estimations) without any random factor were used to analyse the between-habitat variation in the rate of nest visits because measures were collected in a single nest per breeding site.

Food availability – We first selected from all invertebrates collected in the traps only the prey types that were shown to be used for the diet of the nestlings based on our video-recording sequences (see Results). We then analysed invertebrate prey abundance (continuous response, log-transformation) and prey size (continuous response) relative to habitat (class variable: farmland and forest), year (class variable: 2008 and 2009), study area (class variable: area 1 and 2) and two interaction terms of interest: 'habitat x year' and 'habitat x study area'. The interaction terms were included to examine whether differences in prey abundance and size between habitat types were stable over time and in space, respectively. Trap type (pitfall or yellow-pan trap) and sampling period (end of June or mid of July) were used as covariates (class variables) in the GLMM because their effects on the response variables were to be accounted for but were not of direct interest in our study.

Food provisioning – We analysed food provisioning at the level of the nest and at the level of the individual visit of the parent birds to the nest. First, we examined whether the rate of nest visits (continuous response) differed between habitat types. Offspring quantity and nestling age were included as covariates in the GLM analyses. Second, we tested whether prey size (multinomial categorical response) during the parental visits to the nest differed between habitat types. Recording date, offspring quantity, nestling age, sex of the parent, time since the previous visit and weather conditions the day prior to recording were included as covariates in the GLMM analyses. Weather conditions included the mean ambient temperature, wind velocity and precipitation during the daytime (for details see Hollander et al. 2011, Chapter 4). The rate of nest visits and the size of prey delivered to the nests might be correlated in time if parent birds do not exploit randomly the food resources in their territories. To control for this possible temporal autocorrelation in the parental visits to the nest, we fitted a first-order autoregressive covariance structure to this GLMM.

Offspring quality – We analysed variation in offspring quality (continuous response) at two different levels. First, we tested whether offspring quality differed between habitat types for the sample of nests located in the territories where food provisioning data were also recorded in 2010. Second, we used the full set of data collected in 2008-2010 and we added offspring quantity in the GLMM analyses to examine how offspring quality was linked to the number of nestlings competing for food within the same nest and how this among-nestling competition differed between the habitat types ('habitat x offspring quantity' interaction). We included nestling age as a covariate in both analyses because nestling condition varies with age.

All analyses were performed with R 2.13 using an information-theoretic model selection procedure (Burnham & Anderson 2002) based on AIC_c (Akaike Information Criterion corrected for small sample sizes). Full models included the whole set of independent variables and covariates for the analysis of food availability (prey abundance and prey size), food provisioning (rate of nest visits and prey size) and offspring quality. All possible combinations of variables ('candidate models') were then derived from the full models. Marginality rules were followed so that an interaction was only included in a candidate model when both main effects were also included. The covariates were forced in all candidate models. ΔAIC_c were calculated for each candidate model to reflect the difference with the best candidate model (i.e., the model with the smallest AIC_c). The candidate models were then ranked relative to each other based on ΔAIC_c to retain the best-fitting and most parsimonious one(s) ($\Delta AIC_c < 2$ against the best model was considered as a threshold, Burnham & Anderson 2002). The relative support of the candidate models was then obtained by scaling them according to their AIC_c weight of evidence (AIC_c weights, see Burnham & Anderson 2002). The relative importance of each variable (w_+) was estimated by summing the AIC_c weights across all candidate models in which the

variable occurred. The model-averaged parameter estimates (β), the estimate precision (unconditional standard errors) and the w_+ values were calculated to inform on the strength of importance of each variable.

RESULTS

Table 8.1 shows the set of candidate models that are supported according to the model selection procedure ($\Delta AIC_c < 2$) for the analyses of food availability in the territories, food provisioning to the nestlings and offspring quality.

Table 8.1 – Summary of the supported ($\Delta AIC_c < 2$) and best non-supported ($\Delta AIC_c > 2$, between brackets) models for the different response variables related to food availability, food provisioning and offspring quality. The AIC_c weight indicates the support for each model. ΔAIC_c refers to the differences in AIC_c between the model and the best candidate model with the smallest AIC_c. The number of parameters (K) is also reported for each model.

Analyses	Response	Supported and (best non-supported) models	K	Log Likelihood	R^2	ΔAIC_c	AIC_c weight
FOOD AVAILABILITY	**Prey abundance**	- habitat + year	7	-4508.4	0.33	0.00	0.38
		- habitat + year + study area	8	-4508.2	0.33	1.70	0.16
		- (habitat + year + habitat x year)	(8)	(-4508.3)	0.33	(2.03)	(0.13)
	Prey size	- habitat + year + study area	8	-1611.9	0.54	0.00	0.50
		- habitat + year + study area + habitat x year	9	-1611.8	0.54	1.80	0.20
		- (habitat + year + study area + habitat x study area)	(9)	(-1612.0)	0.54	(2.00)	(0.18)
FOOD PROVISIONING	**Number of visits x h^{-1}**	- habitat + (covariates)	5	-217.4	0.78	0.00	0.91
		- (covariates)	(4)	(-220.9)	0.42	(4.68)	(0.09)
	Prey size	- habitat + (covariates)	10	-3130.5	0.38	0.00	0.88
		- (covariates)	(9)	(-3133.5)	0.28	4.06	(0.12)
OFFSPRING QUALITY	**Body condition** (video-recorded nests)	- habitat + (covariates)	5	-62.2	0.56	0.00	0.90
		- (covariates)	(5)	(-65.7)	0.32	(4.54)	(0.10)
	Body condition (all nests)	- habitat + offspring quantity + habitat x offspring quantity + (covariates)	7	-534.5	0.64	0.00	0.77
		- (habitat + offspring quantity + covariates)	(9)	(-536.8)	0.63	(2.49)	(0.22)

Food availability

Prey abundance

A grand total of 52187 invertebrates relevant to the diet of the Red-backed shrike nestlings were sampled in the different traps (Mecoptera: 38%, Coleoptera: 36%, Arachnidae: 19%, Hymenoptera: 3%, Diptera: 2%, Orthoptera: 1%, Other: 1%). Prey abundance was on average 41% lower in forest

than in farmland (Table 8.1, 'habitat': β = - 0.22 ± 0.05, w_+ = 100%). Although the supported models included year and study area, there was only weak support for differences in abundance between years (Table 8.1, 'year': β = 0.02 ± 0.02, w_+ = 55%) and study areas (Table 8.1, 'study area': β = 0.02 ± 0.03, w_+ = 45%). The higher abundance of invertebrates in the farmland habitat was consistent over time and space (Table 8.1, 'habitat x year' and 'habitat x study area' interactions: all w_+ < 20%).

Prey size

Prey items were on average 6% larger in forest than in farmland (Table 8.1, 'habitat': β = 0.8 ± 0.3 mm, w_+ = 97%). There was clear support for differences in invertebrate size between years (Table 8.1, 'year': 2009 > 2008, β = 1.1 ± 0.2 mm, w_+ = 100%) and also between the study areas (Table 8.1, 'study area': 2 > 1, β = 1.0 ± 0.3 mm, w_+ = 100%), but differences between habitat types were consistent over time and space (Table 8.1, 'habitat x year': β = - 0.05 ± 0.1 mm, 'habitat x study area': β = - 0.04 ± 0.2 mm, all w_+ < 28%).

Food provisioning

Nest visits by the parents

On average, the rate of nest visits was 22% lower in forest than in farmland (Table 8.1, 'habitat': β = - 5.6 ± 2.1, w_+ = 91%, Fig. 8.1A), thereby indicating that, on average, parent birds delivered prey to their offspring more often in the farmland than in the forest habitat.

Prey size delivered by the parents

Figure 8.1B illustrates that large-sized prey items are more often delivered to the nests in farmland, whereas small-sized items constitute a more important part of the diet in the forest habitat. Intermediate-sized prey items were delivered with a similar frequency in both habitat types. Hence, prey items delivered to the nests are larger in farmland than in forest (Table 8.1, 'habitat': β = - 0.36 ± 0.07, w_+ = 88%).

Offspring quality

Offspring quality was higher in farmland than in forest, both for the video-recorded nests (Table 8.1, 'habitat': β = - 0.44 ± 0.17, w_+ = 90%, Fig. 8.2) and for all nests sampled in 2008-2010 (Table 8.1,

'habitat': β = - 0.5 ± 0.1, w_+ = 100%, Fig. 8.3). Offspring quality decreased with an increasing offspring quantity in the forest habitat, but not so in the farmland habitat (Table 8.1, 'habitat x offspring quantity': β = - 0.5 ± 0.2, w_+ = 78%, Fig. 8.3).

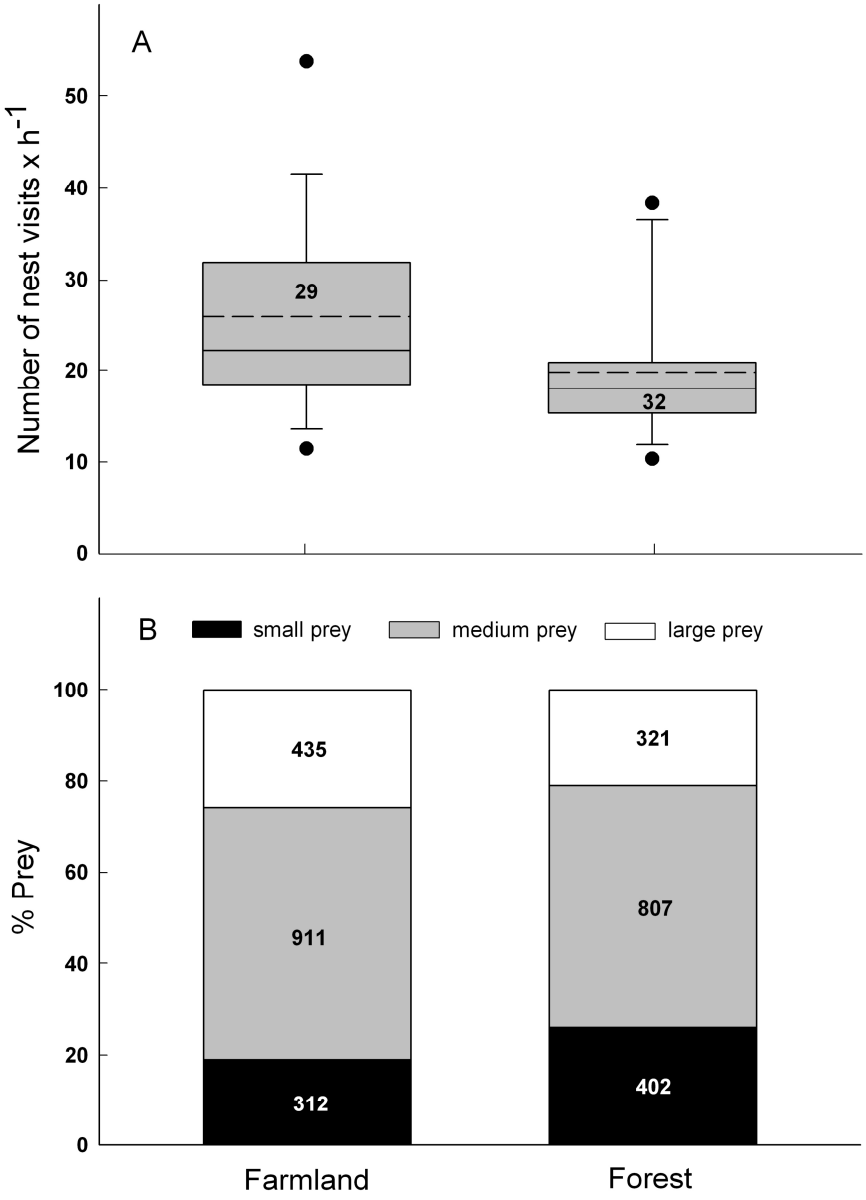


Figure 8.1 – (A) Box-and-whisker plots (5th and 95th percentiles [⊥ and ┬], min-max [•], mean [--] and median [–]) for the number of nest visits by the parent shrikes in farmland and forest habitats. (B) Size of prey items delivered to the nestlings by the parent shrikes in farmland and forest habitats (black: prey size < bill length; grey: prey size = bill length; and white: prey size > bill length). Sample sizes indicate the number of nests (A) and the number of nest visits by the parent birds (B).

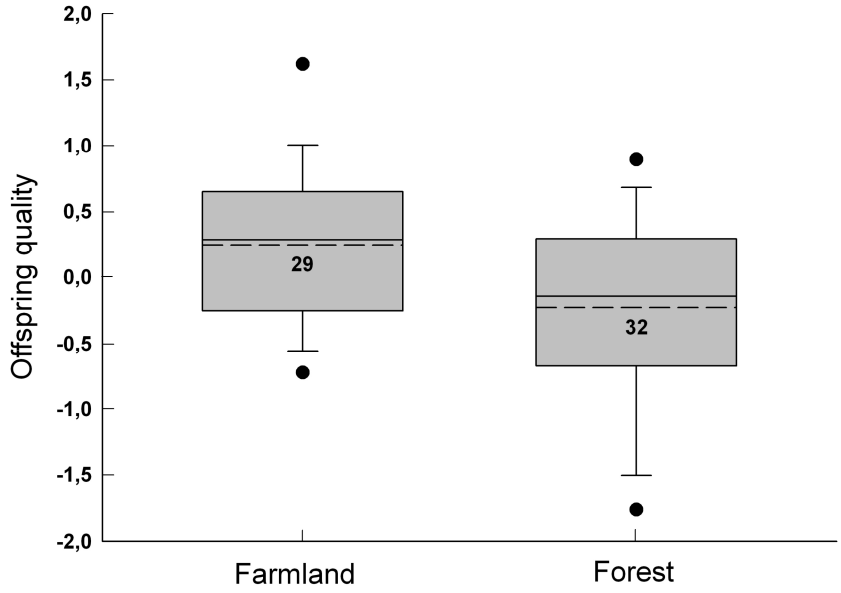


Figure 8.2 – Box-and-whisker plots (5th and 95th percentiles [⊥ and ┬], min-max [•], mean [--] and median [–]) for offspring quality (i.e. average nestling body condition per nest) in video-recorded nests in farmland and forest habitats. Nestling body condition is the first axis of a principal component analysis (PCA) based on tarsus length, wing length and body weight. Sample sizes indicate the number of video-recorded nests in 2010.

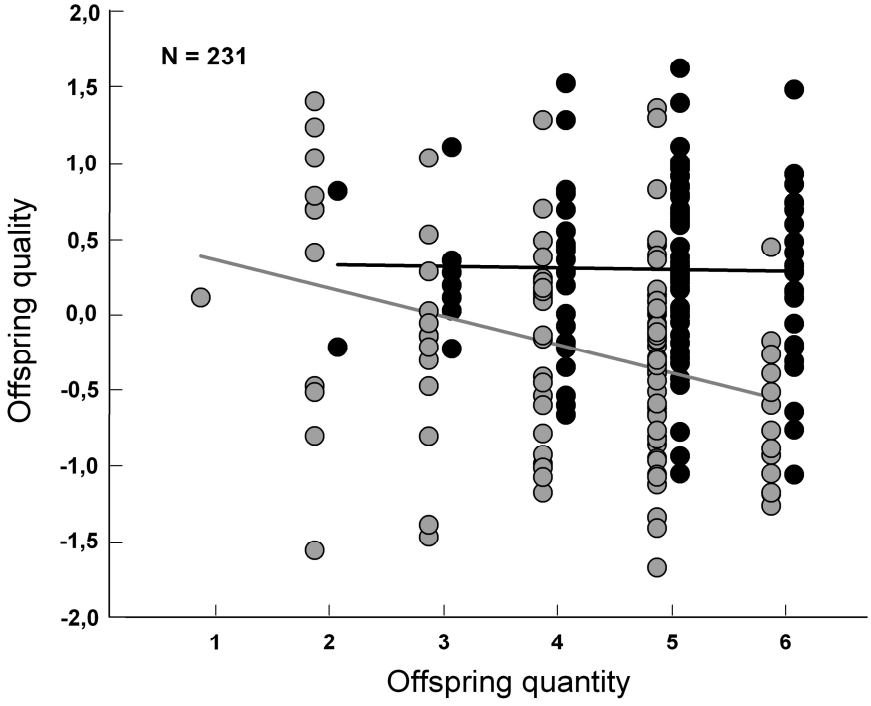


Figure 8.3 – Relationship between offspring quality (i.e. average nestling body condition per nest) and offspring quantity (i.e. number of nestlings older than 12 days) in farmland (N = 126, black circles and black line) and forest (N = 105, grey circles and grey line) habitats. Nestling body condition is the first axis of a principal component analysis (PCA) based on tarsus length, wing length and body weight. Linear regression lines for farmland: y = -0.011x + 0.348, for forest: y = -0.186x + 0.532.

DISCUSSION

Food is one of the most important determinants of survival and reproductive performance in a variety of organisms. Therefore, it is expected that individuals exhibit a strong preference for settlement in food-rich habitats. A large variety of environmental cues with a positive link to food availability have been shown to be used by the organisms during their habitat selection (Marshall & Cooper 2004, Hromada et al. 2008, Mestre & Lubin 2011). Migrants are particularly time-constrained during habitat selection and have to rely on such environmental cues (Orians & Wittenberger 1991, Marshall & Cooper 2004, Hromada et al. 2008, McGrath et al. 2009, Fuller 2012). In contrast with less time-constrained species, migratory organisms are probably more likely to become trapped in case of sudden anthropogenic habitat changes that may uncouple the link between the habitat selection cues and some components of habitat quality like food availability (Battin 2004). Resident species might for instance benefit from a larger time-window to collect information during their habitat selection in order to evaluate the future state of food resources in their environment (e.g. Forsman et al. 2008).

In our study system, the Red-backed shrike prefers to settle in a novel habitat (i.e. harvested areas in plantation forests) where food abundance was much lower than in the traditionally used habitat (i.e. farmland with hedgerows and bushes). As a consequence, the rate of nest visits by the parent shrikes to feed their offspring was reduced in the forest habitat type compared to farmland. Interestingly, this migratory species was shown to be unable to compensate this slower food provisioning with the delivery of larger-sized prey items to the nestlings, even if larger prey items were available in the forest habitat. The observed pattern of food availability in farmland and forest habitats was consistent over years and between study areas, thereby indicating that this maladaptive habitat selection relative to food resources does not represent a transient situation. We also showed that food limitation affected offspring quality only in forest because the average nestling body condition decreased with offspring quantity in that habitat type only. This suggests that kin competition for the same food resources in the nests was only apparent in the preferred forest habitat, whereas there was no link between offspring quality and quantity in the alternative, farmland habitat where food availability was higher. Altogether, our results indicate a strong preference for a habitat type that is associated with fewer (but larger) prey items and where parent birds delivered less (and smaller) prey items to their offspring. Shrikes were therefore shown to be unable to correctly predict and deal with the future conditions in terms of food availability in the breeding sites.

The link between food-related habitat quality and preference has been largely neglected in the context of ecological traps (but see Kloskowski 2012). Beyond the case of a single bird species in a specific human-modified landscape, this study indicates that food-related mechanisms may underlie maladaptive habitat selection in a wide range of organisms relying on environmental cues to guide their habitat selection. Although we showed that a misevaluation of habitat quality relative to food availability induced a fitness loss via an effect on food provisioning to the offspring, we acknowledge, however, that the mechanisms underlying this food-induced ecological trap remain to be identified. Based on our study, we suggest that cues related to prey abundance and/or the size of important prey items are potential candidates. For instance, global prey abundance or the abundance of key prey items for the diet of the shrikes could be higher in forest than in farmland habitat during settlement in spring and a seasonal change in this pattern from settlement to breeding period (e.g. Orians & Wittenberger 1991) may explain the maladaptive habitat selection in the shrikes. Alternatively, prey size may be used by the birds as a cue for habitat quality during settlement and may explain the observed pattern of habitat preference. The effect of habitat structure on food detectability later in the breeding season may then differ between habitat types (Butler & Gillings 2004) because of a lack of management in forest compared to farmland (e.g. mowing). Hence, the larger prey items in forest could become less accessible to the birds during summertime. Of course, mechanisms other than food-related ones may also play a role during habitat selection by the shrikes. Lower predator abundance, higher microclimate or higher vegetation cover may for instance constitute (additional) habitat selection cues and explain the preference of shrikes for the forest habitat. If such cues are used during settlement, recent changes in management activities may have altered food availability and hence, habitat quality, in forest without any impact on habitat attractiveness for the shrikes, which would constitute a variant of ecological trapping (Robertson & Hutto 2006).

Food-related choice experiments are to be conducted to examine how the perception shrikes have of prey quantity and quality in the territories may influence their decision-making during habitat selection. Recently, Kloskowski (2012) showed that the Red-necked grebes (*Podiceps grisegena*) used fish size as a cue to select among a mosaic of artificial fish ponds varying in prey quality. In the Red-backed shrike, Hromada and colleagues (2008) have shown that the presence of food caches from a sister species (i.e., the Great-grey shrike, *Lanius excubitor*) is used by the Red-backed shrikes as an indicator of food availability and as a cue to guide territory selection during settlement. Carlson (1983) showed that the Red-backed shrikes are able to differentiate between prey sizes and that this ability influences decision-making on nestling provisioning. Hence, between-habitat differences in food availability and size may play important roles in determining the maladaptive habitat selection

pattern observed in this migratory shrike species (Hollander et al. 2011). In contrast with most studies on ecological traps examining the impact of nest predation on avian brood success in different habitat types (e.g. Flaspohler et al. 2001, Weldon & Haddad 2005, Gilroy et al. 2011, Hollander et al. 2011, Latif et al. 2011), we draw attention to the importance of food availability and food use as a part of the functional mechanisms underlying an ecological trap in the wild. Dynamic environments under intense human use may involve a biased perception of habitat quality relative to food availability and may induce maladaptive habitat selection especially in mobile or time-stressed organisms that allocate only a limited time budget to settlement decision-making.

From a conservation perspective, there is also clear interest in the consequences of ecological traps for farmland wildlife using novel habitat types in forests because such an understanding of the system may guide the management options for attracting organisms back into undervalued, high-quality habitats in farmland and/or for improving habitat conditions in the low-quality habitats in forest (Gilroy & Sutherland 2007). In this context, our study clearly sheds light on the conservation interest of understanding how food quality and quantity could act as proximate cues to habitat attractiveness and ultimate determinant of fitness in such organisms. Modern forest management practices may interfere with food-related cues and hence, trigger the settlement of farmland wildlife in open areas in forest, but such practices may also affect important resources and conditions (e.g. food resources) in such a way that species-specific habitat quality is lower than the perceived habitat quality by the organisms during habitat selection.

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Red-backed shrike (male), 25 May 2008, Wissembach. Picture: F. Hollander

Chapter 9

GENERAL DISCUSSION

In Europe and elsewhere in the world, disturbance regimes such as fire or grazing maintained early-successional vegetation within climax broad-leaved forests, attracting open-habitat wildlife (Pykala 2000, Vera 2000, Svenning 2002, Swanson et al. 2011). During and after the Neolithic period, natural forests have been intensively exploited by humans and were gradually replaced by agricultural land. This has probably been favourable to open-habitat wildlife, at least to those species which were able to adapt to such drastic anthropogenic changes (Wilson et al. 2009). To date, harvesting in commercial plantation forests might to some extent imitate the effect of natural disturbance regimes, attracting again open-habitat wildlife from farmland to open, human-impacted forests. Farmland and forest management activities may thus create anthropogenic habitats for open-habitat wildlife although they may differ in many respects from natural systems with natural disturbance regimes. Therefore, studying the adaptiveness of habitat selection in human-modified environments and understanding the patterns of habitat preference and ultimate fitness consequences in such systems is of general interest in ecology (Robertson & Hutto 2006).

More specifically, the aim of this thesis was testing whether the Red-backed shrike – a typical farmland bird species – is expanding its habitat use into open areas of forests plantations, in an adaptive way or alternatively, this constitutes a case of ecological trap. The latter option would occur if shrikes are attracted to forest plantations with lower fitness returns compared to the traditionally used farmland habitat. The results of this PhD thesis relative to the different research objectives (p. 23) can be summarized as follows (see Figure 9.1):

1) **Habitat preference**: each year, male shrikes settled earlier in forest than in farmland during the habitat selection phase. Moreover, males with a larger body size and a larger face mask (ornamental trait) were observed to breed more often in forest than in farmland, supporting the idea that higher-quality males arrive earlier and preferentially settle in plantation forests. Based on a field experiment, arrival dates were found to be relevant, individually-motivated

surrogates of habitat preference in this migratory species, since early arriving males were also much more aggressive in defending their territorial resource compared to later arriving males. In addition, territorial defence was found to be on average higher in plantation forests independently of the arrival date and body condition of males. These behavioural data support the overall pattern of habitat selection of the shrikes in the studied farmland-forest landscape: plantation forests were preferentially chosen over farmland habitat.

2) **Habitat quality**: reproductive performance (brood size and nestling body condition) and reproductive success were measured and these traits were found to be consistently lower in the plantation forests compared to farmland. Hence, based on these traits, we identified a lower fitness in high-quality phenotypes breeding in forest.

These results showed a case of maladaptive habitat selection in the Red-backed shrike breeding in farmland-forest landscapes, and provide evidence for an ecological trap given a preference for lower-quality habitat.

In order to determine which processes could lead to the mismatch between habitat preference and habitat quality in the Red-backed shrike populations breeding in farmland-forest landscapes, our research objectives (Fig. 9.1) focused on the key environmental resources and conditions for the shrikes that are likely to differ between both habitats and, hence, to interfere with habitat preference and habitat quality.

1) **Nest predation pressure:** the Red-backed shrike preferred breeding in the habitat with low predator abundance. Despite the lower abundance in forest, we found that nest predation rate was higher than in farmland. This mismatch offers an explanation for the lower reproductive success in forest habitat, and hence, part of the ecological trapping. Lower nest concealment in forest compared to farmland habitat was identified as an important mechanism determining the lower reproductive success in the preferred habitat.

2) **Food availability and microclimate conditions:** food availability for the Red-backed shrike (above-ground and ground-dwelling invertebrates) was consistently lower in forest compared to farmland habitat. This pattern of higher food availability in farmland was correlated with a warmer ground-level microclimate in this habitat type compared to forest. On the other hand, it was found that average prey size was slightly larger in plantation forests. Data on food provisioning to the offspring indicated that nest visits were more frequent and that the parents delivered larger prey items in farmland in contrast with the pattern of prey availability in both habitat types. This pattern of food provisioning most likely

explains part of the differences in nestling body condition between farmland and forest habitats. Moreover, among-nestling competition for food in the same nests was found in the forest habitat only, whereas there was no link between offspring quantity and quality in farmland.

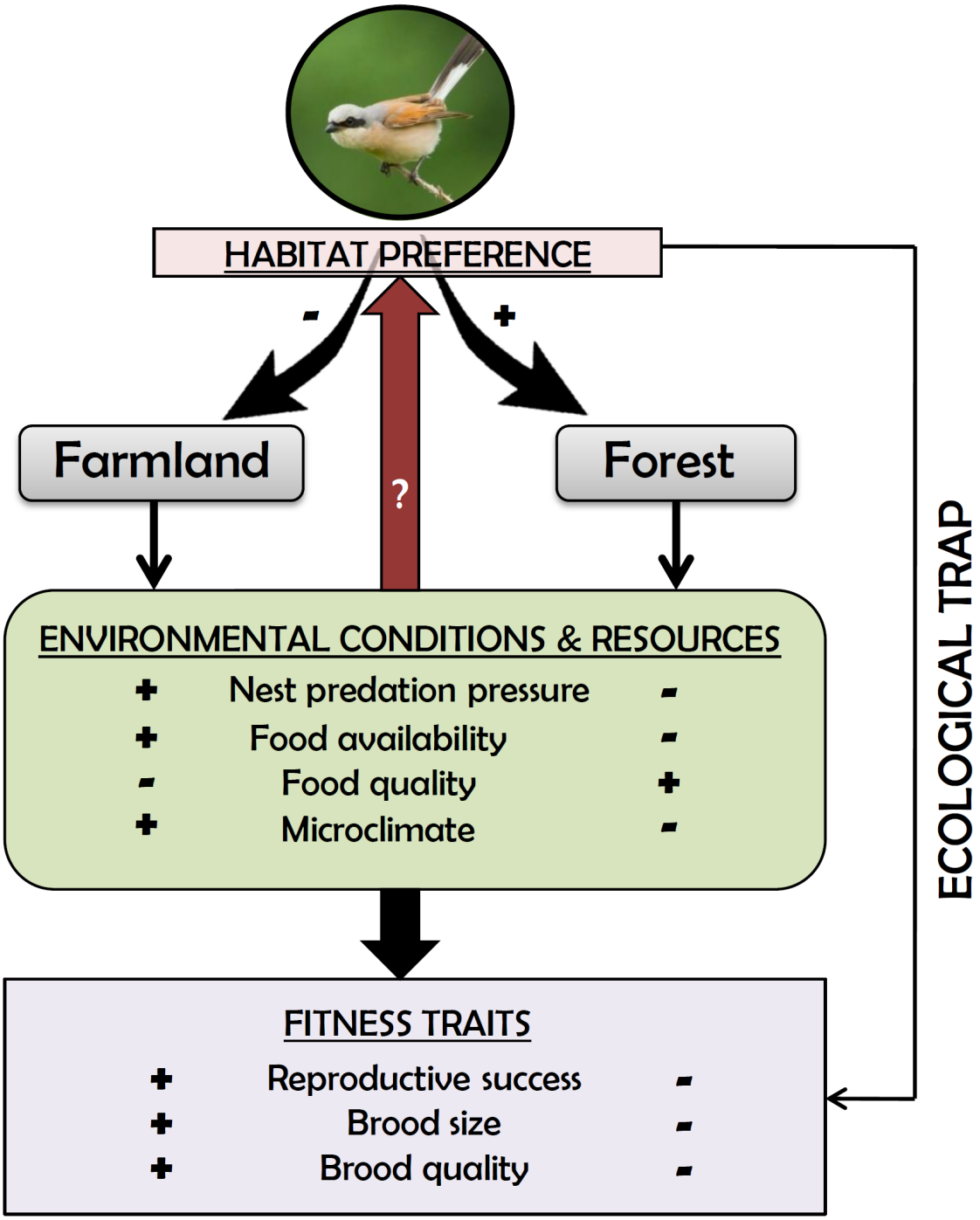


Figure 9.1 – Schematic illustration of the ecological trapping occurring in the Red-backed shrike breeding in farmland-forest landscape of southern Belgium. Shrikes prefer to breed in forest habitat overall yielding lower fitness. Differences in environmental conditions and resources between forest and farmland are indicated. Among other candidates, lower nest predation pressure and/or higher food quality in preferred forest habitat could explain the preference for this habitat type. Higher nest predation rate and lower food availability was shown to decrease fitness traits of the shrikes.

Altogether, our results indicate that the preference of the shrikes for plantation forests leads to fitness loss in terms of the number and quality of nestlings produced compared to the alternative farmland habitat. Reproductive success is reduced in forest due to higher nest predation rates although predator abundance is lower. A series of behavioural (e.g. nest concealment, food provisioning) and environmental factors (e.g. food availability, microclimate) were examined and were found to explain, at least for a significant part, the lower reproductive performance in the preferred habitat. In the following section, we will 1) emphasize the relevance of our results to provide evidence of the existence of an ecological trap in the studied system, 2) synthesize the known mechanisms that underlie the trap and the processes that remain to be identified, and 3) point out the added value of the results for the conservation and management of open habitats in mixed farmland-forest landscapes, as well as for the clarification of the 'habitat' concept.

Meeting the ecological trap: linking habitat preference and fitness

The ecological trap should firstly be considered at the individual level. This is so because habitat preference reflects the result of an individual decision-making process as a response to environmental variability. Hence, relevant data need to be sampled at that level. However, the individual preference for a lower-quality breeding habitat type might trap a significant part of a population in case this behavioural mistake is repeatedly made by a significant part of the population. We found in the literature both individual-based definitions of ecological traps referring to reproductive performance (Robertson & Hutto 2006), and population-based definitions referring to habitat-dependent survival estimates (Delibes et al. 2001, Kristan 2003). Note that both definitions are complementary, and unfortunately life-time reproductive success has not been really considered although it would be an even better fitness measure. In this study, we considered the definition of an ecological trap *sensu* Robertson & Hutto (2006). In any case, several criteria have to be met to confirm the existence of an ecological trap: 1) individually-based habitat preference should be measured, 2) fitness-related measures relative to habitat quality need to be collected, and 3) results may not reflect a transient situation only. In their review, Robertson & Hutto (2006) found only weak evidence of ecological trapping in the wild, but more recent studies have given stronger evidence (e.g. Horváth et al. 2010, Rantanen et al. 2010, Latif et al. 2011). However, many studies claiming to identify a trap actually fail to meet the criteria. For instance, some studies still provide irrelevant estimates of habitat preference as these are not based on an individual decision-making (e.g. Klein et al. 2007, Nordby et al. 2009, Rodewald et al. 2010, Dempster et al. 2011, Zuberogoitia et al. 2013) or use population density as a surrogate of habitat preference without testing the underlying

assumption (e.g. Mänd et al. 2005, Leston & Rodewald 2006, Leighton et al. 2008, Hedin et al. 2008, Keesing et al. 2009, Villard et al. 2012).

In the next sections, we will first discuss how habitat preference could be further evaluated at a fine-grained level of detail in the Red-backed shrike, as well as the evaluation of habitat quality.

One important objective of the present thesis was to identify an individualbehaviour associated with habitat preference measured in the field in order to investigate ecological trapping. Experimental manipulations in the field to measure territorial defence proved to be a helpful approach to evaluate the biological meaning (i.e. individual, motivation-related behaviour) of the measures used to quantify habitat preference (i.e. arrival dates). A next step could be the use of GPS-devices (i.e. geolocators) that allow tracking the complete migration route of long-distance migratory birds (Stutchbury et al. 2009). This system allows considering migration efforts in terms of energy expenditure (i.e. migration speed, travel distances), better reflecting the mechanisms beyond the variation in arrival timing. This has recently been achieved in the Red-backed shrike; individuals showed clear variation in migration routes, stopover sites, travel speed, departure and arrival dates (Tøttrup et al. 2011, see Fig. 9.2, 9.3). Moreover, the authors showed a correlation between autumn departure and the following arrival in spring, showing that migration timing was based on individual behaviour. Individual migration histories might therefore provide insights into habitat selection patterns on the breeding grounds relative to preceding efforts during the migration route. It would thus considerably increase our understanding of the process and consequences of habitat selection in a framework of the organism's complete annual life cycle (Beyer et al. 2010).

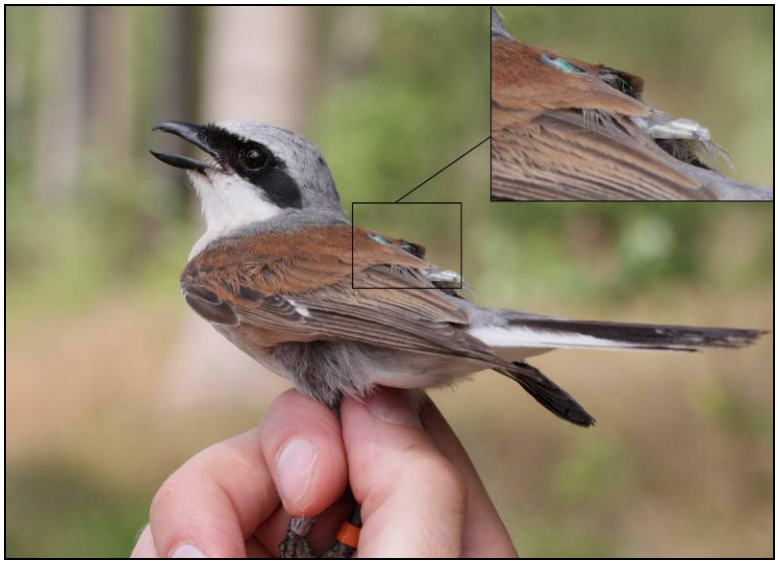


Figure 9.2 – Male Red-backed shrikes provided with a geolocator on its back. Picture from A.Tøttrup.

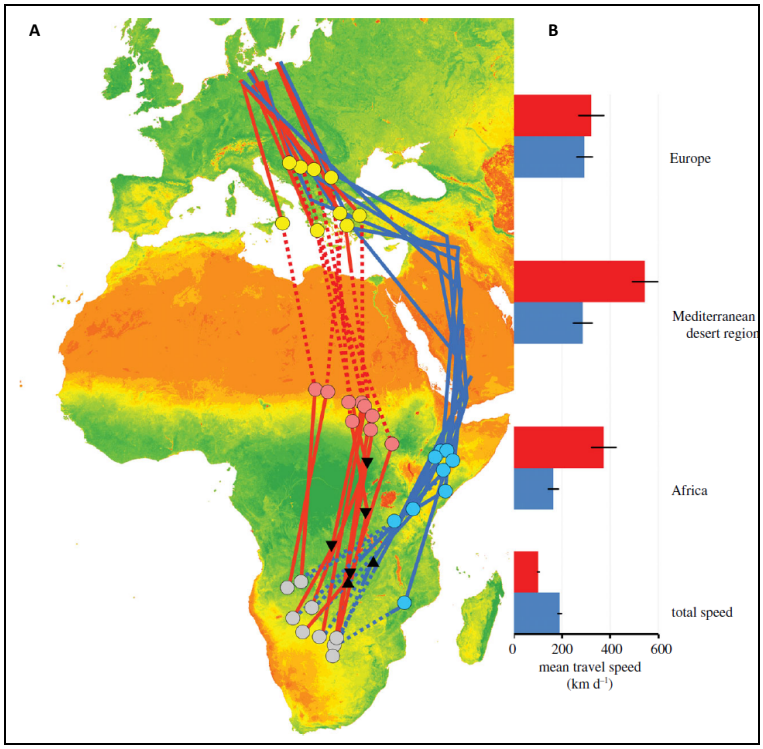


Figure 9.3 – Individual migration routes of nine Red-backed shrikes provided with geolocators. A) Individual migration routes in autumn (red) and spring (blue) are shown as well as stopover sites (circles). B) Regional average migration speeds and total migration speed during spring (blue) and autumn (red) are illustrated. Reproduced with permission from Tøttrup et al. (2011).

In contrast with the Ideal Free Distribution and source-sink models, the ecological trap theory estimates habitat preference and habitat quality separately. We have mentioned above the importance of providing reliable and direct estimates of habitat preference, and of fitness measures. With regard to habitat quality, population density is often used as a fitness measure but it may be only weakly correlated with reproductive success or survival (Van Horne 1983, Tyre et al. 2001, Aldridge & Boyce 2007). In some systems, density may, however, be an appropriate estimator of reproductive performance or survival, but the relation needs to be tested and not only assumed (e.g. Johnson et al. 2006a, Pérot & Villard 2009). This brings us to the problematic issue that density is sometimes used to quantify both habitat preference and habitat quality; this should be avoided when examining whether habitat selection is adaptive because the ecological trap theory focuses on the relationship between both.

Here, we compared the mean reproductive performance (i.e. number and quality of nestling produced) and nest success between preferred and alternative habitats as a surrogate of habitat quality. These measures have been shown to be strongly correlated with habitat quality (Pidgeon et al. 2006). Moreover, they were measured during the complete breeding season (i.e. both first and replacement broods) and so, they approach season-long reproduction estimates (i.e. number of

nestlings produced per year per female) (Nagy & Holmes 2004, Grzybowski & Pease 2005, Etterson et al. 2011). Following the review of Johnson (2007), the best strategy to measure habitat quality is to quantify multiple indicators and to define habitat quality as the *per capita* rate of population increase expected from a given habitat type. Besides reproduction, one would hence need to measure habitat-dependent survival estimates. This is, however, rarely achieved in field studies as it requires long-term datasets (Johnson 2007). Especially in migratory birds such as the Red-backed shrike, this can be really difficult as first-year birds show high natal dispersal tendencies (Pasinelli et al. 2007, Schaub et al. 2011). It is highly relevant to combine different fitness measures (i.e. reproduction *and* survival) to determine habitat quality, given that different ecological conditions and habitat resources might affect differently these measures.

In Chapter 4, we already discussed putative reasons why lower reproductive performance is probably not compensated by higher survival rates of adults and/or nestlings in preferred habitat, mainly because: 1) nestling condition was observed to be consistently lower in the preferred habitat and this trait is expected to affect first-year survival rates in birds (e.g. Naef-Daenzer et al. 2001, Monrós et al. 2002, Tilgar et al. 2010), and 2) higher brood failures in the preferred habitat are likely to have an effect on adult survival (e.g. Schaub et al. 2011). In the Red-backed shrike, the survival probability of unsuccessful adults have been found to be 20% lower compared to successful adults (Schaub et al. 2011). Although this has been observed in shrike populations likely subject to other environmental variability than in the Belgian populations, it is conceivable that higher brood failures in forests have a negative impact on adult survival despite the occurrence of higher-quality phenotypes. Given mortality in long-distance migratory birds are especially high during migration trips (Alerstam et al. 2003, Newton 2006), the long-term use of GPS-technology offers an interesting scope for addressing the relationships between inter-individual variation in survival relative to phenotypic trait values (.e.g. body condition) and habitat preference (Becker et al. 2008, Tomkiewicz et al. 2010).

In conclusion, this PhD-study provides evidence that shrikes are attracted by a habitat inferring lower reproductive performance and success, leading to an ecological trap *sensu* Robertson & Hutto (2006). We acknowledge that additional data are needed to estimate survival in order to identify the potential effect of this ecological trap at the population level (e.g. Delibes et al. 2001, Kristan 2003, Fletcher et al. 2012). Our work contributes to the timely field of maladaptive habitat selection in human-modified environments; maladaptive habitat selection is likely to be more frequent than previously thought.

The mechanisms behind the pattern of ecological trapping

To date, many studies have speculated about the mechanisms that are responsible for fitness loss in the preferred habitats, but, to the best of our knowledge, almost none of them have unequivocally demonstrated such mechanisms. This PhD thesis focussed on two mechanisms that could explain the pattern behind ecological trapping. First, we examined food availability, which is a key resource for reproduction and habitat preference. Second, we investigated nest predation effects as the Red-backed shrike is a bird experiencing high nest predation rates and we assumed that adults prefer settling in habitats with lower predation pressure, and hence, lower expected nest predation rates.

Food availability and its importance for habitat selection

Food availability is a major evolutionary force for avian life histories (Lack 1954, Martin 1987), affecting habitat choice (e.g. Orians & Wittenberger 1991, Pierotti & Annett 1991, Gawlik 2002), body condition (e.g. Strong & Sherry 2000, Brown & Sherry 2006), reproduction (e.g. Lanyon & Thompson 1986, Hau et al. 2000, Nagy & Holmes 2005, Cury et al. 2011) and survival (e.g. Vieyra et al. 2009, Grüebler et al. 2010). Natural selection is, therefore, assumed to favour the preference for breeding habitats with rewarding feeding conditions. Several studies have found support for birds that actively choose and select food-rich habitats for breeding (e.g. Petit & Petit 1996, Burke & Nol 1998, Johnson & Sherry 2001, Sergio et al. 2004, Mänd et al. 2005, Shochat et al. 2005, Bonnot et al. 2009, Dupuch et al. 2009, Diggs et al. 2011, Tozer et al. 2012). Moreover, some studies report that food-rich habitats are often pre-empted by dominant or individuals with a higher body condition (e.g. Huhta et al. 1998, Blondel et al. 2006, Diggs et al. 2011, Tozer et al. 2012); a pattern that suggests adaptive, despotic habitat selection (Fretwell 1972). Under an adaptive habitat selection scenario, food availability is thus correctly valuated during the habitat selection phase, either directly or by means of food-related cues (e.g. Marshall & Cooper 2004, McGrath et al. 2009, Hromada et al. 2008).

Our results show that shrikes preferred the forest habitat with a markedly lower food availability compared to the alternative farmland habitat (Chapter 8). This involved a lower rate of feeding visits with smaller-sized food items, which in turn, affected nestling condition. This pattern indicates that future food availability is probably not valuated correctly during habitat selection, with negative impact on the future breeding conditions of the shrikes in the preferred habitat. This general result provides a new contribution to the literature on ecological traps and reinforces our knowledge of avian habitat selection. Only a few study settings have hitherto provided evidence of the preference for a habitat with lower food availability. Based on nestbox occupation in Estonian forests, Great tits (*Parus major*) were shown to prefer deciduous over coniferous habitat where food availability was,

however, higher (Mänd et al. 2005, Mägi et al. 2009). In non-preferred coniferous habitat tits layed smaller clutches, but nestling condition was found to be higher compared to preferred deciduous habitat. The higher nestling condition in coniferous habitat was attributable to higher-quality food (based on prey size) delivered to the nestlings. Although some doubts remain on individual preference estimates (e.g. nest box occupation not corrected for highly biased nest box availability between habitats), these results indicate that tits preferentially select a habitat with higher food availability, but that there is a mismatch later on during the breeding season regarding food quality. In the Red-necked grebe (*Podiceps grisegena*) it seems to be just the opposite. This aquatic species breeding on artificial fish ponds prefers to settle on ponds with larger prey but that did not yield the expected fitness advantages later on during breeding. Brood failures were caused by lower food delivery on preferred ponds irrespective of food size (Kloskowski 2012). These results resemble those of our study given that maladaptive behaviour in shrikes occurred as 1) the marked preference for a habitat with low food availability that induced lower rate of nest provisioning and, 2) the availability of larger-sized prey items in the preferred habitat did not result in the delivery of larger-sized prey items to the offspring. Finally, another recent study showed a preference of Yellow-bellied sapsuckers (*Sphyrapicus varius*) for 1-5 year or > 60 year old logged forests compared to intermediately aged logged forests, but nest success and reproductive performance was lower in these two preferred habitat types. Food availability was also investigated, but was found to be higher in the preferred habitat, which suggested that this resource was correctly valuated in this ecological trapping scenario (Tozer et al. 2012). A variety of mechanisms are thus susceptible to cue the preference to low-quality habitat.

Food-related cues and their importance in avian habitat selection

Two possible reasons could explain the preference for a habitat with low food availability: 1) food availability is not evaluated during habitat selection as other environmental conditions and resources are used to cue habitat preference, or 2) food availability is evaluated during habitat selection (directly or through food-related cues) but became uncoupled from habitat quality. Both options need experimental manipulation in the field in order to test which conditions attract organisms in a habitat conditioned by lower food availability during habitat selection.

A study system using artificial water ponds attracting wading birds (i.e. herons, ibis, and egrets) showed promising results in this respect. Gawlik and co-workers manipulated the conditions and resources of these ponds to understand habitat selection patterns and feeding success (Gawlik 2002, Gawlik & Crozier 2007, Lantz et al. 2010, 2011, see Fig. 9.4).



Figure 9.4 – Mixed species flock wading in one of the several artificial ponds. Reproduced with permission from Gawlik et al. 2002.

In this system, water height, vegetation density, food density and the presence of other foraging birds (social attraction through the use of decoys) were manipulated experimentally and in synergy, given that all conditions are important for the habitat preference of wading birds. At equal food density between ponds, the following factors defined habitat preference: 1) shallow water, 2) presence of submerged aquatic vegetation, and 3) social attraction. On the other hand, wading birds are attracted by high-density food ponds (Gawlik 2002). Hence, this experimental work showed that a combination of cues attracts wader birds for feeding to the ponds. Unexpectedly, Lantz et al. (2010) showed however that the efficiency of food capture was lower in preferentially selected water ponds. More insights are thus needed in this promising study system, as it shows that some cues (e.g. water depth) indicate favourable habitat in terms of foraging but may deviate from feeding success. Food-related cues might therefore become uncoupled from true feeding conditions. Unfortunately, the authors did not provide any fitness data, which would have been insightful to test the ecological trap and its link with food-related cues.

For logistic reasons, it would be difficult in the case of the shrikes to efficiently manipulate a complex combination of food-related cues in the field as for the experiments by Gawlik and colleagues. Simple experimental manipulations could be feasible. In Chapter 8, we already discussed the possibility that shrikes, at the time of habitat selection, could be attracted by the availability of larger-sized prey in forest compared to farmland habitat as a cue for habitat preference such as observed in the study on Red-necked grebes (Kloskowski 2012). Although the natural distribution of food is difficult to modify in the field, choice experiments relative to alternative food items may be conducted in the field.

Almost three decades ago, Carlson (1983) conducted food choice experiments in the Red-backed shrike with the aim to test predictions of the optimal foraging theory. The predictions were supported as larger offered prey items were preferentially selected in case of higher travel and handling costs, but in case of short travels, small but easily handled prey items were preferred. Hence, it is possible to manipulate prey offer during the breeding season and to test how variation in prey size and nutritional quality would influence prey choice. This could also be achieved during the habitat selection phase, by offering impaled prey (Fig. 9.5) varying in quantity and quality between habitat types. This kind of setup has already been used in the Red-backed shrike. It was shown that settlement occurred earlier in territories with the presence of impaled prey compared to control territories (Hromada et al. 2008).



Figure 9.5 – *Geotrupes sp.* (Coleoptera) stored on a barbed wire by a Red-backed shrike as food reserve. Picture taken by D. Sevrin on the 31st July 2011 at Hotton (Beauraing, Belgium).

Such experiments are needed to identify the importance of food-related cues for the process of habitat preference, and to test which conditions (e.g. food quantity and/or quality) trigger the settlement of the shrikes in the preferred habitat.

Nest predation-related cues and their importance in avian habitat selection

Nest predation represents the most common source of brood failure among open-cup nesting passerines (Martin 1987, Thompson 2007). It has also been reported to be an important factor explaining ecological traps in the wild (Robertson & Hutto 2006, but see also Gilroy et al. 2011, Latif et al. 2011, Tozer et al. 2012). According to our results, the Red-backed shrikes were subject to higher rates of nest predation in the preferred habitat and we examined some of the potential mechanisms underlying this pattern. Interestingly, we found that predator abundance was lower in the preferred habitat but nests were better concealed in the alternative habitat. This general pattern resulted in a higher rate of nest predation in the preferred habitat type. Hence there was a clear

mismatch between predator abundance and predation rate. Poorly concealed nests in the preferred forest habitat increased the probability of nest predation and so, nests were probably detected more easily by predators even if predators were less abundant than in the alternative farmland habitat.

Adaptive habitat selection often involves settlement in habitats characterized by low predator abundance (e.g., Velando & Márquez 2002, Weidinger 2002, Morton 2005, Schmidt et al. 2006, Marzluff et al. 2007, Trnka et al. 2011), a pattern also observed in the Red-backed shrikes breeding in farmland (Roos & Pärt 2004, Roos 2006) and forest (Söderström 2011, see also Chapter 6) habitats. This demonstrates the accurate response to nest predation pressure during habitat selection. The most insightful studies experimentally manipulated predation pressure and measured the behavioural response of the birds during habitat selection and/or breeding. After significant nest predator removal, several migratory species were shown to settle in higher density in predator-removed plots than in control plots (Fontaine & Martin 2006a, b). In these predator-removed plots, nest predation strongly decreased (Fontaine & Martin 2006a, b) and reproductive investment in terms of clutch size and feeding rates increased considerably (Fontaine & Martin 2006b). Although unrelated to predator abundance *per se*, Eggers and co-workers (2006) increased the level of predation pressure by exposing an acoustic cue (playback experiment) of predator presence in several territories of the Siberian Jay (*Perisoreus infaustus*), and measured the reproductive response compared to control territories. In territories with predator calls, Jays placed their nest in more protective vegetation and significantly reduced clutch size. Emmering & Schmidt also observed that Ovenbirds (*Seiurus aurocapilla*) and Veery's (*Catharus fuscescens*) bred further away from predator vocalization (playback experiment) compared to control territories. These studies clearly support the idea that birds can perceive predation pressure (in terms of abundance or presence) during habitat selection, and consequently make behavioural decisions to minimize the expected cost of nest predation later on during breeding. Mönkkönen et al. (2009) altered nest predation pressure for the migratory Pied flycatcher (*Ficedula hypoleuca*) by adding the odour of a natural predator to some nest boxes compared to control nest boxes. Flycatchers avoided breeding in risky nest boxes, but apparently laid larger clutches compared to control nest boxes which is an unexpected result given the potential reproductive cost of a brood failure due to nest predation is not anticipated. The authors proposed that decision-making for reproductive investment is based on other habitat-related cues than those acting on settlement patterns such as predation pressure. As collecting information can be costly for birds, the authors argued that quick and simplified decision-making relative to nest predation pressure might occur and overrule reproductive decisions. Finally, Forsman et al. (2013) recently showed through predator scent experiments that entire bird communities might avoid settling in environments with a high risk of nest predation.

In the light of this literature, we suggest the Red-backed shrike most probably uses the abundance of its natural predators as one of the cues for settlement. Abundance could be assessed directly, but also indirectly through the vocalization or activity of the corvids during habitat selection. Surprisingly, our study shows that nest predation rate is higher in the preferred habitat with lower predator abundance. This is a new finding in the ecological trap literature as the opposite effect is often suggested but rarely tested. To the best of our knowledge, only two studies investigated predator abundance in the avian ecological trap context. First, in American tallgrass prairie habitat, several early-successional bird species prefer (based on density) to breed in managed (burned) plots compared to natural plots. Food abundance was higher in preferred managed plots, but nest predators (mainly reptiles) had a higher density and reduced nest success for these bird species (Shochat et al. 2005). Second, Robertson & Hutto (2007) studied the existence of an ecological trap for the Olive-sided flycatcher (*Contopus cooperi*) and found lower nest success in preferred habitat hosting a higher abundance of nest predators. Hence, we show in our study that lower nest success can be uncoupled from predator abundance. More studies are, however, needed to reveal whether, and how, predation pressure is valuated during habitat selection in strongly human-modified landscapes. Experimental manipulation in the field would again offer the best scope for explaining habitat preference in the wild relative to nest predation pressure, and its relationship with ecological trapping.

We showed that higher predation rates in the preferred habitat could be caused by weaker nest concealment compared to the alternative habitat. Nest concealment is known to be a critical factor for nest disclosure to nest predators (e.g. Weidinger 2002, Albrecht & Klvana 2004, Colombelli-Négrel & Kleindorfer 2009, Latif et al. 2012, Matsui & Takagi 2012). This is also the case in the Red-backed shrike, as poorly concealed nests have a higher probability to be nest-predated (Jakober & Stauber 2002, Müller et al. 2005). Other studies failed, however, to show any effect of nest concealment. This can be the case in habitats with low predation pressure (Latif et al. 2012), or with the additive effect of a behavioural adaptation of the parents (i.e. modification of the rate of feeding visits to the nest) in case of high predation pressure. Both might tone down the effect of nest concealment on reproductive success (e.g. Remeš 2005, Peluc et al. 2008, Ibáñez-Álamo & Soler 2012). In Chapter 6, we showed similar effects as parents decreased their rate of nest visits after a simulated predator intrusion, and this change varied according to the degree of nest concealment, irrespective of the habitat type. Hence, nest concealment *per se* influenced nest predation in our study. From our results, we argue that weak nest concealment in the preferred habitat type may result from 1) the fact that predation pressure is perceived to be lower, 2) the potential prey-site hypothesis (Chalfoun & Martin 2009) where higher nest site availability leads to higher search costs

for predators in forest habitat, and 3) the vegetation structure limits nest concealment. It is worth to mention that these factors are not mutually exclusive and it is now warranted to further investigate their combined effect through manipulation of predation pressure (Fontaine & Martin 2006a), nest site availability or vegetation structure (Chalfoun & Martin 2009). Moreover, integrating the behaviour of predators (i.e. search tactics) and the relationship between nest concealment and the probability of nest detection in the study design would offer a promising avenue of research.

The combination of low-food availability and high nest predation forging an ecological trap

Both food availability and nest predation are the most important factors determining realized fecundity (number of nestlings produced per year per female) in birds and other organisms, as they cause important variation in reproductive success (brood size and the number of successful breeding attempts during the breeding season; Thompson 2007). Moreover, food availability and re-nesting affect the body condition of nestlings, a pattern we also observed in this study. Knowing that the survival rate of nestlings idepends on their condition, and that condition depends in turn on both food and nest predation (i.e. nestling of a first or replacement clutch), studying both food and nest predation jointly will be highly warranted to explain the variation in habitat quality and habitat preference; this has been the scope of different field studies (e.g. Oro et al. 1999, Zanette et al. 2003, Nagy & Holmes 2004, Fontaine & Martin 2006a, Hromada et al. 2008, Dunn et al. 2010). Traditionally, nest predation has been shown to be particularly important (rather than food availability) to explain the annual variation in fecundity, but in certain study systems food availability appears to be the most significant factor (e.g. Nagy & Holmes 2004). Hence, testing the relative contribution of both mechanisms for fecundity will allow a better understanding of the mismatch between the proximate and the ultimate habitat selection factors that eventually lead to an ecological trap. Unfortunately, it was not feasible to statistically determine such relative importance, mainly as food availability could for logistical reasons not be measured separately in first and replacement broods of each breeding pair. Despite this, our data suggest food limitation and higher nest predation probably acting jointly to explain the overall lower reproductive performance and nest success in the preferred habitat, but they do not necessarily act on the same fitness attributes. Experimental manipulation is now necessary to determine under which conditions each of these factors act as a selective force to fitness variation and helps explaining fitness loss in preferred habitat. For instance, Zanette et al. (2006) conducted a well-designed experimental study on the Song sparrow (*Melospiza melodia*) to assess the relative contributions of these changes for nest success: they showed that food and nest predation had an additive effect on nest success. A similar pattern could be observed in the case of

an ecological trap and may explain negative effects of both food limitation and higher nest predation on fitness in the preferred habitat.

An appraisal of the resource-based habitat definition in farmland-forest landscape

This PhD study addressed the comparison of habitat preference, fitness and environmental resources and conditions between two habitats that strongly differed in vegetation structure. Structural differences between habitat types may induce differences in the environmental conditions and resources, and hence determine unbalanced habitat preference and differences in fitness for the organisms. The opposite may also happen: several studies report similar fitness in structurally different habitats, which suggest that these contrasting habitats offer resources and conditions that meet the requirements of the species and lead to similar fitness returns (e.g. Bosch & Sol 1998, Weidinger 2000, Zanette 2001, Good 2002). Although the avian literature offers ample studies investigating habitat-dependent resource-use and selection in birds, the concept of the resource-based definition of the habitat as a tool for conservation has been less intensively explored, or at least not in an integrative context as it has been done in studies on invertebrates (Dennis et al. 2003, Dennis 2010 and references therein). For instance, butterflies have been shown not to use the entire area of an apparently homogeneous vegetation unit (Vanreusel & Van Dyck 2007). Instead, discrete patches are used as feeding resources, oviposition or roost places, and the resources needed for eggs, larvae, pupae or adults might considerably vary among these vegetation units (Dennis et al. 2003). Functional differences can thus be found between mating, breeding or foraging places within a single structural habitat unit. Nectar and host plant availability, quality and selection, microclimatic conditions, mating places or predator shelters are important resources for butterflies and have been integrated into the globalized concept of an organism-centred 'functional habitat'.

The consideration of the functional habitat is of great interest, not only for conservation and management, but also for understanding the functioning of habitat selection and use, and the processes underlying habitat quality in heterogeneous landscapes (Van Dyck 2012). In this view, the mechanisms of (mal)adaptive habitat selection might be considerably better understood through a mapping of the availability of resources and an analysis of their use and selection by the individuals in time and space. This might help to determine the variation in habitat preference and habitat quality between structurally different habitat types. This integrative, mechanistic way of dealing with functional habitat needs to be further integrated in avian ecology and conservation applications, rather than the investigation of single resources or conditions on habitat quality. In the Red-backed shrike, an elegant study has considered jointly the effect of several social and environmental

conditions (i.e. nest predation, timing of breeding, altitude, parental quality, territory quality, population density and weather conditions) on the reproductive performance and local recruitement of the species, hence its habitat quality (Müller et al. 2005). Using the Ferruginous pygmy-owl (*Glaucidium brasilianum*) as model bird, Flesch & Steidl (2010) used the availability and use of several important resources for this locally endangered species over wide spatial gradients to understand what determines nest site selection (habitat choice) and reproductive performance (habitat quality). Analyses were based on the large-scale comparison of available and used resources between successful and unsuccessful nests to identify which resources affected habitat choice and habitat quality. Although such studies are time consuming and need intensive sampling, they result in a detailed assessment of the important resources and conditions that constitute the functional habitat for a species.

Our study also investigated a series of resources that were assumed to be of importance for habitat preference and habitat quality of the shrikes at the landscape level. We showed significant and consistent differences in terms of predation pressure, nest predation rate, food availability, food quality and microclimate conditions between forest and farmland habitats. Such differences indicate that at least some resources were not evenly distributed among the structural habitats, thereby showing that structural differences between both habitats are translated into functional differences for the organisms. Beyond this comparison of resources between habitats used by the species, further work should now identify how these might differ with structurally similarly-looking farmland and forest habitats that are not used by the species. This could help to determine which set and quality of resources trigger settlement and to better identify the most important cues during habitat selection in this species. Beyond their conceptual interest, such research avenues have also important consequences for the conservation of the species, because this approach would allow identifying undervalued resources and perceptual traps in case high-quality resources are found to e available in habitats that are not used by the species (Gilroy & Sutherland 2007).

This PhD study also addressed another important aspect of the resource-based habitat concept: how do resources affect preference and fitness separately? This separate consideration of habitat preference and quality is of paramount importance to guide conservation actions that aim to protect and/or restore habitats and their associated high-quality resources. Identifying the resources or habitat features that trigger settlement and that yield highest fitness is not a common practice in conservation planning so far. The main reason for this lies probably in the cost-effectiveness dilemma of conservation management where there is an urge to quickly conserve threatened biodiversity (e.g. Wätzold & Schwerdtner 2005, Rodirguez & Brooks 2007), and this might compromise the idea of investing time to detect, conserve or restore high-quality resources. Often, conservation strategies

focus on the creation of protected areas such as nature reserves or protection/restoring of the wider countryside which might indeed prove to be useful (e.g. Fabricius et al. 2003, Lovejoy 2006, Cantú-Salazar & Gaston 2010). However, ignoring the important ecological conditions and resources important for the organisms of conservation interest might lead to a waste of conservation and restoration effort and budget.

To delimitate important areas that need protection status, some studies rely on the use of environmental surrogates to identify suitable areas for species of conservation concern. In their recent study, Brambilla & Ficetola (2012) established the link between the local presence of the Red-backed shrike and a series of environmental features such as grassland and shrub lines based on land cover data. The authors then projected this link beyond the locations of the known species' presence to identify unknown suitable areas. They tested to what extent the projection of their habitat suitability index correlated with the local reproductive performance (i.e. brood size) of the shrikes and they found a good fit between both factors. Given this correlation, suitability indices could provide important guidance to designate suitable areas in the landscape without further sampling of fitness or even detailed environmental conditions and resources other than land cover data. Hence, this study shows the need for tools to rapidly assess high-quality areas for conservation purposes. Although this approach may be useful, such shortcuts could, however, be dangerous to use without a detailed assessment of the mechanism(s) beyond the observed patterns. For instance, which conditions and resources constitute the functional link existing between land cover data and fitness? Can this method be extrapolated to other populations or species than those under study? Maladaptive habitat selection might invalid the use of such suitability indices based on species presence records because they may prove to provide misleading information on habitat quality. At least, careful preliminary assessment of the mechanism leading to habitat preference and quality is needed, and the use of different modelling tools chould be favoured (e.g. Girardello & Morelli 2012). Alternatively, the integration of parameters reflecting reproductive performance (in addition to species presence) in such approaches may be relevant (Titeux et al. 2007). This leads to the conclusion that understanding the resources underlying high habitat quality is a priority for conservation biology. Hence, although there is a need to quickly detect areas of conservation concern, there is also a need to understand more precisely the resources determining habitat quality.

Management of open habitats in human-modified landscapes

Open or semi-open habitats were present in the natural, forested landscapes of Europe before human settlement and activities. It is therefore believed that natural openness attracted early-

successional wildlife (Vera 2000, Svenning 2002, Sutherland 2002, Fuller 2012). To date, natural open habitats are much scarcer, but still some interesting examples can be found. For instance, the Red-backed shrike breeds locally in natural, open forest patches with little or complete absence of any human impact (Fig. 9.6). Such examples tend to suggest that the natural forest gaps were probably present and used by the Red-backed shrike and other early-successional birds before the Neolithic period, and that recent open areas in Spruce plantations are attractive for these species as they probably share some features with the historical habitat. Other examples include the use by early-successional, farmland wildlife of open habitats in forest after natural wildfires or wind storms (e.g. Brotons et al. 2008, Zmihorski 2012, Zozaya et al. 2012).







Figure 9.6 – Examples of a natural opening in forests used as breeding sites by the Red-backed shrikes in (A, B) Belgium, in (C) Norway and (D) in Poland. The first two pictures (A,B) are open gaps in deciduous forests which are probably kept open through intensive grazing by herbivores. In Norway (C) the example illustrates a naturally open plain in a Pine forest, while in Poland (D) shrikes were found to breed in large clearing following wind storms. The second (B), third (C) and fourth (D) pictures are used with permission from Vandevyvre (2009), Lislevand (2012) and Zmihorski (2012), respectively. Picture A: F. Hollander.

Given the rapid decline of farmland wildlife with the ongoing intensification of agriculture, open areas in forest due to modern management practices have been considered an interesting alternative habitat for threatened farmland wildlife (Spellerberg & Sawyer 1996, Paquet et al. 2006, Stephens & Wagner 2007, Paz Acuña & Estades 2011, Swanson et al. 2011). However, a comparison

of the quality of both open farmland and forest habitats in terms of fitness consequences for the individuals is needed to fully understand the value of such anthropogenic environments. From our study, it is clear that post-harvesting sites in Spruce plantations create an ecological trap for the Red-backed shrike. This conclusion could be extended to other farmland species currently breeding in plantation forests, although it requires a deeper understanding of the system because, even for a single species like the Red-backed shrike, the habitat selection pattern may differ among geographical areas (Hollander et al. 2011, Söderström & Karlsson 2011).

Modern forest management practices in plantation forests alters several environmental conditions, and these practices have been shown to decrease nest success in different open-cup nesting species compared to their 'natural' habitats (e.g. Darveau et al. 1997, Duguay et al. 2000, Manolis et al. 2002, Griesser et al. 2007, Powell et al. 2010, Wilson et al. 2012). Our study demonstrates that not only nest success, but also reproductive performance, may be lower in open areas in forest than in farmland. Therefore, such environments could provide negative fitness returns, but it remains to be tested how this affects population dynamics in farmland-forest landscapes.

Some forestry practices aim to minimize the negative impact of harvesting on early-successional wildlife by imitating more close-to-nature disturbances. For instance, single-tree selection harvesting aims to cut local trees varying in age to maintain sufficient heterogeneity in the forest structure. Under such management, there is evidence of lower impact on invertebrate abundance (e.g. Smith et al. 2012) or on reproductive performance for birds (e.g. Richmond et al. 2012). Similarly, group-selection harvesting is the removal of a small group of trees at rather short intervals and is expected to stimulate the creation of smaller gaps and uneven-aged forest structure compared to large-scale clearcutting. This technique has also been shown to minimize the effects of harvesting on the structure of avian populations, at least in forested areas (e.g. Forsman et al. 2010, Campbell et al. 2012). However, small gaps might also alter reproductive performance, as observed in different bird species (e.g. Robinson et al. 1995, Burke & Nol 2000, Zanette et al. 2000, Rush & Stutchbury 2008), and may even inhibit the occupancy of some farmland bird species if gap size is insufficiently attractive to them. Therefore, forestry practices should favour the settlement of farmland birds into artificial forest gaps as an alternative to farmland, but also increase the quality of these environments by creating structural heterogeneity (different tree age classes) or the plantation of mixed tree composition (e.g. Felton et al. 2010), enhancing dead tree retention (e.g. Magura et al. 2005), favour natural regeneration or burning practices (e.g. Simon et al. 2002) and disfavour the practice of thinning as well as the use of herbicides (e.g. Hartley 2002). Since our study showed food limitation in forest habitat, such practices could increase the occurrence of invertebrates during breeding. Hence, management actions could reduce the strength of ecological trapping for the Red-

backed shrike by increasing the quality of its preferred habitat, i.e. the availability of resources needed for the species to achieve high fitness. It would be highly interesting to set up an applied and integrated research program in Spruce plantations in order to evaluate different methods to improve conditions for invertebrates and birds.

Maladaptive habitat selection can also be considered from the viewpoint of undervalued resources (i.e. perceptual trap), which in contrast to the ecological trap refers to the low attraction for high-quality habitat (Gilroy et al. 2007). Another (mutually non-exclusive) option would be to increase the attractiveness of the farmland habitat to reduce the intensity of the trap in Spruce plantations. This is more difficult to achieve since it would imply determining the cues that need to be restored or modified to increase the attractiveness of this habitat. A simple example could be illustrated by the rapid increase of corvids known to have occurred with the intensification of agricultural practices in farmland (Wilson et al. 2009). This potentially altered the habitat preference of the shrikes but not the underlying habitat quality as we did not find a link between predator abundance and nest predation rate. Therefore, the regulation of corvid abundance through local hunting activities (e.g. Côté & Sutherland 1997) could be a possible solution to attract shrikes and other early-successional wildlife back in high-quality farmland habitat. Obviously, this is only achievable at a local level. Alternatively, specific agri-environment schemes favourable to enhance the habitat quality for farmland birds could be implemented. These are known to increase food availability, hunting and roosting sites and reproductive success (e.g. Donald & Evans 2006, Baker et al. 2012). Such schemes could hence increase the attractiveness of farmland habitat.

Further research perspectives on ecological trapping

The occurrence of ecological trapping in wild organisms has gained a growing interest over the last few decades and is important to evaluate the impact of global change on the behavioural decision-making and fitness consequences of organisms in environments recently created by human activities. Further work should continue to identify relevant measures of habitat preference and habitat quality to unequivocally demonstrate the existence of ecological traps for other species in other human-modified environments (e.g. urban areas). This should help answering whether ecological traps are widespread in anthropogenic landscapes (Robertson & Hutto 2006). Fitness estimation is often limited to reproduction parameters because estimates of survival rates are time-consuming. Such a complete estimate of individual fitness is, however, needed to determine local recruitment, lifetime reproductive performance and so, population growth rates. Ecological trapping refers to maladaptive individual decision-making relative to habitat selection and may (or not) lead to population declines

(Delibes et al. 2001, Battin 2004, Fletcher et al. 2012). The existence of such phenomena remains only poorly explored in the wild. More investigations should therefore consider how a preference for low-quality habitat at the individual level might turn into an attractive sink habitat at the population level.

Experimental manipulation of habitat selection cues and/or habitat quality also constitutes promising research avenues because such approaches would allow identifying the resources and conditions that underlie habitat preference and fitness consequences. Hence, such manipulation will lead to a deeper understanding of the mechanisms beyond the pattern of ecological trapping. Particular attention is to be paid to the variation in phenotypes and/or genotypes of breeders between preferred and alternative habitat types. This again would help to link the ecological trap theory with the other habitat selection models that address the phenotypic quality and condition of the organisms relative to the habitat types (i.e. ideal free distribution or the source-sink models). Long-term studies will be necessary to investigate the consistency of ecological trapping over time, and to evaluate whether populations could come out of an ecological trap through learning and natural selection.

We still know little about the ability of organisms to avoid an ecological trap by changing habitat preferences and colonize high-quality habitat types. In case habitat preference is heritable, natural selection could filter out maladaptive habitat selection with time. Individuals could also learn to recognize low-quality habitat with previous experience and respond quickly to maladaptive habitat selection (Kokko & Sutherland 2001, Fletcher et al. 2012). In the case of shrikes, site faithfulness could represent an interesting study case as it deals with behavioural plasticity in regard to environmental variability (Schmidt 2001, Hoover 2003). If reproductive output is low in a given environment, an individual may opt for not breeding at the same location the following year, but will breed elsewhere and this will involve again habitat selection. Some support for such plasticity in habitat selection has been observed in the Red-backed shrike (Pasinelli et al. 2007). If the same cue is used to select a new habitat as before, the individual is, however, likely to end up again with low fitness returns. A typical case would be a repetitive preference for human-modified habitat edges where nest predation is often higher compared to core habitats (Flaspohler et al. 2001, Ries et al. 2004). In this case, the naive re-use of previous cues would lead to selecting again the same environment with high nest predation pressure. In the other case, another habitat could be selected, even a previously unexplored one, and eventually restore high reproductive performance and/or success. To the best of our knowledge, such ideas have only been treated theoretically at this stage (Kokko & Sutherland 2001), but not yet by field experiments. A related issue is to understand how new selection regimes due to recent habitat modifications and associated ecological trapping might

favour microevolutionary changes on fitness-related traits such as timing of breeding or clutch size or on other life-history traits (e.g. Roff 1992, Stearns 1992, Charmantier et al. 2004, Sih et al. 2011).

The concerns on improving the conservation of ecologically trapped organisms are at the first stages of development. Although it has been pointed out that ecological traps might lead to population declines, few studies have dealt with the managing efforts to reduce the effect of the traps, except in the case of undervalued resources (Gilroy & Sutherland 2007). Recently, Robertson (2012) proposed practical guidelines for the management of the Olive-sided flycatcher (*Contopus cooperi*) that take into account the environmental conditions and resources triggering the ecological trap in this species. For declining or endangered species subject to ecological trapping or other forms of maladaptive habitat selection, such studies are to be welcomed in specific conservation schemes.

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CURRICULUM VITAE

Professional experience

- 2011-2012: CSD Ingénieurs Namur – Environmental impact studies (http://www.csd.ch/)
  Biodiversity monitoring (birds, bats), Agri-environmental schemes for biodiversity protection, Environmental studies on Natura 2000 sites
- 2007-2011: Catholic University of Louvain-la-Neuve - Biodiversity Research Centre – Earth & Life Institute (http://www.uclouvain.be/en-eli.html) – Phd thesis
- 2010-2011: CSD Ingénieurs Namur – Environmental impact studies (http://www.csd.ch/)
  Assessment of landbird migration on construction sites of wind turbines
- 2005: AIG EUROPE (Insurances) *Student job*
- 1999: CBR (Heidelberg Cement Group) *Student job*

Publications

- **Hollander, F., Van Overveld, T., Tokka, I. & Matthysen, E.** (2008). Personality and nest defence in the great tit (*Parus major*). *Ethology* 114, 405-412

- **Hollander, F., Van Dyck, H. San Martin, G. & Titeux, N.** (2011). Maladaptive habitat selection of a migratory passerine bird in a human-modified farmland-woodland landscape. *PLoS ONE* 6, e25703.

- **Hollander, F., Titeux, N. & Van Dyck, H.** (2012). Territorial resource valuation deviates from habitat quality in an ecologically-trapped, long-distance migratory bird. *Behavioral Ecology & Sociobiology* 66, 777-783.

Poster presentations & seminars

- 2012: Aves (BE), "Journée d'études Aves", 4 March - *Seminar*

- **2011**: University of Rennes (FR), "7th Ecology & Behaviour Meeting", 2 – 6 May - *Seminar*

- **2010**: - University of Lesbos (GR), "3rd Eurasian Ornithology Congress", 8 – 11 April – *Seminar*
  - Natuurpunt (BE), "Vlaamse Ornithologische Studiedag", 7 Novembre – *Seminar*
  - UCL (BE), "Biodiversity seminars", 16 December – *Seminar*

- **2009**: - Oxford University (UK), "Student Ornithology Conference", 7 – 9 January – ***Best poster price***
  - University of Lyon (FR), "5th Ecology & Behaviour Meeting", 6 – 10 April - *Seminar*
  - UCL (BE), "Biodiversity seminars", 17 December - *Seminar*

- **2008**: University of Liège (BE), "Benelux Congress of Zoology", 30 - 31 October - *Poster*

- **2007**: Oxford University (UK), "Student Ornithology Conference", 3 – 6 January - *Seminar*