ANTIPREDATOR BEHAVIOURS IN PREY AND PREDATORS DURING BREEDING:

FROM HABITAT SELECTION TO PARENTAL CARE

by

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To my family, far far away but very very close at the same time

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LIST OF ORIGINAL PAPERS

This thesis is based on the following publications and manuscripts which are referred to in the text by their Roman numerals:

I)   Morosinotto C., Villers A., Thomson R.L., Varjonen R., Korpimäki E. – Mind your neighbours: competition and predation risk modify settlement patterns and breeding success of intra-guild prey. *Manuscript*

II) Morosinotto C., Thomson R.L., Hänninen M., Korpimäki E. (2012) Higher nest predation risk in association with a top predator: mesopredator attraction*?* *Oecologia* DOI: 10.1007/s00442-012-2320-1

III) Morosinotto C., Thomson R.L., Korpimäki E. (2010) Habitat selection as an antipredator behaviour in a multi-predator landscape: all enemies are not equal. *Journal of Animal Ecology* 79: 327-333

IV) Morosinotto C., Ruuskanen S., Thomson R.L., Siitari H., Korpimäki E., Laaksonen T. - Predation risk increases the levels of maternal immune factors in eggs. *Submitted manuscript*

V)   Morosinotto C., Thomson RL., Korpimäki E. - Plasticity in incubation behavior under experimentally prolonged vulnerability to nest predation. *Submitted Manuscript*

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1.   INTRODUCTION

Predation is a major evolutionary and ecological process shaping prey behaviour, decision making and population dynamics (Lima and Dill 1990, Abrams 2000, Caro 2005). The importance of strategies used by individuals to avoid predation, and the consequences of these behaviours in producing community structure, has been extensively studied (Lima and Dill 1990, Schmitz et al. 1997, Lima 2009). In addition, competition among individuals of the same or different species has important implications for the life of an animal. Competition may result in a reduction of growth, survival, and reproduction for at least some of the competitors due to limited resource supply or to aggressive interactions that may even lead to death (Charnov et al. 1976, Schoener 1983, Fernandez et al. 1998, Eccard and Ylönen 2007, Watts and Holekamp 2008). Furthermore, predation may also occur among competitors that share similar resources; this is defined as intra-guild predation (IGP; Polis et al. 1989, Polis and Holt 1992) and has great consequences not only for the life of the individual but also for all the species directly or indirectly involved (Ritchie and Johnson 2009).

A direct predation event generally results in the death of the prey (i.e. lethal effects) and, through the active reduction of prey numbers, it may influence prey population dynamics. This may lead to cascading effects to trophic levels below, for example on the prey's own resources. The cascading effects that predation has on species abundance at several trophic levels is termed a trophic cascade (Pace et al. 1999, Polis et al. 2000). Therefore, in a natural environment, top predators will reduce the abundance of smaller predators (mesopredators) through intraguild predation (Ritchie and Johnson 2009), which in turn will affect not only their prey population but, indirectly, also the abundance of resources (plants or smaller animals) consumed by prey.

Predators may however greatly affect behaviour, sociality and reproductive success of prey through the so called non-lethal effects of predation; by simply being perceived by prey (Lima and Dill 1990, Lima 1998, Caro 2005, Cresswell 2008). Variation in prey behaviour as a response to perceived predation risk may have implications to the animal community structure (Schmitz et al. 1997, Preisser et al. 2005), since changes in prey habitat selection or foraging pattern will probably affect the distribution of prey's resources. Behaviourally mediated trophic cascades have been shown in invertebrates: for example, grasshoppers modify their foraging behaviour according with the perceived risk from spiders, thus indirectly affecting grass biomass (Schmitz et al. 1997). Therefore, perceived predation risk may not only strongly influence individual behaviour but can also influence prey populations as much as the direct predation.

1.1   Predation risk

Animals breeding under high predation risk might reduce reproductive investment (Doligez and Clobert 2003, Cresswell 2008, Sheriff et al. 2009, Zanette et al. 2011) and produce offspring of lower quality (Scheuerlein and Gwinner 2006, Sheriff et al. 2009, Coslovsky and Richner 2011a) compared to animals breeding in areas of low predation risk. To reduce the costs of predation, animals can adopt several antipredator strategies, thus decreasing the probability of predator encounter (Lima and Dill 1990, Lima 1998, Caro 2005). These behaviours include high vigilance towards predator presence, decreased activity and changes in activity time. However this results in a trade-off between time invested in antipredator behaviours and other important activities linked to survival and individual maintenance, like foraging (Lima and Bednekoff 1999). Individuals adopting antipredator strategies may pay costs both in terms of reduced energy intake (van der Veen and Sivars 2000, Pérez-Tris et al. 2004) and of lower body condition with consequent low fitness (Boonstra et al. 1998, Persons et al. 2002).

Predation risk will not be constant, but will vary temporally. Predator activity may increase at a certain time of the day or may vary according to breeding season or time of the year (Heithaus and Dill 2002, Mukherjee et al. 2009, Kotler et al. 2010). When predation risk varies in time, an animal should optimize the allocation of antipredator behaviours versus the time spent in foraging, mating and parental care. This temporal optimization of the behaviour depending on variable perceived risk is known as the "risk allocation hypothesis" (Lima and Bednekoff 1999). This hypothesis suggests that animals under high short term predation risk will strongly respond to predator presence, whereas under a prolonged high predation risk animals will optimize the time spent in vigilance and the time allocated in other activities. For example, female elk (*Cervus elaphus)* living in areas where wolves (*Canis lupus*) are present exhibit lower vigilance, after a direct encounter with wolves, compared to elks living in wolf-free sites (Creel et al. 2008). Similarly, pied flycatchers (*Ficedula hypoleuca*) living in close proximity to sparrowhawk (*Accipiter nisus*) nests are faster in resuming nestling feeding, after a direct predator encounter, than parents breeding far from the hawk nest (Thomson et al. 2011).

Predation risk will also vary spatially. The distribution of predators, their behaviour, territoriality and mobility will influence the spatial distribution of risk. When predators move in the landscape actively searching for food, prey will constantly need to adjust their behaviour and vigilance in response to the changing levels of predation risk. The animals will therefore be living in a landscape with differing degrees of risk or fear of predation: a "landscape of fear" (Brown et al. 1999, Laundré et al. 2001). When different predator species with variable hunting strategies coexist in the environment, prey will modify their space use by avoiding both the area where different predators are common

and those where there is higher probability of attack due to the habitat structure (Thaker et al. 2011). When instead the predator is a central-place forager for a given time, the predation risk will be more localized to the vicinity of the predator nest; therefore the risk in that territory will be more predictable. This has been defined as the "predation risk landscape", where prey settle after their predator and can use information related to predator location to optimise the level of predation risk experienced during their breeding (Thomson et al. 2006).

During breeding the cost of perceived predation risk can be particularly high because it affects not only adults but also their offspring. But most animals breed multiple times. Animals should allocate energy in the current breeding attempt at a level that would maximise their lifetime reproductive success. Reduced investment in the current breeding attempt could be a result of the trade-off between current and future reproductive output. Animals breeding under high predation risk can have low reproductive success and fitness due to either reduced number of eggs or offspring (Doligez and Clobert 2003, Eggers et al. 2006, Thomson et al. 2006, Martin and Briskie 2009, Travers et al. 2010), or because of low survival of the young (Martin and Briskie 2009, Zanette et al. 2011). Therefore, parents might invest less in the current brood, if they have a good probability of survival to the next breeding attempt, to preserve energy that can be allocated in a future brood (Clutton-Brock 1991).

Low breeding success could also be a consequence of physiological stress experienced by the mother due to predator presence. Previous studies have shown that stressed mothers might differently allocate hormones and immune factors in the eggs or in the embryo (McCormick 1998, Scheuerlein et al. 2001, Bian et al. 2005, Saino et al. 2005). The allocation of different levels of these factors might have negative implications for the growth of the young (Bian et al. 2005, Saino et al. 2005, Scheuerlein and Gwinner 2006) and reduce the immune response (Coslovsky and Richner 2011b), both of which can lead to high offspring mortality.

To reduce the risk of nest and adult predation, animals modify their behaviour during the breeding period (Caro 2005, Martin and Briskie 2009). In birds the strategies adopted differ depending on the phase of the breeding, starting from the selection of the habitat and nest-site (Lima 2009) to a reduction in parental activity both during the incubation and the care of the young (Ghalambor and Martin 2000, Martin et al. 2000, Fontaine and Martin 2006a, Peluc et al. 2008, Kovařik and Pavel 2011).

1.2   *Habitat selection and perceived predation risk*

Territory location decisions of animals seem to be based on direct and indirect sources of information. Choices are based partly on direct environmental cues such as resource

availability and presence of enemies. However information gathered indirectly from other individuals of the same or different species appears to be used too (Valone and Templeton 2002, Doligez et al. 2003, Seppänen et al. 2007). Public information, gathered by observing the behaviour and reproductive success of other individuals, indirectly reflects the quality of the environmental resources and can be used during foraging and breeding habitat choices (Valone and Templeton 2002). For example, collared flycatcher (*Ficedula albicollis*) choose the breeding sites according with information on reproductive success gathered during the previous breeding season via prospecting (i.e. visiting) neighbouring nests (Pärt and Doligez 2003).

In addition, previous studies have shown that the use of public information occurs also among individual of different species. For example, migratory birds choose their breeding territories depending on the location or densities of resident species (Thomson et al. 2003, Seppänen and Forsman 2007) and can have higher reproductive investment and success when breeding in vicinity of their potential competitors (Forsman et al. 2002).

When choosing the breeding territory, information about predator presence will be crucial. Selecting a safe breeding site should reduce the probability of a direct predator encounter and of nest detection, increasing thus fitness (Fontaine and Martin 2006b, Lima 2009). Information regarding ambient predation risk is likely included within the cue using of conspecific and heterospecific density. Warning calls of both con- and heterospecifics already settled in the area can be a valuable source of information on predator presence, type and location (Zuberbühler et al. 1997, Rainey et al. 2004, Schmidt et al. 2008, Magrath et al. 2009). In addition animals can also collect information on the predation risk in the area directly from the predator, for example through predator's territorial calls (Templeton et al. 2005, Adams et al. 2006, Thomson et al. 2006, Mönkkönen et al. 2007), or through indirect predator cues, like scent or scats (Amo et al. 2008, Roth et al. 2008, Mönkkönen et al. 2009).

1.2.1 Habitat selection during interspecific interactions: competition, intraguild predation, and protective nesting associations.

Spatial segregation from predators can be crucial, because species breeding or foraging far from a predator will have reduced probability of direct encounter with it (Lima and Dill 1990). For example, birds will occupy more often sites without predators and, in these sites, will have overall a higher reproductive investment (Fontaine and Martin 2006a, b). In addition, birds breeding at larger distance from predators will have higher reproductive success and reduced stress (Thomson et al. 2006, Thomson et al. 2010). Also individuals of the same or of different species, that compete for similar resources, might benefit from reciprocal avoidance and spatial segregation to reduce competition

costs, which may lead to reduced fitness (Ziv et al. 1993, Fernandez et al. 1998, Wilkin et al. 2006).

The killing and eating among competitor species is defined as intraguild predation (IGP; Polis and Holt 1992, Sergio and Hiraldo 2008). Alternatively, if species are both predators but do not compete for the same prey the interaction is defined as food chain omnivory (Aunapuu et al. 2010). Individuals of species involved in intraguild predation interactions will therefore have to face fitness consequences not only of predation risk (especially for the IGPrey) but also the costs of competition (for all the species involved). Therefore, the antipredator behaviours adopted by IGPrey will probably be particularly exacerbated to avoid not only the predator but also to reduce both exploitative and interference competition. Spatial segregation between individuals can be vital to reduce the costs of coexistence when intraguild predation occurs. Previous studies have shown that IGPrey avoid to breed and forage in the vicinity of IGPredators territories (Hakkarainen and Korpimäki 1996, Heithaus and Dill 2002, Sergio et al. 2003, Sergio et al. 2007) and might modify their activity pattern and hunting strategies to reduce the probability of encountering the IGPredators (St-Pierre et al. 2006, Sergio et al. 2007, Zuberogoitia et al. 2008).

Some species might benefit from the intraguild predation and interference competition existing among other species. In protective nesting associations, prey can select territories near large predators (top predators), that usually prey upon other smaller dangerous species (mesopredators), to reduce their own predation risk (Bêty et al. 2001, Quinn et al. 2003, Quinn and Ueta 2008). Protective nesting associations may also occur where the protector species is not a top predator but is a species with intense nest defence behaviour, with consequent low predation risk in the surrounding of their nests (Norrdahl et al. 1995, Bogliani et al. 1999, Quinn and Ueta 2008). In these nesting associations the "protected" species will benefit from a reduced predation risk around the site because predators species will not be frequent in this area, either due to direct intraguild predation (Ritchie and Johnson 2009) or because of changes in the behaviour of smaller predators that avoid larger species (St-Pierre et al. 2006, Sergio et al. 2007, Mukherjee et al. 2009).

Close association with a top predator may also entail costs for prey. Costs may originate if the protector species occasionally predates also upon the species that is gaining protection (Norrdahl et al. 1995, Larsen and Grundetjern 1997). If the protector species constitute a risk for the protected species, either due to aggression or predation, the protected species might settle at a distance from the predator nest where the benefits exceed the costs. In predator-prey systems it has been observed that prey can select a territory at an optimal distance (not too close and not too far) from their predators where the costs (predation risk) and benefits (protection) are in balance (Quinn and Kokorev 2002, Thomson et al.

2006). This seems to occur also in some protective nesting associations. For example, red-breasted geese (*Branta ruficollis*) associate with peregrine falcons (*Falco peregrinus*) to reduce the predation risk from arctic foxes (*Vulpes lagopus*). However, due to high frequency of attacks from the falcons, geese settle at an optimal distance that allows to benefit from the nest defence of falcons versus foxes but without paying too high costs for frequent attacks (Quinn and Kokorev 2002). When the costs of protective nesting association are elevated, individuals will select breeding sites close to protective species only when the benefits of such associations exceed the costs, for example when predation risk is high (Haemig 1999).

1.2.2 Multiple predators

Natural environments are characterized by a multitude of different predators sharing the same habitat. For prey, it will be vital to cue on the multitude of predators and even identify different predators. This is especially important since behaviours evolved to avoid a certain predators could either increase or decrease the risk represented by other predators in the same habitat (Lima 1992, Sih et al. 1998). Some predators might take advantage of behavioural changes that prey adopt to avoid other predators species in the area, so called "predator facilitation". For example gerbils in captivity are more exposed to risk of predation by owls, when snakes are also present in the environment. Gerbils avoid dense structurally complex patches where snakes are more active, thereby increasing their exposure to owls in open areas (Kotler et al. 1992).

Previous studies have shown that animals can indeed distinguish between different predators and behave according to predator presence. Primates in captivity can respond uniquely to playbacks of different predators (Zuberbühler et al. 1997), while passerines in aviaries can recognize several predators species depending on their size and can adopt different alarming calls according to the danger they represent (Templeton et al. 2005). In addition, prey behavioural responses to multiple predators vary according to the predator species detected (Kotler et al. 1992, Korpimäki et al. 1996, Van Buskirk 2001, Botham et al. 2006, Eccard et al. 2008). When different predators are present in the area simultaneously, animals will have to adopt behavioural strategies that reduce the overall risk of predation. These trade-off behaviours may be imperfect for individual predators but help to optimise the predator facilitation effect, from different types of predator. For example, mountain log skink (*Pseudemoia entrecasteauxii*) show a predator-specific behaviour when in the presence of different predators that are visible one at the time. However when there are simultaneously two predators, with different hunting strategies (Preisser et al. 2007), these lizards will adopt a non-specific antipredator behaviour: a reduction of the overall activity (Stapley 2004).

At a landscape level, when different predator species with variable hunting strategies coexist in the environment, prey will modify their space use while trying to reduce both the risk of direct encounter and the risk of being killed (Willems and Hill 2009, Thaker et al. 2011). For example several African ungulate species avoid both areas where different predator species are common, especially sit-and-pursue predators that are easier to locate, and areas that are dangerous due to the habitat structure (Thaker et al. 2011).

1.3 Parental investment and care under predation risk

Parental care is vital for successful reproduction in numerous species. Increased investment in care should produce better quality offspring with greatest chances of survival. However, parental care also entails substantial costs to parents. Therefore, species parental care strategies have evolved as a result of the trade-offs between fitness costs and benefits of care provision (Montgomerie and Weatherhead 1988, Clutton-Brock 1991, Klug and Bonsall 2010). Parental care can be divided between the care given to the eggs and the care given to the young. The relative costs and benefits of care giving vary according to the quality of the brood, which can affect the future reproductive success of the parents (Montgomerie and Weatherhead 1988, Clutton-Brock 1991, Klug and Bonsall 2010), but depends also on the probability for the adult to survive to a future reproductive attempt (Clutton-Brock 1991).

The quality of the brood depends, along with other factors, on clutch and brood size and on the probability of survival of the offspring. Clutch size in birds has been hypothesized to depend on the maximum number of chicks that the parents can feed until fledgling (Lack 1947, Klomp 1970), and will therefore be dependent on the availability of food in the breeding territory (Högstedt 1980). Along with food availability also predation has been suggested as one of the main forces determining clutch size (Lima 1987, Martin 1995). Indeed, birds breeding under high predation risk have shown reduction in clutch size in response to the perceived risk (Eggers et al. 2006, Thomson et al. 2006).

1.3.1 Maternal allocation in eggs

Parents can increase the probability of offspring survival before hatching through differential maternal allocation in eggs (Mousseau and Fox 1998). During egg formation the mother allocates not only nutrients necessary for the development of the embryo, but can also transfer immune factors, hormones and carotenoids which might influence survival, development and future reproductive success of the offspring (Saino et al. 2002, Grindstaff et al. 2003, Hargitai et al. 2006, Gil 2008, Hasselquist and Nilsson 2009).

The allocation of immunoglobulin in eggs can increase the resistance to parasites in nestlings (Grindstaff et al. 2003), whereas high carotenoid levels in eggs might reduce

the amount of free radicals and oxidative stress (Blount et al. 2002, Török et al. 2007). The allocation of hormones has both costs and benefits for the offspring. The benefits of hormone allocation include faster growth, larger body masses and increased begging behaviour and survival. However higher levels of androgen hormones might also suppress immune activity, which might in turn reduce offspring survival when breeding in low food condition or in the presence of high density of parasites (Gil 2008).

Maternal investment partly depends on stimuli gathered before laying, at the time of egg formation (Mousseau and Fox 1998). Therefore, during nest building phase and egg formation, females might collect information from the environment and allocate differential levels of hormones, immune factors and carotenoids accordingly. Females breeding in stressful conditions, such as in high conspecific densities or under predation risk, can transfer different levels of immune factors and hormones to eggs, either adaptively, to increase the fitness of the offspring, or simply as a consequence of the level circulating in their own blood (Saino et al. 2005, Hargitai et al. 2009). Previous studies have shown that females exposed to predation risk during egg formation produce larger eggs with higher levels of cortisol (Giesing et al. 2011) or corticosterone (Saino et al. 2005). In addition, mothers that have been exposed to high predation risk will produce offspring with lower immune activity (Coslovsky and Richner 2011b), lower body growth (Coslovsky and Richner 2011a) and that may exhibit stronger antipredator behaviours (Storm and Lima 2010, Giesing et al. 2011).

1.3.2 Minimizing risk at the nest

Nest predation is attributed as the main cause of nest failures in many species of birds, which has promoted the evolution of a variety of behavioural strategies to minimise nest predation risk (Martin 1993, Martin and Briskie 2009). Parents can actively defend their nest by alarming and attacking predators, but this active nest defence has great costs due to the risk of predation for the parent itself, and can be used only when the predator is already in a close proximity to the nest (Caro 2005). Parents can also adopt passive antipredator strategies aimed at decreasing the probability of nest detection, reducing so both nest and adult predation risk (Caro 2005). When breeding in area of high nest predation risk, a common antipredator strategy is to reduce the activity at the nest during all phases of breeding (Martin et al. 2000, Chalfoun and Martin 2010).

In species with uni-parental incubation, the incubating parent, which is generally the female, invests a lot of energy to incubate eggs at an optimal temperature. This energetic investment is in addition to the cost in terms of loss of self-foraging time (Conway and Martin 2000a). To reduce the energetic costs of incubation, the non-incubating parent, generally the male, may provide food to the female via incubation feeding. This behaviour has been shown to reduce the self-feeding trips of the incubating parent (Lifjeld and

Slagsvold 1986), therefore increasing the probability that the eggs will be maintained at an optimal temperature, and increasing hatching success.

When breeding under high predation risk males seem to reduce the number of feeding trips, probably to reduce the probability of nest detection (Martin and Ghalambor 1999). In addition, several studies have shown that incubating females perceiving high risk might reduce the number of trip to and from the nest, while prolonging the time spent incubating in each trip (on-bout duration) (Conway and Martin 2000b, Ghalambor and Martin 2002, Kovařik and Pavel 2011), so reducing the activity around the nest. Similar behavioural adaptations of incubation behaviours occur also after a failure of the first breeding attempt due to predation (Chalfoun and Martin 2010). Also during the care of the young the parents can reduce the activity at the nest to reduce the predation risk for both the nestlings and themselves (Martin et al. 2000, Fontaine and Martin 2006a, Thomson et al. 2011).

1.4   *Aim of the thesis*

Predation can negatively impact the life of animals not only via the direct death of a certain individual, but also through non-lethal effects caused by the perceived risk, which may lead to decreased reproductive success and increased physiological stress. In this thesis I am investigating the antipredator behaviours adopted by parents to reduce both adult and nest predation risk in both avian prey and predators. Although there is a vast literature on antipredator strategies, and on their costs and benefits, the majority of the studies are conducted in captivity or by studying the response to short high pulses of predation, which can exacerbate the behaviour observed. In this thesis I studied the response of breeding birds to naturally occurring predation risk (**I,II,III,IV**), or where the perception of predation risk was experimentally manipulated for several days, through either predator cues (**IV**) or using special nest-boxes that allowed to increase both parental perception of risk (**V**) and actual predation rate (**II**).

The thesis is organized in a hierarchical approach following the breeding phases of birds, going from the choice of a safe breeding territory to changes in parental care to reduce predation risk. In the first three chapters of the thesis I study the habitat selection, reproductive success and survival of both prey and predators depending on competitive and predatory interactions occurring in boreal forests. I especially focused on the spatial segregation occurring as a consequence of intra- and interspecific competition and intraguild predation among two owls species (**I**), the interactions between passerines, meso- and top predators during breeding and their consequences on passerine nests survival (**II**) and finally on the habitat choice of passerines when multiple adult predators are settled in the area (**III**).

Once the territory has been selected a breeding pair will invest in reproduction through egg laying, incubation and care of the young, and in all these phases the perceived predation risk will have a great impact on the fitness. From this perspective I investigated how a passerine deals with the risk after settlement and in particular on how females exposed to risk during nest building and egg laying vary their maternal allocation in eggs (**IV**) and how parents modify their incubation behaviour under experimentally increased perception of risk (**V**).

In the first chapter I investigated the spatial settlement of pygmy owls (*Glaucidium passerinum*) depending on habitat structure and on the overall density of neighbouring nests of both conspecifics and of Tengmalm's owls (*Aegolius funereus*) (**I**). I hypothesized that pygmy owls will avoid to breed at high densities of both conspecifics and intraguild predators (IGP) to reduce the costs of food and territorial competition and predation risk. In addition, the presence of high density of both con- and heterospecifics should cause a reduction in the breeding success of pygmy owls.

After studying the direct interactions within the predator guild, I investigated if intraguild predation could indirectly affect survival of passerines. I wanted to see if pied flycatchers (*Ficedula hypoleuca*) would actively seek protection from a top predator, the Ural owl (*Strix uralensis*) against small mesopredators that are both common predators of passerines nests and prey of Ural owls (**II**). If Ural owls reduce densities of mesopredators in their territories through intraguild predation, this should indirectly weaken the predation pressure on passerines nests. However protective nesting associations could also be beneficial for small mesopredators; breeding at an optimal distance from a large predator could indeed potentially reduce predation risk of mesopredators from other larger predators which represent a higher danger for them. Through the study of pied flycatcher habitat selection and nest predation rate I aim to differentiate between the two possible protective nesting associations (**II**).

Several different predators can therefore coexist in the same environment and their spatial distribution depends on both competition and predation risk. The presence of different predators in the area will increase the predation risk for the prey, especially since antipredator behaviours that are effective against a certain predatory species might not be effective in the presence of others. I investigated the spatial settlement and reproductive success of pied flycatchers breeding in patches with nests of either pygmy owls or Tengmalm's owls and respective controls (**III**). I hypothesized that pied flycatchers will first settle in sites without predators and then settle close to the less dangerous predators. In addition, the perceived risk due to owl presence in the sites should results in lower reproductive investment.

Breeding in sites under high predation risk might induce physiological stress, which will cause a reduction in animal reproductive success. Therefore females breeding under

highly stressful conditions might be able to allocate differentially in eggs to increase the probability of survival of the chicks. I analyzed the levels of immune factors and carotenoids in pied flycatcher eggs laid under both naturally occurring and experimentally increased high predation risk and in respective controls (**IV**). I hypothesized that females will allocate higher levels of immune factors in eggs as an adaptation to the perceived predation risk to increase the probability of offspring survival.

Finally, the presence of predators in the breeding environment will also affect parental care. Parental presence at the nest might increase the probability of nest detection by predators. In this study I use an innovative methodology that allows me to study the behavioural response of pied flycatcher parents when the perception of risk, and the nest susceptibility to predation, is constantly high (**V**). I expect both parents to reduce the time spent at the nest and to increase the vigilance at the nest while incubating to reduce both female's and eggs' predation risk.

2.   METHODS

2.1   *Study species and systems*

The pied flycatcher (*Ficedula hypoleuca*) is a migratory passerine that arrives in Finland in mid-May for breeding. Early arriving flycatchers are generally in good body condition, settle first in high quality patches and have higher reproductive success (Lundberg and Alatalo 1992). Pied flycatchers breed in cavities, either in natural cavities or nest boxes, and predation rate in natural nests is higher than in nest-boxes. Clutches average between 5 to 8 eggs and only females incubate, generally for thirteen days, whereas the care of the young is bi-parental and last in average fifteen days (Lundberg and Alatalo 1992).

The pygmy owl (*Glaucidium passerinum*) is a forest-dwelling species, and is the smallest owl in Europe. The hunting strategy is flexible, characterized by the ability of both hunt while flying and the use of a sit-and-wait strategy (Kullberg 1995). Pygmy owls are diurnal, with activity peaks at dusk and dawn (Kullberg 1995), and their home range is on average 1.5 km^2 (range 0.2-4.0 km2; Strøm and Sonerud 2001). In Finland the breeding phase generally starts from late March to early May (Lehikoinen et al. 2011). The diet of pygmy owls consists of vole species (*Microtus* and *Myodes* spp.) and passerine birds. The proportion of birds in the diet can be relatively large, especially during the poor vole years (25% - 80 % of diet; of which 1.8% are pied flycatchers; Kellomäki 1977, Kullberg 1995).

The Tengmalm's owl (*Aegolius funereus*) is a small forest-dwelling owl species. It is mainly nocturnal (Korpimäki 1981) and utilizes a sit-and-wait hunting strategy (Bye et al. 1992). Tengmalm's owl diet mainly consists of voles (both *Microtus* spp. and *Myodes* spp.), which in North Europe follow high-amplitude (50-200 fold) 3-year cycles with sequential low, increasing and decreasing densities (Korpimäki et al. 2005). During low vole years Tengmalm's owls hunt also birds but in small proportion (20 % - 36 %; 0.1% are pied flycatchers; Korpimäki 1988). Tengmalm's owl males start hooting already in February, which is followed by nest site choice from March to April, after which mostly unpaired males hoot (Korpimäki 1981). The home range of hunting Tengmalm's owls male during breeding season is 1.5 km^2 in the increasing phase and 2.3 km^2 in decreasing phase of the vole cycle (Korpimäki and Hakkarainen 2012, Santangeli et al. 2012). Previous studies indicate that Tengmalm's owls sometimes predate upon pygmy owls since their remains have been found in the diet of Tengmalm's owls (Korpimäki and Hakkarainen 2012). In addition, Tengmalm's owls also seem to decrease the hunting success of neighbouring pygmy owls in late autumn and winter, probably due to food competition and predation risk (Suhonen et al. 2007).

The Ural owl (*Strix uralensis*) is a large boreal forest-dwelling species that mainly prey upon two *Microtus* species (the field vole *M. agrestis* and the sibling vole *M. levis*) and bank voles (*Myodes glareolus*). In low voles years their diet also includes a variety of small predators, like red squirrels (*Sciurus vulgaris*), great spotted woodpeckers (*Dendrocopos major*) and small mustelids (Korpimäki and Sulkava 1987). Ural owls are present in their territories all year round and might be present in the site despite not breeding due to scarcity of main food (voles) (Lundberg 1981, Pietiäinen 1989). During breeding, Ural owls aggressively defend their nests and territories from intruders (Kontiainen et al. 2009).

Small mesopredators inhabiting boreal forests can be divided in two main groups depending on their main prey. First, small mustelids such as stoats (*Mustela erminea*) and least weasels (*M. nivalis*), that subsist mainly on *Microtus* and *Myodes* voles but shift to alternative prey, such as passerine nests, when vole density is low (Korpimäki et al. 1991). Second, there are generalist nest predators, such as the great spotted woodpecker, the European Jay (*Garrulus glandarius*), the pine marten (*Martes martes*) and the red squirrel; all of them are common predators of passerine nests (Weidinger and Kočvara 2010). Small mesopredators in our study area are predated upon by Ural owls (red squirrels being 0.5% of total prey number, least weasels and stoats 0.9%, woodpeckers 0.3%, corvids 0.4%; Korpimäki and Sulkava 1987) but also by larger predators such as eagle owls (*Bubo bubo*) and goshawks (*Accipiter gentilis*).

2.2 Experimental design

2.2.1 Spatial analyses

To study the settlement of pygmy owls in respect to nests of both con- and heterospecifics (**I**) I used Marked Point Pattern Models (Baddeley and Turner 2005) to estimate the intensity (~density) of point patterns. Each occupied nesting site was represented by a point in the model and classified according to the species, either pygmy owl (PO) or Tengmalm's owl (TO). I studied repulsion or attraction between species, both among pygmy owl conspecifics (PO-PO) and among pygmy owls and Tengmalm's owls (heterospecifc interaction, TO-PO). I included in the analyses also habitat characteristics obtained from the classification of three years Landsat satellite images and the proportion of each type of environmental covariate was computed for 5 different ranges (500, 1000, 1500, 2000 and 2500 m from a focal nest). Habitat characteristics were included in the analyses at the best range describing the proportion of a certain habitat in the landscape. The repulsion and attraction among con- and heterospecifcs was then calculated, while taking into account the habitat characteristics, with a MultiStrauss pairwise interaction function which indicated the value of gamma (with $\gamma \leq 1$ indicating repulsion between points). In the analyses of pygmy owls breeding success (**I**), I took into account the presence of both con- and heterospecifics by calculating the kernel

density of neighbouring pygmy owls and Tengmalms's owls per each pygmy owl nest at different range values, according with species home ranges.

2.2.2 Enlarged boxes

In chapter **II** and **V,** I used innovative methodology to experimentally increase the long-term perception of predation risk of breeding pied flycatchers. In both experiments I set up groups of nest boxes in several forest patches, both treatment boxes (called "enlarged" in **II**) and control boxes (called "normal" in **II**). Treatment nest-boxes appeared normal during settlement and egg-laying periods, with a small entrance hole (diameter 3.2 cm), but a panel was removed during incubation revealing an enlarged entrance hole (diameter 5.5-6 cm; Fig. 1A). Our aim, through the manipulation of the entrance hole, was to increase both perceived (**V**) and actual risk (**II**) of predation at the nest. Control boxes initially appeared normal with the small entrance hole, but when the front panel was removed during incubation it revealed an entrance hole of the same size, not altering the susceptibility to nest predation risk (Fig. 1B).

In experiment **II** the front panel of both control and treatment boxes was removed on the 6-8th day of incubation and was replaced when chicks were 2-3 days old. Nests in treatment boxes were exposed to nest predators on average for 8-9 days. Predation events were checked after cover removal and predator type was identified whenever possible on the basis of tracks, hair, teeth marks or scent (**II**). In chapter **V** instead, the front panel was removed approximately on the 8th day of incubation and nests were exposed on average for three days, to either increased or normal predation risk. Thereafter I recorded parental activity at each nest with digital video-cameras. Recordings lasted on average 2 hours at each nest. From each video I scored: the nest attentiveness, on-bouts duration, female vigilance, male presence at the nest and incubation feeding (**V**). The nest box manipulation method was approved by the Finnish Environmental centre (permission number: LSU-2009-L-497).
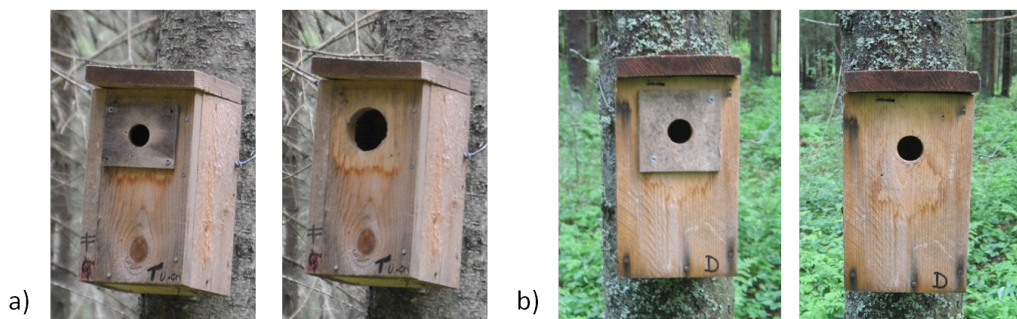

Figure 1: a) Treatment (enlarged) nest-boxes appear normal during habitat choice and laying but a panel was removed during incubation revealing an enlarged entrance hole increasing nest predation risk. b) Control (normal) boxes appeared normal but a panel was also removed revealing a normal sized entrance hole underneath and not altering nest predation risk.

2.2.3 Nest box settlement

In chapters **II**, **III** and **IV,** I studied the responses of pied flycatchers to perceived predation risk by setting up nest boxes in different patches where either an owl species was breeding or where predation risk was experimentally simulated at the nest via use of predator cues.

In studies **II** and **III,** I set up pied flycatcher boxes in forest patches containing actively nesting Ural owls (**II**), or either pygmy or Tengmalm's owls nests (**III**). In addition, in both experiments I used as control sites forest patches (with an empty owl nest-box) that were unoccupied during the current year but that had been previously used as breeding site by one of the owl species (**II**, **III**). In the second experiment, I placed 5 nest boxes per forest patch (two of which were control nest boxes and three enlarged boxes; see "*Enlarged boxes*" chapter), approximately at 100 m from the owl box, either in the presence of Ural owl nests or in control sites. In the third experiment, I settled four pied flycatcher nest boxes in all forest patches, at approximately 80 m from the owl nest-box. In both these studies (**II, III**) I measured the clutch size of pied flycatchers nests in treatment and controls sites to study the reproductive investment depending on the habitat selection choice. In both studies I classified the clutch size as either small or large. The majority of the clutches included either 6 or 7 eggs (with only few cases of 5 or 8 clutches in both experiments) and therefore the binomial distribution was the best to describe the reproductive investment.

In study **IV,** I collected pied flycatcher eggs from nests under predation risk from either pygmy owls or least weasels. In the pygmy owl experiment, I set up nest boxes in the surrounding of an active pygmy owl nest or in control sites, which were currently unoccupied but that have been occupied by pygmy owls in previous years (same methodology as in **III**). The weasel treatment sites were instead patches where all the boxes were sprayed every other day with least weasel urine (**IV**). Spraying lasted from the nest building phase until the laying of the first egg. In addition weasel hairs were glued on the entrance hole of the nest box to increase the perception of risk with a visual cue and finally a mounted stoat was presented for five minutes when the nest was completed or latest on the day when the first egg was laid. The weasel control sites were instead sprayed every other day with water and a drop of glue was put on the entrance of the nest box; finally a mounted chaffinch was presented on top of the nest just before egg laying. In all boxes, both pygmy and weasel treatments and controls, the fourth egg was collected and replaced with a dummy egg (**IV**).

2.2.4 Laboratory analyses

Laboratory analyses were conducted to determine the content of pied flycatcher eggs laid under high predation risk (**IV**). The yolk and albumen of each egg was separated in the

laboratory and part of the yolk was used for carotenoid and immunoglobulin analyses. Yolk and albumen samples were frozen at -20 °C and analyses of eggs were conducted in the laboratory at the Department of Biological and Environmental Science of University of Jyväskylä, Finland.

The antibody concentration was measured using an indirect enzyme-linked immune-sorbent assay (ELISA) (Pihlaja et al. 2006, Ruuskanen et al. 2011). The levels of immunoglobulins were measured as U/ml. The lysozyme was determined with a turbidometric assay by measuring the change in absorbance of the solution of albumen with a phosphate buffer after the addition of a *Micrococcus lysodeikticus* (Sigma M-3770) suspension (Jokinen et al. 2003, Ruuskanen et al. 2011). The results are given as lysozyme activity = change in absorbance units x 1000/min. The carotenoids analyses were done by adding in three different phases 300 µl of pure acetone to 50 mg of the frozen yolk. The samples were vortexed, centrifuged for 10 minutes at maximum speed and then supernatant was isolated at every phase. Absorbance at 450 nm was then measured from the *ca.* 900 µl of total supernatant so obtained (Multiskan Ascent, Therma oy, Finland) and then was corrected for the original yolk mass, the resulting concentration was in µg/mg.

3.   RESULTS AND DISCUSSION

3.1   Habitat selection under predation risk

3.1.1 Predation risk and competition under fluctuating food abundance

Spatial settlement and reproductive success of pygmy owls depended on the local densities of both conspecifics and inter-specific competitors (**I**). Pygmy owls avoided breeding at high densities of conspecifics independently of food abundance. When breeding at high conspecific densities, breeding success was reduced. A strong avoidance of intra-specific competitors, probably due to competition for food and territories, has been shown in some large birds of prey (Ferrer and Donazar 1996, Fernandez et al. 1998, Martínez et al. 2008).

Pygmy owls also avoided breeding close to Tengmalm's owls. When breeding in an area with high densities of Tengmalm's owl, pygmy owl hatching date was delayed. In addition, the reproductive success was reduced when both con- and heterospecifics were breeding at the same time, probably as a consequence of both competition and predation risk (**I**). The spatial and temporal segregation of IGPrey from their intraguild predators/competitors has been shown previously (Hakkarainen and Korpimäki 1996, Heithaus and Dill 2002, Sergio et al. 2003, St-Pierre et al. 2006, Sergio et al. 2007, Mukherjee et al. 2009). Distinguishing between the prey responses to intraguild predation risk and to interference/encounter competition can be difficult in some species, especially since the behaviour evolved to reduce predation risk or aggressions from competitors are similar (Ziv et al. 1993, Palomares and Caro 1999, St-Pierre et al. 2006, Mukherjee et al. 2009, Kotler et al. 2010). In addition, lethal effects of intraguild predation may be difficult to identify, for example when the killings are either difficult to record or occur rarely because of low encounter rate between species due to antipredator strategies evolved previously, like a shift in time activity (Lima and Dill 1990, Palomares and Caro 1999).

Here I used spatial analyses that allowed me to study aggregation or repulsion among individuals taking into account the habitat characteristics (**I**). Including habitat is essential because habitat structure and type can strongly affect the patterns of aggregation/ repulsion (Cornulier and Bretagnolle 2006). When neglecting to account for the habitat characteristics, aggregations among individuals can be seen as a result of conspecific attraction whereas, in reality, the spatial patterns are a direct consequence of abiotic environmental factors, like nest site availability (Cornulier and Bretagnolle 2006). Since my results take into account the characteristics of the habitat in the surrounding of both

pygmy and Tengmalm's owls nests, I can conclude that the repulsion observed both among con- and heterospecifics is due to behavioural avoidance among individuals. In addition to habitat, further studies should also include the spatial distribution of the prey of the species under study in the analyses, to determine the impact of food availability on the habitat selection and spatial distribution of the species.

3.1.2 Protective nesting association and mesopredator attraction

In experiment **II,** I investigated the possible protective nesting association between passerines and top predators. Overall I found that in patches where Ural owls were breeding, pied flycatcher nests were predated at higher rates than in patches without a top predator. High nest predation rates suggest a high abundance of predators in the area, which imply higher mesopredator densities in the proximity of Ural owl nests compared to control forest patches.

Protective nesting associations are characterized by a species actively selecting to breed close to a large predator to gain benefits in terms of reduced nest predation risk (Quinn and Ueta 2008, Ritchie and Johnson 2009). Although it has not been hypothesized so far, protective nesting associations could also involve species from the same guild because small mesopredators may choose to breed near large or aggressive predators, which represent for them a low risk of predation, to avoid more dangerous predators. It seems appropriate that this type of nesting association will be called "mesopredator attraction".

A mesopredator breeding close to a larger predator will face high costs in term of predation risk for itself; however, if the benefits of associating with the large predator are outweigh the costs, then such an association could evolve. A few previous studies have indirectly supported this hypothesis, showing that small species, occasionally predators of vertebrates, might associate with larger predators. For example, azure-winged magpies (*Cyanopica cyana)* and choughs (*Pyrrhocorax pyrrhocorax*) are occasional predators of vertebrates and breed close to the Japanese lesser sparrowhawk (*Accipiter gularis*) and the lesser kestrel (*Falco naumanni*), respectively, to reduce their own predation risk (Ueta 1994, Blanco and Tella 1997). Associations among predators could have consequences for several species at different trophic levels, because it would create an area with high density of mesopredators which would increase the predation risk for all the species that are generally or occasionally predated by those small predators.

A higher density of mesopredators in top predator nest sites, suggested by high predation rate on pied flycatchers nests, could however be explained also by shared habitat preferences among top and mesopredators. Both groups might choose similar habitats leading to a spatial association. Similar spatial aggregation due to nest-site availability has been previously observed (Cornulier and Bretagnolle 2006). However in

our study we used as control patches sites that were previously occupied by Ural owls, without large changes in the habitat between years; this design makes spatial association unlikely. Indeed, if both mesopredators and Ural owls would choose the same habitat characteristics we would expect mesopredator presence (i.e. predation events in our pied flycatchers nests) to be equal or even higher also in control sites, whereas this occur only in one of the study year. Admittedly, Ural owls and mustelid mesopredators share food resources, and both may spatially select territories with high current vole densities. However this would successfully explain the presence of mustelids around Ural owls sites, but would not justify the presence of the full range of mesopredators (woodpeckers, squirrels and jay) that do not depend on voles abundance. Therefore, the mesopredator attraction hypothesis rather than the spatial association due to habitat characteristics could be the apparent cause of the predation rates observed. Additional data on abundances of voles among sites, mesopredators distribution and on the cues used by mesopredators during habitat choice are however needed to better separate between mesopredator attraction and spatial association hypotheses.

Although, pied flycatcher nest predation rates were higher in Ural owl sites compared with controls, there was substantial variation in nest predation rates between years (**II**). In two of the years of study (2008 and 2010) predation rate was high in Ural owl nest sites (71% and 50%) but completely absent in control sites; in 2009 there was instead an overall high nest predation rate with no obvious differences between controls and Ural nest sites (83% and 55%). It appears that the environment was largely saturated with mesopredators in 2009, which may be linked to the abundance of *Microtus* voles, which follow a three year population cycle (Korpimäki et al. 2005) and are the main prey of both Ural owls (Korpimäki and Sulkava 1987) and small mustelid mesopredators (Korpimäki et al. 1991).

Pied flycatcher habitat selection did not appear to be dependent on the presence of Ural owl nests in the forest patch, since laying date (which is a proxy of pied flycatcher settlement choice) did not vary between sites. Pied flycatchers did not change their settlement according to the top predator presence, which is also in agreement with what suggested by a previous study (Mönkkönen et al. 2007). Pied flycatchers are able to choose the breeding territory according to the predation risk posed by avian adult predators (**III**, Thomson et al. 2006), however this may be more difficult with less conspicuous predators, such as nest predators (Chalfoun and Martin 2010). Passerines might thus not be able to assess precisely the nest predation risk in the patch during settlement. In addition, we found that pied flycatchers laid smaller eggs in nests close to Ural owls, which suggests that females perceived predation risk after settlement and varied their reproductive investment accordingly.

3.1.3 Multiple predator species affects habitat selection and reproductive investment of a prey

Pied flycatchers are able to distinguish among different predators and adjust their habitat selection decision and reproductive investment according to the perceived predation risk (**III**). Pied flycatchers avoided breeding in vicinity of pygmy owls but did not show differing occupation rates when breeding close to Tengmalm's owls or in control sites. In addition, pied flycatchers breeding in sites with pygmy owls showed a prolonged nest building period, delayed laying date and smaller clutches than birds in control sites or in vicinity of Tengmalm's owls. The low occupancy and the reduced reproductive investment in pygmy owl nesting sites indicates that pied flycatchers perceive these as risky sites.

The lack of avoidance of Tengmalm's owl sites and the similar reproductive investment between owls nest-sites and control sites suggests that pied flycatchers do not perceive the Tengmalm's owl as a serious threat. This is despite Tengmalm's owls occasionally preying on pied flycatchers. Pied flycatcher settlement in Tengmalm's owl nest sites could be due to a lack of information on the presence of Tengmalm's owls in the forest patch, since this owl species is mainly nocturnal. However it seems unlikely that a passerine would be unaware of predator presence a few meters from the nest. This is especially true in northern latitudes, where this study was conducted, characterized by very short nights and therefore where nocturnal animals are active also at dusk and dawn. Another explanation could be that pied flycatcher might gain some benefits from the presence of Tengmalm's owls in their breeding sites, for example because smaller predators might avoid these territories due to intraguild predation (Quinn and Ueta 2008, Sergio and Hiraldo 2008).

This study shows how a passerine, breeding in natural multi-predator environment under naturally occurring predation risk, can recognize different predators and modify its territory choice according to the perceived predation risk (**III**). My results are in agreement with previous studies indicating that prey can recognize different predators (Templeton et al. 2005, Adams et al. 2006) and adopt different antipredator behaviours accordingly (Korpimäki et al. 1996, Van Buskirk 2001, Stapley 2004).

3.2 Reproductive investment and parental care under predation risk

3.2.1 Maternal allocation of immune factors in eggs

In experiment **IV** I showed that pied flycatchers breeding under high predation risk, either due to the presence of a breeding predator or due to constant presence of predator cues in the nesting sites, transfer high levels of immunoglobulin to eggs. Parents breeding under high predation risk might reduce their effort in feeding the nestling, even if this will be costly for the nestling, because high activity in the surroundings of the nest might attract

predators to the nests, increasing so both adult and nest predation risk (Martin et al. 2000). High immunoglobulin levels in eggs might however increase the probability of survival of chicks that are poorly fed and therefore the transfer of high levels of immune factors might be adaptive. However, females breeding under high predation risk have high levels of immunoglobulins circulating in the blood (Thomson et al. 2010, Sheriff et al. 2011), due to the stress of predator presence, and therefore might also transfer a part of these immunoglobulins directly to eggs without any adaptive allocation (Saino et al. 2005). This experiment is the first evidence for higher transfer of immune factors in eggs when females are exposed to naturally occurring predation risk, however further studies are needed to determine if this transfer is adaptive.

In addition, the level of lysozyme differed between sites with a breeding pygmy owl and controls, but the levels were opposite in different years, being higher in controls in 2007 but higher in pygmy owls nest sites in 2009 (**IV**). This significant difference in lysozyme levels in eggs laid under predation risk seems to suggest that lysozyme transfer may interact with some environmental factors, but the mechanisms behind this allocation and their effects are still unknown.

3.2.2 Incubation behaviour

The use of new methodology (Figure 1), allowed me to study plasticity in the antipredator behaviour under constant predation risk (**V**), without the use of high pulses of risk, which can alter the behaviour observed (Lima and Bednekoff 1999). This methodology increased the probability of nest predation (**II**) and therefore the variation in parental behaviours observed in the enlarged nest-boxes, higher vigilance and reduced activity at the nest, is similar to what occur in natural nests.

In this last experiment (**V**), I found that pied flycatcher males reduce their activity in the surrounding of the nest while females increased their vigilance when breeding in experimentally manipulated nest-boxes. Higher vigilance should allow parents to reduce their own predation risk through early predator detection e.g. increasing their flight initiation distance (St Clair et al. 2010). Time spent in vigilance may also reduce nest predation risk because parents may be able to engage in nest defence before the predator approaches (Caro 2005).

In addition, we did not find variation in male incubation feeding trips and females on bouts duration depending on the nest-box manipulation which altered susceptibility to nest predation. Previous studies have instead shown a reduction in incubation feeding and increment in on-bouts duration after a predator encounter (Martin and Ghalambor 1999, Ghalambor and Martin 2000, 2002, Chalfoun and Martin 2010, Kovařik and Pavel 2011). However both these two antipredator strategies present energetic costs for the

females, because of reduction of feeding from the male and of self-foraging time. Under continuous high perception of risk, as in our study, parents might need to optimize the long-term costs and benefits of parental care strategies (risk allocation) by reducing their antipredator response to the continue perceived risk and restore quickly their normal activity after a high risk event (Creel et al. 2008, Ferrari et al. 2009, Thomson et al. 2011).

4. CONCLUSION

In this thesis I studied several antipredator behaviours during breeding in different avian species and considered the impacts of these behaviours on trophic interactions. My results, in agreement with other studies (Hakkarainen and Korpimäki 1996, Sergio et al. 2003, Fontaine and Martin 2006a, Thomson et al. 2006, Lima 2009), show that birds can assess the level of predation risk in a certain territory and therefore carefully choose territory location accordingly (**I**, **II**, **III**). Habitat selection is the first antipredator strategy linked to the reproductive period that an animal can adopt to reduce the risk and costs of predation. Informed territory choices are made both in "normal" predator-prey interactions (**III**) and when competition and intraguild predation are involved (**I**, **II**) to reduce costs of coexistence.

The settlement pattern of a predator might have consequences at several levels of the forest community. For example, the location of a bird of prey will affect the settlement of prey (**III**) but might also be affected by the distribution of other predators (**I, II**). Pygmy owls avoid breeding in high density of Tengmalm's owls nests (**I**) while Tengmalm's owls avoid breeding at close distance to Ural owls to reduce their own predation risk (Hakkarainen and Korpimäki 1996). Passerines and small rodents also modify their spatial distribution according to the spatial settlement of predators to reduce predation risk (**III**, Korpimäki et al. 1996). These complicated interactions among species, due to perceived predation risk and antipredator behaviours adopted, modify the overall spatial distribution of species in the forest community. A deeper knowledge of how predators settle spatially, depending on the presence of competitors and other predators in the landscapes, and the follow-on effects on prey spatial settlement is essential to better define the role of behaviourally mediated trophic cascades among vertebrates in natural environments.

In the second experiment, I suggested that species interactions in animal communities can be more complicated than earlier appreciated. Small predators might associate with larger species to gain protection from other guild predators. IGPrey have been shown to exhibit antipredator strategies (**I**, Sergio et al. 2003, St-Pierre et al. 2006, Salo et al. 2008, Mukherjee et al. 2009) against their IGPredators, to reduce their own costs of predation risk. Therefore protective nesting associations are likely to occur among predators if the benefits of such an association are higher than the costs for the IGP (**II**). My study is the first to suggest such a mesopredator attraction. If mesopredator attraction proves to be a common process, it will have large implications for associations in nature and overall community organisation. This process may also generate several new hypotheses about the direct value of top predators in the landscapes, which will be more complicated than earlier thought (Sergio et al. 2008). Alternatively, there could be a spatial association between top- and mesopredators due to similar habitat characteristics.

This association would also result in the higher predation rates observed for prey of the mesopredators. Further studies are needed to determine if mesopredators actively seek protection from top predators and to study the behavioural mechanisms behind this association. Nevertheless, my studies (**I, II**) suggest that intraguild predation and antipredator strategies, which can be adopted not only by prey but also by predators as prey (IGPrey), might have a strong impact on defining the community structure at a landscape level through their effects at several trophic levels.

Habitat selection in an environment with multiple predators requires an ability to recognize different predators (Templeton et al. 2005). In addition, if predators differ in hunting strategy, prey are required to adopt different antipredator strategies according to the predator species encountered (Stapley 2004, Preisser et al. 2007). My results highlight how prey appear to distinctly recognize between predators breeding in the area and modify not only their habitat selection behaviour but also their reproductive investment accordingly to the risk that each predator imposes (**III**). That the predator species involved are two quite similar owl species, further highlights a fine-tuned ability of the pied flycatcher in predator recognition. My results provide an understanding of how prey may respond, through their settlement in the landscape, to the presence of different breeding predators in a natural environment. This is especially important since the majority of the others studies conducted so far are in captivity or in enclosures, which does not allow study of free prey habitat choice.

Prey appear to have further possibilities to fine-tune their reproductive effort following their territory location decision, and increasing thus their fitness. Avian prey may alter their clutch size to match conditions of ambient adult (**III**) and nest predation risk (**II**). In addition to the investment in the clutch, I show that females may allocate substances in the eggs to even further fine-tune investment according to the perceived predation risk (**IV**). Female flycatchers transferred higher levels of immunoglobulins in eggs laid under either naturally occurring or experimentally increased constant predation risk. This appears to be the first evidence of variation in maternal allocation of immune factors in eggs depending on long-term perceived predation risk (**IV**).

The mechanism behind this transfer of immune factors is however still unknown; it could be either due to adaptive allocation in eggs or be a mere consequence of the level of immunoglobulins circulating in the female blood. Adaptive maternal allocation in eggs when breeding under high predation risk has been previously suggested by a comparative study among passerines where a correlation between eggs' testosterone levels and daily nest predation rate was found (Schwabl et al. 2007). The discovery that the predation risk perceived by the female during the early breeding affects the allocation in eggs (**IV**, Saino et al. 2005, Giesing et al. 2011), which may lead to consequences to the survival of the offspring, increases our understanding of predation as agent in the evolution of

both maternal effects and parental investment. A next step will be to investigate how the compounds found at higher levels in eggs laid under high risk (**IV**) affect chick performance in a high predation risk environment.

In the last chapter of this thesis I showed that parents modify their behaviour, through a reduction of parental activity and increased vigilance, when breeding under continuous high predation risk (**V**). Several studies have shown changes in parental care after a direct predator encounter, but the majority of these have used experimentally simulated short high pulses of risk (Dale et al. 1996, Ghalambor and Martin 2002, Peluc et al. 2008, Požgayová et al. 2009). Although investigating the response to a direct predator encounter is useful to increase our knowledge of animals antipredator behaviours, the behaviours observed under high pulses of risk might be exacerbated and thus may not reflect the responses to continuous risk (Lima and Bednekoff 1999). An animal living in a natural environment will more often live in a "landscape of fear", where the predator presence is perceived often in variable degrees but where the encounters with the predator are infrequent (Brown et al. 1999, Laundré et al. 2001), partly due to avoidance behaviours adopted by the prey. Therefore, to fully understand the behavioural responses to predation risk used by animals living in natural environment, we need to test the response under a continue perception of risk, like the one allowed by my methodology (Figure 1). This study highlights how the plasticity in parental behaviour evolved to reduce the predation risk but allows, at the same time, the animal to perform also other behavioural activities, like foraging, that are essential to survival.

To conclude, my thesis highlights the importance of predation and competition in determining species distribution in the landscape and the consequences at different trophic levels of these individual choices (**I, II, III**). In addition, it highlights the importance of using spatial analyses with characterization of the habitat to reach accurate conclusions on the aggregation/repulsion patterns between species (**I**). I also suggested a new mechanism, mesopredator attraction (**II**) that could deeply affect the community structure. The aggregation of mesopredators close to top predator nests will indeed create area on the landscape with high risk for their prey and this will have indirectly consequences also on the prey's resources availability. My thesis focuses also on the consequences of predation risk on reproductive investment and parental care, which both affect the overall fitness of an animal by affecting offspring survival. I showed that predation risk can affect maternal allocation (**IV**) and might thus adaptively increase the survival of the offspring. Finally I investigated parental care under predation risk (**V**) and showed that behaviours previously observed under short term pulses of risk do not occur when the perception of risk is prolonged. In my opinion, future studies need to concentrate on the behavioural responses under constant predation risk that better simulate or match conditions occurring in nature.

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