The effects of habitat changes, conservation measures and interspecific interactions on forest-dwelling hawks

Heidi Björklund

Finnish Museum of Natural History Luomus
Zoology Unit
University of Helsinki
Finland

Faculty of Biological and Environmental Sciences
Department of Biosciences, Ecology and Evolutionary Biology
University of Helsinki
Finland

LUOVA Doctoral Programme in Wildlife Biology Research
Doctoral School in Environmental, Food and Biological Sciences (YEB)
University of Helsinki
Finland

ACADEMIC DISSERTATION

To be presented for public examination with the permission
of the Faculty of Biological and Environmental Sciences of the University of Helsinki
in Auditorium C205, Economicum (Arkadiankatu 7), on June 26th 2015 at 12 noon.

Helsinki 2015

Supervised by: Dr. Toni Laaksonen
University of Turku, Finland
Dr. Jari Valkama
Finnish Museum of Natural History Luomus, Finland

Reviewed by: Priv.-Doz. Dr. Anita Gamauf
Naturhistorisches Museum Wien, Austria

Prof. Jari Kouki
University of Eastern Finland – Joensuu, Finland

Examined by: Prof. Oliver Krüger
University of Bielefeld, Germany

Custos: Prof. Jouni Laakso
University of Helsinki, Finland

Members of the Thesis Advisory Committee:

Dr. Patrik Byholm
Novia University of Applied Sciences, Finland

Dr. Ilpo Hanski
Finnish Museum of Natural History Luomus, Finland

Prof. Otso Ovaskainen
University of Helsinki, Finland

Author's address:
Finnish Museum of Natural History Luomus, Zoology Unit
P.O. Box 17, FI-00014 University of Helsinki
Finland
heidi.bjorklund@helsinki.fi

ISBN 978-951-51-1369-6 (paperback)
ISBN 978-951-51-1370-2 (PDF)
http://ethesis.helsinki.fi
Painosalama Oy
Turku, 2015

To my mother Irma and grandmother Rauha, two strong women,
and to my sons Daniel and Mikael, the burgeoning explorers.

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LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following articles, which are referred to in the text by their Roman numerals:

I **Björklund, H.**, Valkama, J., Tomppo, E. & Laaksonen, T. (Submitted, under review). Habitat effects on the breeding performance of three forest-dwelling hawks.

II **Björklund, H.**, Santangeli, A., Lehtoranta, H., Tomppo, E., Valkama, J. & Laaksonen, T. (Manuscript). Effects of habitat change on nest occupancy of two forest-dwelling hawks.

III **Björklund, H.**, Valkama, J., Saurola, P. & Laaksonen, T. (2013). Evaluation of artificial nests as a conservation tool for three forest-dwelling raptors. *Animal Conservation* 16: 546–555.

IV **Björklund, H.**, Santangeli, A., Blanchet, F. G., Huitu, O., Lehtoranta, H., Lindén, H., Valkama, J. & Laaksonen, T. (Submitted, under review). Intraguild predation and competition impacts on a subordinate predator.

Table of contributions

	I	II	III	IV
Original idea	**HB**	TL, AS	**HB**	**HB**, TL
Study design	**HB**, TL, JV	AS, **HB**, TL	**HB**, JV, TL	**HB**, AS, JV, TL
Empirical data	Luomus, ET	HLe, ET	Luomus	OH, HLe, HLi
Analyses	**HB**	**HB**	**HB**	**HB**, FGB, OH
Manuscript preparation	**HB**, JV, TL, ET	**HB**, JV, TL, AS, ET	**HB**, TL, JL, PS	**HB**, AS, FGB, TL, JV, OH, HLi

HB = Heidi Björklund, TL = Toni Laaksonen, JV = Jari Valkama, AS = Andrea Santangeli, ET = Erkki Tomppo, HLe = Hannu Lehtoranta, OH = Otso Huitu, HLi = Harto Lindén, FGB = F. Guillaume Blanchet, PS = Pertti Saurola, Luomus = Finnish Museum of Natural History Luomus; raptor nest card data gathered by volunteer raptor ringers, see Acknowledgements.

The summarising report includes previously unpublished research results not included in the article manuscripts in sections 4.2.1. (pp. 19–20) and 4.4. (p. 22). These results are referred to as Björklund et al., unpublished data. Unpublished results on the page 17 are referred to as Finnish Museum of Natural History Luomus, unpublished data.

ABSTRACT

Human-caused habitat changes are a major reason for the loss of biodiversity and population declines of many species. Habitat changes, such as habitat loss, fragmentation and habitat degradation, have direct and indirect impacts on species and their interactions with other species, which all affect their occurrence, survival and reproduction. In Northern Europe, intensive forestry has transformed boreal forests and worsened living conditions of especially those species dependent on mature and old forests. Populations of many forest-dwelling species have declined but the mechanisms by which habitat changes affect these species are often not known.

In this dissertation, I examined habitat changes, habitat-change effects and habitat-associated breeding performances of three declining forest-dwelling hawks, the northern goshawk *Accipiter gentilis* (goshawk), the common buzzard *Buteo buteo* and the honey buzzard *Pernis apivorus*. These species can compete for nest sites, but are also involved in intraguild predation (goshawk can predate the buzzards). The hawks may lack nest sites in managed forests on account of which their nesting possibilities have been supported by constructing artificial nests. I studied the breeding success of the hawks in artificial nests since the benefits of this intervention as a conservation measure had not been previously analysed. Finally, since dominant species in interspecific interactions can exclude subordinate ones from the remaining habitat patches, I studied the conditions when this could occur.

According to my results, the area of old forests has decreased throughout southern Finland while young forests have increased. These habitat changes are particularly adverse for the goshawks because their breeding success improves with an increasing proportion of old spruce forests and a decreasing proportion of young forests around their nests. The breeding performances of the common buzzard or honey buzzard were not significantly associated with habitats, probably because factors other than habitat have a greater effect on their reproduction. However, common buzzards were not eager to re-occupy nests that were surrounded by a vastness of old forests.

The breeding success of all three species was lower in artificial nests than in natural ones, although the difference in breeding success between the nest types was not significant for the honey buzzard. This suggests that conservation measures aimed at enabling the breeding of hawks in managed forests conflict with their conservation objectives. I discuss the possible contributing factors of this unexpected result and directions for further investigations. In the meantime, artificial nests could be used to replace fallen natural nests if the re-construction of natural nests is not possible for the hawks.

Interspecific interactions with other raptors proved to be a decisive factor in whether or not a subordinate raptor species occupied a territory. The occupancy stage is critical for common buzzards, most likely because a breeding failure later in the season (due to a disadvantageous occupancy decision) would involve a considerable waste of breeding investment. Common buzzards prefer to occupy safe territories, where the threat of intraguild predation by the goshawk and interference competition with other raptors are small. My results also suggest that adverse interspecific interactions with other raptors can impede a subordinate raptor species from fully exploiting the periodic food peaks. Although high prey levels would benefit common buzzards, they often preferred to avoid food-rich areas if that abundance had attracted interspecific raptors. These results suggest that other raptors that are predators or interspecific competitors, can exclude subordinate raptors from their territories, and thus contribute to the occurrence and population levels of subordinate raptors.

Finally, my dissertation shows that for each species, it is crucial to know the most relevant spatial and temporal scales in order to identify where external disturbances affect them most. Therefore, long-term data is of paramount importance to detect these scales, which can differ even for similar-sized species with rather similar ecological requirements.

TIIVISTELMÄ

Ihmisen aiheuttamat elinympäristömuutokset ovat suurimpia syitä eliölajien monimuotoisuuden katoon ja monien lajien kantojen pienenemiseen. Elinympäristömuutoksilla, kuten elinympäristön häviämisellä, pirstoutumisella ja huonontumisella, on suoria ja epäsuoria vaikutuksia lajeihin ja niiden vuorovaikutuksiin muiden lajien kanssa, ja nämä yhdessä vaikuttavat lajien esiintymiseen, selviytymiseen ja lisääntymiseen. Pohjois-Euroopassa tehometsätalous on muokannut boreaalisia metsiä ja heikentänyt erityisesti täysikasvuisesta ja vanhasta metsästä riippuvaisten lajien elinoloja. Monet metsälajit ovat taantuneet, mutta elinympäristömuutosten vaikutusmekanismeja näihin lajeihin ei aina tunneta.

Tutkin väitöskirjassani kolmen taantuvan metsähaukkalajin, kanahaukan *Accipiter gentilis*, hiirihaukan *Buteo buteo* ja mehiläishaukan *Pernis apivorus*, elinympäristön muutoksia, elinympäristömuutosten vaikutuksia sekä näiden lajien pesimistulokseen vaikuttavia elinympäristötekijöitä. Tutkimuslajit voivat kilpailla pesäpaikoista, mutta ovat osallisia myös killansisäiseen saalistukseen (kanahaukka voi saalistaa hiiri- ja mehiläishaukkoja). Talousmetsissä voi olla niukasti haukoille sopivia pesäpaikkoja, joten haukkojen pesimismahdollisuuksia on tuettu rakentamalla niille tekopesiä. Tutkin haukkojen pesimismenestystä tekopesissä, sillä tämän puuttumiskeinon hyötyjä suojelutoimenpiteenä ei ole aiemmin tarkasteltu. Vahvemmat lajit voivat lajien välisissä vuorovaikutuksissa jopa häätää alisteiset lajit pois jäljelle jääneistä elinympäristölaikuista, ja tutkin lisäksi, missä oloissa näin voi käydä.

Tulosteni mukaan vanhat metsät ovat vähentyneet haukkojen reviireillä ja Etelä-Suomessa, kun taas nuorten metsien pinta-ala on kasvanut. Nämä elinympäristömuutokset ovat erityisen haitallisia kanahaukalle, koska kanahaukan pesimismenestys kasvoi vanhan kuusimetsän osuuden kasvaessa ja nuoren metsän osuuden vähentyessä reviirillä. Hiiri- ja mehiläishaukalla ei havaittu merkitsevää yhteyttä elinympäristön ja pesimistuloksen välillä luultavasti siksi, että muut tekijät kuin elinympäristö vaikuttavat niiden lisääntymiseen enemmän. Hiirihaukat eivät kuitenkaan mielellään asuttaneet uudestaan pesiään, joiden ympärillä oli paljon vanhaa metsää.

Kaikkien kolmen haukkalajin pesimismenestys oli alhaisempi tekopesissä kuin haukkojen omissa pesissä, tosin mehiläishaukalla pesätyyppien ero pesimismenestyksessä ei ollut tilastollisesti merkitsevä. Tulos viittaa siihen, että tämä haukkojen pesinnän metsätalousmetsissä mahdollistava suojelukeino on ristiriidassa suojelutavoitteidensa kanssa. Tarkastelen tulokseen mahdollisesti vaikuttavia tekijöitä sekä tarvittavia jatkotutkimuksia, jotta odottamattomalle tulokselle löytyisi selitys. Toistaiseksi tekopesiä voi rakentaa korvaamaan pudonneita haukkojen omia pesiä, mikäli luonnonpesien uudelleenrakentaminen ei haukoilta onnistu.

Vuorovaikutussuhteet muiden petolintulajien kanssa osoittautuivat tärkeiksi alisteisen petolintulajin päättäessä asettumisestaan reviirille. Reviirinasutusvaihe on hiirihaukoille kriittisen tärkeä luultavasti siksi, että huonosta päätöksestä johtuva pesinnän epäonnistuminen myöhemmin pesimiskaudella merkitsisi huomattavaa pesimispanostuksen menetystä. Hiirihaukka suosii turvallisia reviirejä, joilla kanahaukan killansisäisen saalistuksen uhka ja muiden petolintulajien häirintäkilpailun uhka ovat pieniä. Tulokseni viittaavat myös siihen, että epäedulliset vuorovaikutukset muiden petolintulajien kanssa voivat estää alisteista petolintulajia hyödyntämästä täysimääräisesti saalislajiensa ajoittaisia huippuvaiheita. Vaikka runsas ravinto hyödyttäisi hiirihaukkaa, hiirihaukat mieluummin välttävät alueita, joilla saalislajeja on paljon, mikäli runsas ravinto houkuttelee alueelle muita petolintulajeja. Tulosteni perusteella muut petolintulajit, jotka ovat saalistajia tai kilpailijoita, voivat syrjäyttää alisteisen petolintulajin reviiriltä ja siten vaikuttaa sen esiintymiseen ja kannankokoon.

Väitöskirjani osoittaa, että on tärkeää tunnistaa kullekin lajille oleelliset alueelliset ja ajalliset mittakaavat, jotta tiedetään, missä mittakaavassa tapahtuvat ulkoiset häiriöt vaikuttavat lajiin todennäköisesti eniten. Lajien pitkäaikaiset aineistot ovat ensiarvoisen tärkeitä selvitettäessä näitä mittakaavoja, jotka voivat vaihdella jopa samankokoisten ja ekologisilta vaatimuksiltaan samankaltaisten lajien välillä.

SUMMARY

1. INTRODUCTION

1.1. Habitat change effects on species

Anthropogenic environmental and land use changes impact many wildlife species and biodiversity worldwide (Sala et al. 2000, Foley et al. 2005). For instance, habitat destruction and degradation are globally the main threats to 86% and 88 % of threatened bird and amphibian species, respectively (Baillie et al. 2004).

Anthropogenic habitat changes involve the loss, fragmentation, and degradation of habitats, and these have various effects on organisms (Fahrig 2003, Fischer and Lindenmayer 2007, Schwitzer et al. 2011). Smaller, isolated and degraded habitat areas support smaller populations of organisms (Begon et al. 1996). Habitat loss is usually more critical than fragmentation for the persistence of populations and biodiversity (Begon et al. 1996, Fahrig 1997, 2003), while habitat cover and configuration are important determinants of species presence in fragmented landscapes (Villard et al. 1999). Reductions in habitat cover hamper movements of even highly mobile species such as birds during the breeding season (Bélisle et al. 2001). Habitat changes can also disrupt the biology and behaviour of species, thus impeding reproduction (Fischer and Lindenmayer 2007). On the other hand, habitat change effects and responses can be species-specific (Villard et al. 1999). Species that have large territories and require vast areas of specific habitats (Kurki et al. 2000), or species favouring habitat interiors (specialists) are prone to suffer from fragmentation, while habitat generalists can manage or even thrive in fragmented landscapes (Schmiegelow et al. 1997). This is because generalist species often use exterior areas in addition to specific habitats (Andrén 1994), while for specialist species, areas of the preferred habitat are further reduced due to various edge effects (Fahrig 1997). Consequently, habitat loss and fragmentation can alter species compositions even without actual habitat changes in the remaining patches (Nee and May 1992). Finally, habitat loss and fragmentation can lead to population declines or at worst, extinctions (Begon et al. 1996, Fischer and Lindenmayer 2007).

In addition to direct effects on species, habitat changes can have complicated indirect impacts. Habitat loss may cause crowding, an often temporary increase in species abundance in remaining adjacent habitat patches (Schmiegelow et al. 1997). Consequently, more frequent encounters between species can alter their interactions (Nee and May 1992, Fischer and Lindenmayer 2007). For instance, intra- or interspecific competition or predation can be higher in fragmented landscapes (Møller et al. 2012).

Dominant species can then displace weaker competitors and reduce the amount of habitat available to them (Krüger 2002a, but see Nee and May 1992). Habitat change effects can also escalate in food webs when declines in prey populations lead to a decrease in their predator population or to a diet shift of the predator (Widén 1997, Sulkava et al. 2006), or when disappearances of top predators lead to a mesopredator release and consequent suppression of its prey (Crooks and Soulé 1999). Shortage of the main food can even make predators predate other predators (Bijlsma 2004, Rutz and Bijlsma 2006). Multiplicative effects can obscure the prediction of habitat change effects on species; for instance fragmentation in association with anthropogenic disturbance can have a stronger impact on species richness than fragmentation alone (Ross et al. 2002).

1.2. Challenges in studies of habitat change effects

Various documented effects of habitat changes on species were reviewed above. Here, we take one step backwards to discuss some challenges that may arise when studying the habitat change effects on a species. For a detailed discussion, see e.g. McGarigal & Cushman (2002). First, it is often unknown what habitat parameters are important for a species (Kouki et al. 2001), and so, a multitude of measurements are taken. However, a trade-off between the level of detail and areal coverage of the study affect the sample size, especially for species with wide home ranges. Some pre-selection of habitat parameters is usually needed but the relevant ones can easily be missed. Secondly, habitat data should be acquired from at least two periods in order to detect changes. Thirdly, it can be difficult to identify the appropriate temporal scale in which habitat changes affect a species (Sverdrup-Thygeson et al. 2014). The species responses may not have developed after recent habitat changes (McGarigal and Cushman 2002), or the truly influential habitat changes may have already occurred in the past (Kouki et al. 2001), but due to lag effects the species have not yet disappeared (extinction debt in Hanski 2000). Therefore, the currently observed habitat associations are potentially not ideal for the species. As another example on the relevance of temporal scale, habitat changes can exert the strongest effect on a specific phase of the life or breeding cycle. Habitat changes may have no effect on the productivity of individuals that were able to reproduce, even when half a population found no sites for reproduction. Fourthly, assessing an appropriate spatial scale is also challenging (as discussed in Kouki et al. 2001). Effects of habitat change can be analysed close to reproduction sites, while doing so also at the landscape scale would be more relevant (Kurki et al. 2000, Squires and Kennedy 2006, Sverdrup-Thygeson et al. 2014).

1.3. Habitat change and conservation

Conservation efforts aim to mitigate negative impacts of habitat changes on species. Such efforts include measures to sustain habitats, for example by establishing protected areas (Groom et al. 2006) and leaving habitat corridors (Bennett 2003) or buffer zones (Santangeli et al. 2012). Efforts to counteract the loss of essential habitat structures include construction of artificial nests (**III**, Ivanovski 2000) and nest boxes for birds (Lambrechts et al. 2011). However, sometimes conservation measures can have unexpected consequences and even harm species by luring them to low-quality habitats, i.e. 'ecological traps' (Battin 2004). For instance, nest boxes can attract birds to breed in unsuitable or dangerous environments (Klein et al. 2007). Therefore, an evaluation of the impact and efficiency of conservation efforts should be routinely performed, but it is currently often not done (Ferraro and Pattanayak 2006).

1.4. Birds of prey in changing environments

In this work, we used birds of prey to study habitat changes, habitat change effects on species and species interactions. Birds of prey are suitable study organisms for these purposes because they often use the same nests and nest sites for breeding over several years (Jiménez-Franco et al. 2014). Either the availability of food or nest sites drives the natural population ecology of birds of prey (Newton 1979), and habitat changes can affect both. Thus, consequences of environmental changes around the nests can be followed and associated with breeding variables connected to the nests (such as occupancy and productivity). Since predators are at the top of the food web, any habitat changes affecting the lower levels have potential repercussions for them. Top predators have been used as indicators of environmental conditions or surrogates in conservation programs (Sergio et al. 2008). Raptor nest sites are also associated with high biodiversity values (Sergio et al. 2006, Burgas et al. 2014) and as such, adverse environmental changes at raptor nest sites can imply unfavourable changes for several other species. Therefore, conservation measures for raptors and their nest sites could also benefit other taxa.

Habitat change effects in birds of prey are potentially complicated (but interesting) because of the variety of interspecific interactions they have with each other. Birds of prey can compete for nest sites, territories, food or some combination of these (e.g. Schmutz et al. 1980, Korpimäki 1987, Poole and Bromley 1988, Kostrzewa 1991, Clouet et al. 1999). Due to competition, birds of prey are often territorial intra- but also interspecifically (Newton 1979, Janes 1984, Kostrzewa 1991, Martínez et al. 2008) since continuous conflicts with neighbouring interspecifics can lead to breeding failures of both competitors (Kostrzewa 1991, Clouet et al. 1999). In addition, birds of prey are involved in various interspecific predatory interactions including superpredation, intraguild predation (IGP) and interspecific competitive killing (Mikkola 1976, Sergio and Hiraldo 2008, Lourenço et al. 2011, Lourenço et al. 2014). Superpredation occurs when a top predator kills and consumes another (often smaller sized) predator as prey, when the victim is not a competitor of the top predator (Lourenço et al. 2014). IGP refers to events when a predator kills and consumes another predator species that is a potential competitor (Polis et al. 1989, Polis and Holt 1992). In interspecific competitive killing, the killer and the victim predators are competitors but the victim is not consumed. It represents an extreme case of interference competition where the victim dies during a fight or defence of shared resources (Lourenço et al. 2014). Superpredation and IGP are often asymmetric, such that one species predates the other but not vice versa (Sergio and Hiraldo 2008). As anti-predator responses, subordinate predators can try to avoid the dominant ones spatially, temporally, or behaviourally (Sergio and Hiraldo 2008). For instance, subordinate predators may try to become inconspicuous when a dominant predator arrives (Zuberogoitia et al. 2008), or they may avoid the nest sites of the dominant species (Poole and Bromley 1988) and habitats where an encounter is probable (Sergio et al. 2007). The dominant predator can choose nest sites and territories irrespective of the subordinate predators (Pakkala et al. 2006, Rebollo et al. 2011) while the displaced subdominants may need to move to other areas (Kostrzewa 1991, Chakarov and Krüger 2010). Therefore, the loss or decrease in preferred habitats of both species could especially harm subordinate predators.

2. OUTLINE AND AIMS OF THE THESIS

Continuous population declines of several birds of prey species in Finland, including both diurnal and nocturnal raptors, were an impetus for this thesis (Saurola 2008, Saurola and Björklund 2011). Since the declining raptors have different migratory patterns (resident, migratory, nomadic) and food sources (from mammals and birds to insects), but all inhabit forests, this raised our concern for the state of managed boreal forests and whether the raptor declines are associated with changes in the forests. For instance the Tengmalm's owl (*Aegolius funereus*) benefits from old forests (Laaksonen et al. 2004, Hakkarainen et al. 2008) and its decline in Finland is probably associated with reductions in old-growth forests in the 1900s (Östlund et al. 1997, Myllyntaus and Mattila 2002, Korpimäki and Hakkarainen 2012). However, several diurnal hawks have also declined, but the possible associations of these decreases with forest habitat changes are not fully understood.

Our three study species, the northern goshawk *Accipiter gentilis* (hereafter goshawk), the common buzzard *Buteo buteo*, and the honey buzzard *Pernis apivorus*, are middle-sized forest-dwelling hawks that have declined in Finland in recent decades (Valkama et al. 2011, Honkala et al. 2013). The species are potential nest site competitors but the goshawk is an intraguild predator of the buzzards (see details in 3.1.). The population declines of the buzzards are steeper than that of the goshawk (Honkala et al. 2013). This has evoked suspicions that the dominant goshawk excludes the buzzards from high-quality habitats (Krüger 2002a, Hakkarainen et al. 2004a) and therefore could have partly contributed to the buzzards' declines. Thus, ecological similarity, population declines and a potential tension in their interaction made these hawks interesting study species.

Firstly, it turned out that there is a lack of detailed knowledge of the breeding habitats of the species in European boreal forests. Despite the array of breeding habitat studies on the goshawk in North America (reviewed by Squires and Kennedy 2006), and on all three species in more southern areas in Temporal and Mediterranean Europe (e.g. Jędrzejewski et al. 1988, Penteriani and Faivre 1997, Selås 1997, Krüger 2002a, Penteriani 2002, Bielański 2006, Lõhmus 2006, Gamauf et al. 2013), there are only few studies on the boreal breeding habitat of the goshawk in Europe (Hakkarainen et al. 2004b, Byholm et al. 2007) and none on the other species. This lack of information is striking considering that the Boreal Zone is the second largest biome in the world and all three hawks are widespread throughout the European Boreal Zone (Cramp and Simmons 1980, Ruckstuhl et al. 2008). Secondly, habitat changes and the effects of changes in breeding habitats are even less well studied, although it is recognized that habitat changes can render a landscape unsuitable for the hawks (Squires and Kennedy 2006). Furthermore, the breeding habitats close to nests are often investigated, even though the habitat composition at the landscape scale is probably also important, and analyses at this scale are needed (Squires and Kennedy 2006) since the hawks have wide territories. Therefore, we studied the breeding habitats of the goshawk, the common buzzard, and the honey buzzard at multiple scales in the Boreal Zone in southern Finland using extensive long-term data on hawk nests and multi-source habitat data (**I**). We analysed the association of the breeding habitats with the breeding success and brood size of the hawks, and changes in the breeding habitats between two periods.

We were also interested in how habitat changes at the nest site and the territory scales around nests affect goshawk or common buzzard nest occupancy (**II**), i.e. an earlier stage of the breeding cycle than in **I**. This assists in understanding whether habitat changes contribute to hawk population declines by reducing the occupancy probability. Hawks can abandon nests whose surroundings change drastically, but different species can have varying abilities to adapt to habitat changes. Moreover, abrupt changes such as forest loss close to the nest are known to decrease occupancy (Penteriani et al. 2002, Santangeli et al. 2012), whereas effects of gradual habitat changes at the territory scale are rarely studied.

Forest-dwelling hawks use large, often old trees with stout forks and thick branches or distorted trees to construct their heavy stick nests (Bielański 2004, 2006, Lõhmus 2006). However, intensively managed forests are logged before trees grow old, and suitable nest trees are prone to be removed due to practices favouring straight trunks and small branches (Bielański 2004, Lõhmus 2006). Consequently, hawks can suffer from a shortage of suitable nest trees in intensively managed forests. For decades, Finnish raptor ringers and volunteers have aided these birds by constructing artificial nests (Honkala et al. 2013). Artificial nests for the goshawk, common buzzard and honey buzzard are stick nests made to resemble natural ones in appearance and in their under-canopy location in a tree. The benefits of this conservation measure had not been evaluated until now. To do so, we compared the breeding performance of the three hawks in natural and artificial nests (**III**).

Finally, since the potential competitive or predatory exclusion of the common buzzard by the goshawk has been suggested, we used a novel way to study the impact of the intraguild predator goshawk on the subordinate predator common buzzard, while taking into account different biotic and abiotic conditions (**IV**). Specifically, we analysed how threat of the goshawk, food levels, presence of competitors (mainly *Strix* owls), and weather affect the occupancy and reproduction of the common buzzard. We hypothesized that common buzzards avoid the proximity of goshawks especially when the main food sources of the goshawk are scarce, as this is when it can switch to predate alternative prey, including raptors. We also took into account food levels of the common buzzard, and weather during spring and summer, which are known to affect their reproduction (Reif et al. 2004, Lehikoinen et al. 2009).

3. MATERIALS AND METHODS

3.1. Study species

Our study species, the goshawk (**I**–**IV**), the common buzzard (**I**–**IV**) and the honey buzzard (**I**, **III**), inhabit similar full-grown coniferous and mixed forests (del Hoyo et al. 1994, Nevalainen 2003) and are potential nest site competitors as evidenced by the species even using the same nests for breeding over different years (**IV**, Lõhmus 2006). However, the goshawk is dominant and can usurp nests of the other species (Kostrzewa 1991, Krüger 2002b, Hakkarainen et al. 2004a).

The goshawk predates mainly forest grouse, corvids, some other birds, and European red squirrels (*Sciurus vulgaris*; Sulkava et al. 2006, Tornberg et al. 2006). The common buzzard preys on *Microtus* voles, forest grouse, and hares (Reif et al. 2001), and the honey buzzard chiefly on wasps (Vespidae), frogs, and small birds (Itämies and Mikkola 1972). The goshawk is also an intraguild predator of the common buzzard, honey buzzard and other raptors (Kostrzewa 1991, Bijlsma 2004, Pakkala et al. 2006). Due to IGP threat, other raptors often avoid settling close to goshawk nests (Kostrzewa 1991, Hakkarainen et al. 2004a, Pakkala et al. 2006, Gamauf et al. 2013). In contrast, common buzzards and honey buzzards are not known to predate other birds of prey (Itämies and Mikkola 1972, Reif et al. 2001) and they can successfully breed close to each other (Kostrzewa 1991).

Adult goshawks are sedentary in Finland, common buzzards are short- or long-distance migrants to Europe and Africa, and honey buzzards are long-distance migrants to Africa (Saurola et al. 2013, Byholm and Valkama 2015). Goshawks establish their territories in March, while common buzzards return from their wintering grounds in March–April (Kontkanen and Nevalainen 2002, Saurola et al. 2013). When honey buzzards arrive to their breeding grounds in May–June, goshawks and common buzzards already occupy the most attractive forests and are incubating (Kostrzewa 1991, Kontkanen and Nevalainen 2002, Gamauf et al. 2013, Saurola et al. 2013, Byholm and Valkama 2015). On the other hand, breeding later than the goshawk and common buzzard decreases the temporal overlap with these species (Hakkarainen et al. 2004a), and honey buzzards can choose nest sites far from goshawks (Gamauf et al. 2013). In addition, honey buzzards possibly avoid detection by being very secretive at their nest sites (Gamauf et al. 2013) and therefore, their nests are hard to find. This is probably the main reason why the number of honey buzzard's nests was low in this study.

3.2. Study area

The data on hawk nests originate from southern Finland (**I** and **III**) and from the region of North Karelia in eastern Finland (21 584 km^2, **II** and **IV**). In both regions, forests are mostly managed and dominated by Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*) and birches (*Betula pendula* and *B. pubescens*; Kaila and Ihalainen 2014). Of the total forest area in southern Finland, 2% is strictly protected (Juntunen 2014).

3.3. Nest data

In this study, we used two datasets on hawk nests, both gathered by volunteer raptor ringers and enthusiasts (see Acknowledgements). *Raptor Nest Card data* has been gathered since 1982 as a part of the Finnish Common Birds of Prey Survey (Saurola 1986), and we used this previously unanalysed data from southern Finland in chapters **I** and **III** for years 1992–2010 and 1982–2009, respectively. Raptor Nest Cards document information on the nests of birds of prey and their breeding attempts. The data enabled analyses on breeding success and brood size in different nest types (**III**) and habitats (**I**). However, Raptor Nest Cards are usually filled in for occupied nests, and rarely for unoccupied ones. Fortunately, the North Karelian Ornithological Society has gathered data on all known hawk nests since the 1980s, including information from those years when nests were unoccupied. Therefore, we used the *hawk nest data from North Karelia* when we wanted to analyse the conditions that affect nest and territory occupancy. We used this data in chapters **II** and **IV** for years 1999–2008 and 1997–2009, respectively.

3.4. Other data

Our *habitat data* was derived from the multi-source national forest inventory (MS-NFI) data of the Finnish Forest Research Institute (2015 onwards Luke, see * below). MS-NFI data combines information from satellite images, field plots of Finnish national forest inventories and other georeferenced data (Tomppo et al. 2008, Tomppo et al. 2009). Each pixel in the raw MS-NFI data (hereafter habitat data) was classified into predefined habitat classes, which were further combined into seven habitat classes suitable for our purposes: old spruce forests, volume ≥ 150 m^3 / ha; other old forests dominated by Scots pine, volume ≥ 150 m^3 / ha; young thinning forests, volume ≥ 60 m^3 – < 150 m^3 / ha; low stocking forests, volume 0– < 60 m^3 / ha; water; arable land; and built-up land. The habitat data was retrieved from circles of different radii around hawk nests: 100 m, 250 m, 500 m, 1000 m, 2000 m and 4000 m for chapter **I**, and 250 m and 2000 m for chapter **II**.

We used two datasets to measure food availability levels of the goshawk and the common buzzard (**IV**). *Grouse data* of the Finnish Game and Fisheries Research Institute (*), which includes yearly abundances of the forest grouse species Eurasian black grouse (*Lyrurus tetrix*), hazel grouse (*Bonasa bonasia*), capercaillie (*Tetrao urogallus*) and willow grouse (*Lagopus lagopus*), was used as a measure of principal food availability for the goshawk and alternative food for the common buzzard. *Vole data* of the Finnish Forest Research Institute (*) consisted of abundances of the two most common vole species, the field vole (*Microtus agrestis*) and the bank vole (*Myodes glareolus*), and was used as a measure of principal food availability for the common buzzard.

(*) From 2015 onwards, the Finnish Forest Research Institute and the Finnish Game and Fisheries Research Institute were incorporated into the new Natural Resources Institute Finland (Luke).

Weather data (**IV**) from the Finnish Meteorological Institute consisted of spring and summer temperatures and precipitation (Venäläinen et al. 2005).

3.5. Study design and analyses

In chapter **I**, we studied the habitat-associated breeding performances of the goshawk, common buzzard and honey buzzard at multiple spatial scales, and habitat changes around their nests. Chapter **I** also provides detailed multi-scale information on the breeding habitat of the goshawk, common buzzard and honey buzzard in the European Boreal Zone. We used the habitat data from four MS-NFI periods to analyse the association of breeding habitat with breeding success and brood size of each species. This way we ensured that the breeding data from a nest and the habitat data around the nest were temporally closely matched (within ± 2 years). We first assessed which scale (100 m, 500 m, 1000 m, or 2000 m) best explained the breeding success and brood size of each species, and then analysed the association of habitat variables with the breeding performance within that scale. Then we analysed differences in habitat proportions at different scales around hawk nests (100 m, 1000 m, and 2000 m) between two periods (median years: 1998 for the first period and 2008 for the last period) to detect changes in breeding habitats. These changes were contrasted with overall changes in forests throughout southern Finland, based on field data of Finnish national forest inventories. We also analysed interspecific differences in the multi-scaled breeding habitats over the two periods (Björklund et al., unpublished data). One nest from each territory for each species was randomly selected from the two periods for this analysis.

In chapter **II**, we studied the effects of habitat changes around goshawk and common buzzard nests on their occupancies of the nests, using similar habitat data as in **I**. (The sample size of the honey buzzard was too small.) We measured changes in the proportion of old forests (≥ 150 m^3 / ha), considered the key habitat, at the nest site and territory scales (within 250 m and 2000 m, respectively) between two periods (2000 and 2005 or 2007), and studied how the habitat changes affect nest occupancy in the later period. We took into account the occupancy history of the nests and the initial proportion of old forests, since habitat changes can be more influential if the initial proportion of old forests was small.

To evaluate the importance of artificial nests as a conservation measure, we analysed the breeding success and the brood size of the goshawk, common buzzard and honey buzzard in natural and artificial nests (**III**). We took into account potential effects of anthropogenic disturbances (proximity to roads and settlement), latitude, longitude, and a higher probability of successful breeding in natural nests in the year when the nest was found (occupied nests are more easily found than empty nests). We also analysed differences in key habitat proportions between the nest types (Björklund et al., unpublished data).

We studied the simultaneous effects of intraguild predator threat, food level, interspecific competitors, and weather on the territory occupancy and the breeding success of the subordinate predator common buzzard in chapter **IV**. Here, the interesting question is how “threat of IGP” is defined and how it should be measured: e.g. whether this is the risk of IGP or how much a subordinate predator fears the intraguild predator and how this can be quantified. This is commonly estimated with a nearest neighbour distance to the closest intraguild predator, but this approach includes only one intraguild predator neighbour, even though the subordinate predator might sense the threat of IGP from several directions. Additionally, IGP threat is assumed to decrease linearly with an increasing distance from the nest of the intraguild predator neighbour, which probably underestimates the risks considering the long hunting distances of breeding goshawks (> 1000–1500 m; Penteriani et al. 2013). Another possibility is to relate an IGP risk to the number of documented IGP events. However, the subordinate species’ degree of fear of the intraguild predator is not directly comparable with the number of IGP incidents. These events can be rare but still enough to sustain IGP fear in the subordinate predator population (Sergio and Hiraldo 2008). For instance, our Raptor Nest Card data included only two verified and eight suspected events when a goshawk predated common buzzards from their nests (N = 4139 common buzzard nest cards; Finnish Museum of Natural History Luomus, unpublished data). An estimation of IGP fear based on these numbers would probably yield values that are too small. Therefore, we measured IGP threat (hereafter goshawk threat) in a novel way, based on locations of occupied goshawk territories in each year. The goshawk threat was considered maximal and constant within a distance (range) around each occupied goshawk territory, and beyond that range the threat decreased towards zero; the decrease was regulated with a standard deviation (SD) value. Thus, the goshawk threat followed a flat-top bivariate Gaussian kernel around a goshawk territory. Since the intensity of the goshawk threat sensed by common buzzards is unknown, we created nine different 'goshawk threat surfaces' for each year across the study region by using all combinations of three ranges (1 km, 2 km, and 3 km) and three SDs (1 km, 3 km, and 4 km). Ranges were based on reported hunting distances of goshawks. Nine goshawk threat values were extracted from the threat surfaces to the common buzzard territories in each year, and for further analyses we chose the goshawk threat that overall best explained common buzzard territory occupancy. For each common buzzard territory, we used the yearly abundances of all grouse individuals as a measure of principal food availability for the goshawk, and abundances of all juvenile grouse as a measure of alternative food for the common buzzard. An interaction between the goshawk threat and the abundance of all grouse was used to determine whether the influence of goshawk threat on common buzzard occupancy and breeding success depended on the main food level of the goshawk. In other words, this was used to test e.g. the hypothesis that the effect of IGP fear on the subordinate predator is higher when the principal food of the IG predator is scarce. In addition, we used a vole abundance index to measure the main food levels of the common buzzard in each year. We also examined if the presence of an interspecific competitor species in the territory – the great grey owl (*Strix nebulosa*), Ural owl (*S. uralensis*) and common raven (*Corvus corax*) – affected common buzzard occupancy, because these nest and food competitors occupy nests before the common buzzards arrive from migration. Finally, effects of spring and summer weather (temperature, precipitation) were taken into account.

Our responses in the analyses were the binomial nest or territory occupancy (**II**, **IV**), the binomial breeding success (successful, unsuccessful; **I**, **III**, **IV**), and the Poisson-distributed brood size (**I**, **III**). We used generalized linear models (glm; **II**), generalized linear mixed models (glmm; **I**, **III**, **IV**) or linear mixed models (lme; Björklund et al., unpublished data) with which the repeated observations from the same sites were taken into account to avoid pseudoreplication (Hurlbert 1984, Bolker et al. 2009). Since closely located observations tend to be more (or less) similar than randomly associated ones and thus non-independent (Legendre 1993), a possibility for this spatial autocorrelation was tested from all model residuals (Bivand 2014) and if found, it was treated as appropriate (**III**). Interspecific differences in the arcsine square-root-transformed habitat proportions in the two periods were subjected to analyses of variance or Kruskal-Wallis tests with associated Wilcoxon rank sum tests (Björklund et al., unpublished data), and the threshold for significant p-values were adjusted with a Bonferroni correction. All analyses were conducted using the R statistical language (R Core Team 2013).

4. RESULTS AND DISCUSSION

4.1. Breeding habitat and breeding performance

The territory scale (2000 m radius) proved to be important for goshawk reproduction since habitat proportions at this scale best explained their breeding success (**I**). This result confirms the need to analyse habitats at the often neglected large scales (Squires and Kennedy 2006, Sverdrup-Thygeson et al. 2014) that are probably important for the goshawk for ensuring the supply of prey. Forest composition at the landscape scale is also associated with the breeding performance of the goshawks' main prey, the forest grouse (Kurki et al. 2000). Goshawk breeding success was higher with increasing proportions of old spruce forest and water, and a decreasing proportion of young thinning forests in the territory. Their preference for mature or old-growth forests is documented in Europe and North America (Penteriani 2002, Hakkarainen et al. 2004b, Lõhmus 2006, Squires and Kennedy 2006), and they favour large forest stands over small ones (Woodbridge and Detrich 1994). Goshawks are adapted to hunting inside mature forests with an open understorey space where prey are more readily available than in dense forests (Widén 1989, Beier and Drennan 1997). They appear to avoid young forests that are too dense for successful hunting and are therefore suboptimal habitats for them (Widén 1989, Bloxton 2002). Water within the territory can be advantageous for hunting waterfowl, an important alternative prey during the breeding season (Tornberg et al. 2009).

Habitat proportions close to nests (100 m radius) best explained the breeding success of the common buzzard and honey buzzard, but none of the habitat variables within that scale were significantly associated with their breeding success. Habitat variables were not significantly associated with the brood size of any of the hawks either (**I**). Other factors than solely the breeding habitat can thus be more important in regulating the reproduction of the common buzzard and honey buzzard. Food levels, weather, interspecific interactions (**IV**) and anthropogenic disturbances are some of the reported factors for the common buzzard (Krüger 2002c, 2004, Lehikoinen et al. 2009, Jonker et al. 2014), and an avoidance of the intraguild predator goshawk directs in some regions the nest site choice of the honey buzzard (Gamauf et al. 2013), a species sensitive to an increase in adult mortality (Bijlsma et al. 2012).

4.2. Changes in the breeding habitat

The proportion of old spruce forests decreased significantly between the two periods within 1000 m around goshawk and common buzzard nests, and within 2000 m around goshawk nests. Low stocking forests also decreased in goshawk territories within 2000 m. In contrast, proportions of other old forests increased at all scales (100 m, 1000 m, and 2000 m) for both the goshawk and the common buzzard. No significant habitat changes were detected for the honey buzzard, which can partly be due to a low number of their nests in the last period (N = 19 nests).

We compared these habitat changes at the hawk nest sites and territories with overall changes in boreal landscapes based on data from field plots of national forest inventories throughout southern Finland. According to national forest inventory data, areas of old spruce forests and other old forests decreased in southern Finland by 24% (to 14,471 km^2) and 10% (to 24,838 km^2), respectively, while the area of young forests increased by 14% (to 48,877 km^2; **I**) during the study period. Considering that old spruce forests are beneficial and young forests disadvantageous for goshawk breeding success, the habitat changes throughout southern Finland are worrying and partially explain the population declines of the goshawk. We have no data on how old forest loggings were distributed, but the habitat changes in hawk territories refer to loggings scattered in the landscape, and to compromises that the hawks are forced to make when looking for territories. For instance, goshawks still breed in old spruce forests (no change in their proportion within 100 m between the periods), but when these forests shrunk in the landscapes, goshawks accepted other old forests (pine forests) rather than young forests in their territories (**I**). A consistently high proportion of young thinning forests at multiple scales around the nests suggests that the hawks were unable to avoid this habitat (**I**).

4.2.1. Interspecific differences in the breeding habitat

We found several interspecific differences in the multi-scaled breeding habitats (Björklund et al., unpublished data). For instance, the proportion of arable land was higher within 100 m around common buzzard nests than around goshawk or honey buzzard nests (mean proportion ± sd in first period, common buzzard CB: 0.07±0.17, N = 231 nests; goshawk G: 0.03±0.10, N = 282; honey buzzard HB: 0.03±0.10, N = 72; $p < 0.001$ Kruskal-Wallis test; differences CB / G $p < 0.001$, CB / HB $p < 0.05$, Wilcoxon rank-sum test). Common buzzards breed in forests near open areas in other regions as well (Jędrzejewski et al. 1988, Kostrzewa 1996, Lõhmus 2006), probably due to easy access to their main prey, *Microtus* voles. Honey buzzard territories (within 2000 m) included more water than goshawk or common buzzard territories, and common buzzard territories more than goshawk territories (mean proportion ± sd in the first period, HB: 0.11±0.13, N = 72 nests; G: 0.05±0.10, N = 282; CB: 0.06±0.10, N = 231; $p < 0.001$ Kruskal-Wallis test; differences HB / G $p < 0.001$, HB / CB $p < 0.05$, G / CB $p < 0.01$, Wilcoxon rank-sum test). In Sweden, honey buzzards favour forests on nutrient-rich soils near lakes, probably due to abundant passerines (Amcoff et al. 1994). Finally, the proportion of old spruce forests close to nests (within 100 m) was not significantly different between the goshawk and the honey buzzard in the first period, while ten years later, this proportion was significantly lower around honey buzzard nests than around goshawk nests (the first period, HB: 0.36±0.32, N = 72 nests; G: 0.36±0.29, N = 282; n.s.; the last period, HB: 0.17±0.22, N = 19; G: 0.34±0.27, N = 208; $p < 0.001$, Wilcoxon rank-sum test; Björklund et al., unpublished data). No difference was found in the proportion of old spruce forests around goshawk nests between the periods (**I**). This can mean that when old spruce forests decreased in the landscape, goshawks managed to dominate the mature stands, while the honey buzzards' nest site selection changed.

4.3. Habitat changes and nest occupancy

The effects of habitat changes (i.e. changes in the proportion of old forests within 250 m and 2000 m) on the nest occupancy of common buzzards in the later period depended on the initial habitat proportion at both scales. When the proportion of old forest was initially low, nest occupancy increased with increasing proportions of old forest, and decreased when old forests were further lost (**II**). When the initial proportion of old forest was high, nest occupancy increased only if parts of old forest were logged. The habitat change as such (as a main effect) had no significant association with occupancy, but only in interaction with the initial proportion of old forest. Additionally, it was more probable that common buzzard nests were occupied if they had been occupied in the previous period. Hawks tend to re-use their nests and territories rather than build new ones or search for new territories, which highlights the importance of nests as resources for hawks (Finn et al. 2002, Jiménez-Franco et al. 2014). The habitat results show that common buzzards tolerate moderate increases in old forest (i.e. some forests grew enough to be classified as old forests), since they are forest-dwellers. However, they are not eager to re-occupy nests that are surrounded with plenty of old forest. This might relate to the common buzzards' preference for landscapes with habitat heterogeneity, with alternating forested and open areas (Sergio et al. 2005). An alternative explanation is that common buzzards avoid re-occupying nests whose surroundings start to resemble the preferred old forest habitats of the intraguild predator goshawk. However, the causal relationship between the habitat preferences and the reasons that have led to these are difficult to establish (Connell 1980).

Habitat changes or initial habitat proportions at the nest site or territory scales were not significantly associated with goshawk nest occupancy in the later period (**II**).

Considering that goshawk breeding success is higher in territories with greater proportions of old spruce forests and sparser young forests (**I**), this result may seem counterintuitive. However, it is possible that the number of goshawk nests in the study was too low (19) or the measured habitat changes were too small to significantly impact nest occupancy. The proportion of old forest around goshawk nests even slightly increased between the periods (median change in the proportion of old forest: +0.06 within 250 m, +0.04 within 2000 m, **II**). It also seems that territorial goshawks tolerate some logging around their nests rather than abandon them due to the disturbance (Mahon and Doyle 2005, Moser and Garton 2009, Saga and Selås 2012). At most, they might search for a new nest site close to the previous one (Penteriani and Faivre 2001), because space for new territories can be difficult to find in landscapes with regularly distributed territories (Solonen 1993). Goshawks may also lack alternative nests in intensively managed spruce forests (Saga and Selås 2012), which makes them reluctant to desert their only nest. In this way, habitat changes may seem to have no obvious effects on nest occupancy, but they can still affect goshawk breeding success through influences on their prey (Kurki et al. 2000).

4.4. Artificial nests – ecological traps?

The breeding success of goshawks and common buzzards was significantly lower, and that of honey buzzards also tended to be lower in artificial nests compared to natural nests (**III**). This result was consistent when the first breeding year in natural nests was taken into account. The breeding success of goshawks improved with decreasing distances to roads. That of common buzzards worsened towards the north of Finland, which was expected, since the species may suffer from climate change effects at the northern limit of its distribution (Lehikoinen et al. 2009). No difference was found in the brood size of the hawks in natural and artificial nests.

Lowered breeding success in artificial nests is the antithesis of their conservation objective. This result is also unexpected because artificial nests are widely used to help eagles (Gieck 1989, Grubb 1995, Ivanovski 2000) and the osprey (*Pandion haliaetus*; Ewins 1996, Martin et al. 2005, Saurola 2011), for which they have been largely useful (Houston and Scott 1992, Ivanovski 2000; but see Ewins 1996, Martin et al. 2005). Artificial nests, mainly exposed platforms on poles or transmission line towers, are also constructed for middle-sized hawks and are considered beneficial especially in areas otherwise lacking suitable nesting substrates (Bohm 1977, Schmutz et al. 1984, Steenhof et al. 1993). However, information on artificial nests that resemble natural hawk stick nests situated in or under the forest canopy is scarce from other regions. Thus, to our knowledge, this was the first study to evaluate their importance.

We did not find evident reasons for the lowered breeding success in artificial nests. Their distances to potential anthropogenic disturbances were adequately optimized, and goshawk breeding success was even higher closer to roads. One possibility is that habitats around natural and artificial nests differ. When selecting locations for artificial nests, ringers can easily evaluate the suitability of forest stands for each species based on their experience, but assessing suitable habitat compositions at large scales is more likely to be difficult. However, it appears to be important as shown with the result that habitat proportions within 2000 m best explained the breeding success of the goshawk (**I**). To study whether habitat differences could explain the breeding success discrepancy between natural and artificial nests, we compared the proportions of those habitats that significantly affected goshawk breeding success within 2000 m around natural and artificial nests using the same habitat data as in **I**. The proportion of old spruce forest within 2000 m was significantly lower around artificial nests (mean ± SE: 11.4% ± 0.5%, N = 108 nests) than around natural nests (12.6% ± 0.4%, N = 741 nests; $t = -2.425$, $p = 0.016$), but proportions of young thinning forests or water were not significantly different between the two nest types (Björklund et al., unpublished data). Artificial nests have on average 15 ha (radius ≈ 220 m) less old spruce forest within 2000 m than natural nests. This area exceeds the goshawk's nest area of 12 ha (Reynolds et al. 1992), which means that one alternative nest area is potentially missing for artificial nests.

Artificial nests become ecological traps (Battin 2004) if hawks desert their good-quality nests and switch to breed in artificial nests with lower breeding success (like owls in Klein et al. 2007). However, artificial nests can be useful if the settling hawks completely lack a nest site, whereupon a lower chance of success is better than nothing. Until we can distinguish between these two possibilities, it is better to carefully consider the suitability of landscapes for each species, and the potential for interspecific interactions (see **IV**) before constructing artificial nests. Since the impact on goshawk breeding success operated at the territory level (**I**), we do not recommend the use of artificial nests to attract them to settle in small patches of otherwise suitable old spruce forest. We likewise do not advise constructing artificial nests in areas dominated by young thinning forests, because they were unfavourable for goshawk breeding success. The safest solution is to replace a fallen natural nest with an artificial one if a re-construction of the natural nest is improbable (lost supporting branches) and if surrounding habitats have not drastically changed.

4.5. Impacts of interspecific interactions on a subordinate predator

Goshawk threat with a range of 1 km and a SD = 1 best explained common buzzard territory occupancy (**IV**). This implies rather short-ranged IGP threat around occupied goshawk territories, and the 1 km range corresponds to the average foraging distance of goshawks in a prey-rich environment (Penteriani et al. 2013). The probability of common buzzard occupancy increased with decreasing goshawk threat, lower total grouse levels in the previous year, lower March temperatures, and when no interspecific competitors were found in the territory. Vole abundance, April temperatures, and the interaction between goshawk threat and grouse levels were not significantly associated with common buzzard territory occupancy, but the presence of competitors in common buzzard territories was associated with high vole levels.

The probability of successful common buzzard breeding was higher with increasing April temperatures, whereas vole abundance, goshawk threat, grouse levels in the current year, June temperatures, and June precipitation were not significantly associated with their breeding success. Most of the breeding failures occurred during the sensitive egg-laying or incubation periods in April or May, while warm spring temperatures favoured breeding.

We found no support for the hypothesis that the effect of goshawk threat on common buzzard occupancy would be higher when the main food of the goshawk (grouse) is scarce. This was tested with the interaction between the goshawk threat and grouse levels, which was non-significant. Instead, common buzzards avoided goshawks in general, irrespective of grouse levels, but they also avoided territories that had high levels of grouse in the previous year, probably because abundant grouse can attract goshawks. Goshawks are opportunistic predators, taking any prey they can catch including occasionally offspring of other raptors (Petty et al. 2003, Bijlsma 2004). Common buzzard chicks in their open nests are rather vulnerable to predators and abundant grouse are no guarantee of safety. Therefore, it is likely that common buzzards avoid the proximity of the intraguild predator in any case. In Germany, common buzzards kept an average distance of 1.5 km to goshawk nests (Kostrzewa 1991). However, by definition, intraguild prey are attracted to the same resources as their intraguild predator, and this contradiction in IGP was also observed in our study. Nests are very important resources for raptors (Jiménez-Franco et al. 2014), and deserted goshawk nests could be immediately occupied by common buzzards; a few common buzzards even bred successfully in goshawk territories concurrently with goshawks. Apparently, some common buzzards tolerate IGP threat better than other individuals (Krüger 2002b) and subordinate species can thus have individual plasticity in their responses. It is also possible that common buzzard pairs bold enough to breed in goshawk territories actually benefit from protection against other nest predators, such as corvids and the competitor Ural owl that avoid goshawks (Krüger 2002b, Pakkala et al. 2006, Rebollo et al. 2011).

Although common buzzards could breed in the same territory with goshawks, they barely did so with their owl-competitors (ravens used a common buzzard nest only once; **IV**). Gause's principle (in Lack 1946) suggests that species with similar ecological niches or resource use cannot coexist. It is likely that such an intensive interspecific competition occurs between Ural owls, great grey owls, and common buzzards as they compete for nests and food. Ural owls and great grey owls are also known to defend their nests and offspring fiercely (Voous 1988), and constant conflicts with interspecifics would jeopardise the breeding investment of the buzzards. In addition, the owls have competitive advantage since they occupy a territory before common buzzards arrive from migration. Finally, since the occurrence of owls in common buzzard territories was associated with high vole counts, common buzzards are at risk of exclusion from their territories when their food levels are optimal.

These results show that common buzzards make important decisions on where to settle at the territory occupancy stage, when they arrive from migration. This early stage is important because a breeding failure later in the season would entail a considerable waste of reproductive investment. Common buzzards prefer safe territories, since a higher goshawk threat and the presence of competitors in the territory both decreased the probability of their occupancy. When common buzzards took interspecifics into account, these same variables were not significantly associated with their breeding success. Our results also suggest that interspecific interactions can impede a subordinate species fully benefiting from the peaks in food availability. Although abundant voles and grouse would be beneficial for common buzzards, they could prefer to avoid areas with high levels of these main and alternative foods when other predators were present, to evade harmful interactions. Such a trade-off between food exploitation and avoidance of interspecific predators was indicated when rough-legged buzzards (*Buteo lagopus*) were not as abundant as expected during a lemming peak year, probably because a bigger predator, the nomadic snowy owl (*Bubo scandiacus*) bred in unusually large numbers at the time (Potapov 1997). In another example, tawny owls (*Strix aluco*) preferred food-rich coppice woodlands when they were far from their potential predator, the eagle owl (*Bubo bubo*), but avoided these habitats in their proximity (Sergio et al. 2007). Both owl species prey on the edible dormouse (*Glis glis*) that is associated with coppice woodlands.

5. CONCLUSIONS AND FUTURE PROSPECTS

We found that an overall reduction in old forests still continues throughout southern Finland and in hawk territories while areas of young forests increase (**I**). These changes are adverse for the goshawk and other species that favour old forests or specific characteristics common in old forests (e.g. dead wood; Sverdrup-Thygeson et al. 2014). The most rapid changes and reductions in old forest already occurred in the 1900s in boreal forests, and despite some reversed patterns in fragmentation, mature forests (with timber volume >100 m^3 / ha) may cover only an estimated 15% of the landscapes (Östlund et al. 1997, Mykrä et al. 2000, Kouki et al. 2001, Löfman and Kouki 2001, Myllyntaus and Mattila 2002). Even the remaining patches of mature forests can be too fragmented, scattered and isolated to satisfy the requirements of old-forest species (Mykrä et al. 2000, Sverdrup-Thygeson et al. 2014). Therefore, a landscape-level and ecosystem-based planning could be useful in ensuring the availability and continuum of suitable mature forest habitats in the landscape (Reynolds et al. 2006, Sverdrup-Thygeson et al. 2014). There is thus an ongoing need to reconcile the socio-economic interests tied to forests and the ecological requirements of species dependent on old forests (Mönkkönen et al. 2011). This can be challenging under the multiple ownership of Finnish forests, but co-operation with landowners can aid in reaching the target (Kurttila et al. 2002, Santangeli et al. 2012).

Our work confirms the importance of studying habitat associations also on wide scales as has been suggested for raptors (**I**, Widén 1997, Squires and Kennedy 2006) and for other taxa (Sverdrup-Thygeson et al. 2014). The appropriate scale depends on the species (Kouki et al. 2001, Sverdrup-Thygeson et al. 2014), and the relevant scale can differ even between similar-sized competitors. Habitats within 2000 m were important for goshawk breeding success, whereas the overall association of habitats with the breeding performance was loose for the common buzzard and honey buzzard (**I**). Instead, common buzzards responded to interspecifics at the nest site and territory scales (**IV**). We suggest that landscape scales should be included in breeding habitat studies so that their potential importance for the species is not missed. Even scales that are larger than what individuals use can influence their occurrence and reproduction (Kurki et al. 2000, Sverdrup-Thygeson et al. 2014). Furthermore, habitat change effects should be investigated in relation to initial habitat quantities (**II**).

We stress the importance of evaluating conservation measures such as the use of artificial nests (**III**). This call is not new yet it is often overlooked. Also, how this intervention affects the whole community should be examined, because artificial nests and nest boxes can increase raptor numbers in the landscape. Since predators have direct and indirect effects on their prey and on other predators (**IV** and below), unnatural increases in predator numbers or favouring one species with artificial nests can disrupt species interactions. For instance, Clayton & Schmutz (1999) provided artificial nests for *Buteo* hawks in Canada, but when their numbers increased, they predated burrowing owls (*Speotyto cunicularia*), a species of conservation concern.

Interspecific interactions (competition and IGP or its threat) between raptors were important in shaping the territory occupancy of a subordinate raptor (**IV**). This can be one mechanism by which a subordinate species is ousted from a landscape covered with dominant species or ones with a competitive advantage. Subordinate species may adapt if they are flexible in their breeding habitat choices, as common buzzards seem to be, but climate change effects associated with pressures from interspecifics are likely to still decrease common buzzard populations in managed boreal landscapes. Additionally, further studies could address how commonly interspecific interactions with other predators restrict the food exploitation of subordinate predators when food is abundant (**IV**), and what role such a trade-off has in regulating populations of subordinate predators.

Factors contributing to the occupancy or breeding success of the inconspicuous honey buzzard in boreal forests remained unsolved in this dissertation, but the potential interaction between the goshawk and honey buzzard deserves more attention in the future.

Since goshawk avoidance seems to govern the breeding site choice of honey buzzards (Gamauf et al. 2013), it is possible that in changing environments honey buzzards select less optimal breeding habitats to avoid goshawks that dominate the optimal old spruce forests (**I**, Björklund et al., unpublished data). Hakkarainen *et al.* (2004a) concluded that goshawks had no significant impact on honey buzzard productivity, probably due to the small temporal overlap of these species during breeding. However, honey buzzards suffer from goshawk predation in areas where quantities of the goshawk's normal prey are low (Bijlsma 2004, Rutz and Bijlsma 2006).

Due to various avoidance or attraction effects, raptors can create spatial heterogeneity in 'landscapes of fear', as shown with other predators (Laundré et al. 2001, Ritchie and Johnson 2009). Raptors shape the spatial distribution of their prey (Thomson et al. 2006, Burgas 2014), and interspecific interactions with other raptors modify the distribution of raptors in landscapes (e.g. **IV**, Chakarov and Krüger 2010, Gamauf et al. 2013). In addition, interspecific interactions between raptors can have multiplicative effects on other fauna. When dominant raptors suppress other raptor species that in turn spatially regulate their own prey, the dominant raptors indirectly impact the prey species of the subdominant raptors. Prey can even seek protection from dominant raptors against their own subdominant raptor predators that avoid the proximity of the dominant raptors (Pakkala et al. 2006). The indirect impacts of raptors' interspecific interactions on prey have only recently been studied (Pakkala et al. 2006, Byholm et al. 2012, Morosinotto et al. 2012) and thus, interspecific interactions in birds of prey and their repercussions on entire food webs should be taken into consideration in both science and conservation. Interspecific interactions should be studied in various environmental conditions since low food levels can enhance intraguild predation (Rutz and Bijlsma 2006, Sergio and Hiraldo 2008). In conclusion, in the future, it would be fruitful to study and consider systems as a whole rather than its species separately.

ACKNOWLEDGEMENTS

This dissertation would not have been realized without many people who provided their advice, knowledge, data and support during my PhD work. I am very grateful for your ample assistance; it is an honour to know you all!

I first want to acknowledge my supervisors, Toni Laaksonen and Jari Valkama. I remember when I first wondered to Jari in 2009 whether it would be possible to do a dissertation on the Finnish Birds of Prey Survey data. Tentatively, you were supportive of the idea. Toni, you started working at the Luomus soon after that, and I presented the Survey materials to you. I recall you too wondering whether a dissertation could be done on the data. Later on, you discussed this with Jari, and it turned out that I was

actually willing to do that. So the process began with lots of optimism and brilliant plans. Eventually, hardly any of my original ideas are as such in this book, which is probably for the best, since as Toni commented, they would be enough for several theses.

Toni and Jari, you have guided me through the PhD work, and for this I am very grateful. Having two supervisors is perhaps not the simplest solution, but I benefitted from two experts who complemented each other well. Toni, you provided sound advice on the study designs, analyses and statistics, and you set limits when the work started to meander. I really admire this ability of yours to quickly pick up the relevant issues and detect possibilities to conduct interesting research. You are good at reasoning in plain Finnish (or English), which makes a student's life easier. Jari, you were my backbone when Toni returned to work in Turku. You gave invaluable comments on the articles and were always willing to listen to my problems even when you were utmost busy with your book projects. Your long field work experience on my study species was extremely helpful in many occasions. You were the epitome of calmness even when sending a funding application two minutes before the deadline. Toni and Jari, I sincerely thank you for these years!

I want to express my gratitude to Prof. Oliver Krüger who agreed to be appointed as the opponent and wade through the dissertation despite the busy field season. Your articles have inspired me during my PhD studies, which is why I am especially honoured to have the possibility to discuss my thesis with you. Furthermore, I acknowledge Priv.-Doz. Dr. Anita Gamauf and Prof. Jari Kouki for their efforts when they pre-examined this thesis. I am also grateful to Prof. Jouni Laakso for acting as custos.

I was very lucky to have Ilpo Hanski, Patrik Byholm and Otso Ovaskainen as the members of my thesis advisory group. I met with this group of external experts and my supervisors once every year, and discussed my progress and future directions. Even though these meetings sometimes made me nervous, these occasions also helped me to see what was already achieved, and the progress compared to the previous year. Thank you so much for your support, constructive comments and suggestions on how to proceed!

My dissertation is based on long-term raptor survey data that volunteer raptor ringers and enthusiasts gathered over several decades. Their enormous amounts of field work made it possible to study interesting questions that can rarely be approached in such a wide spatial scale. Thus, I am most indebted to all the volunteers who I want to specifically address by name at the end of the Acknowledgements. Furthermore, I acknowledge Pertti Saurola, who launched the Common Birds of Prey Survey in Finland, and Hannu Lehtoranta, who coordinates the survey on raptor nests in North Karelia, eastern Finland.

Fortunately, a dissertation involves lots of cooperation, and several co-authors made a significant contribution on the thesis. Andrea Santangeli is an extraordinary person to work with. He provided valuable comments and ideas, and also constructive criticism, always in a polite and respectful manner. Andrea, you were really helpful in various matters ranging from ArcGIS to statistics and reviewing, and you were perhaps always the first to send comments. Your positive attitude and encouragements meant a lot to me, and I really admire your enthusiasm and efficiency in doing science! Erkki Tomppo is probably one of the busiest scientists I know, with all his national and international cooperation projects. Despite this fact, he spent hours producing habitat data for my dissertation. In addition, he gave good comments and was reachable even in the evening by phone or email when I urgently needed advice. Hannu Lehtoranta is both a forest manager and a raptor ringer, and due to his dual expertise, his opinions assisted me greatly. I thank Guillaume Blanchet, who made a significant contribution to chapter IV in terms of statistics, Kernel estimation and proofreading. I had the privilege to cooperate with Otso Huitu and Harto Lindén who provided indispensable data and comments on voles and grouse. I would not be at this point without Pertti Saurola, who originally guided me to the world of raptors when he employed me as the coordinator of the Birds of Prey Survey. I feel really humble and honoured to have all these multidisciplinary experts involved in my dissertation.

In addition, several other persons assisted me in conducting the research and preparing the articles. I owe my gratitude especially to Esko Piirainen who made the essential nest and territory identification and who did great work in creating the nest card database. Aleksi Lehikoinen and Kaisa Välimäki were helpful with the weather data, and Jukka Rintala with the grouse data. I acknowledge Sanna Mäkeläinen for her help in finding articles and reviewing my text as well as for discussions on several issues ranging from geoprocessing to statistics. I thank Marianna Teräväinen and Pepin Marshall, who checked the language of the thesis summary and one of the articles.

The Finnish Museum of Natural History Luomus has enabled this work by providing the working environment and facilities, as well as financial support. I want to warmly thank the director of Luomus, Leif Schulman, and the director of the Zoology Unit, Aino Juslén, for all their support to me and all of us PhD students of Luomus. I acknowledge the Doctoral Programme in Wildlife Biology Research Luova of the University of Helsinki, and especially the coordinator of Luova, Anni Tonteri, who takes good care of the PhD students. Luova organized very useful courses on statistics and on other topics. I am also grateful to Prof. Veijo Kaitala for his assistance through the official steps towards the doctoral degree.

PhD students of Luomus meet regularly to discuss diverse issues and share information on relevant topics. These meetings have been really fruitful and supportive. Thank you Aino, Sanna, Juho, Maria He, Maria Hä, Mari, Andrea, Annina, Gosia, Marianna, Hanna La, Hanna Li, Elina, Diego, Kalle and Sara (some of you already PhDs) for your peer support, encouragement, help, pulla and sharing the show scene to celebrate those of us graduating! I enjoyed taking part in the same courses with PhD students from Viikki: Alex, Christina, Anniina, and Henna, to name just a few. I was also happy to join gatherings of bird researchers originating from Viikki and the Helsinki Lab of Ornithology (Luomus). Thanks Ed, Vilppu, Markus, Andy, Aleksi, Daniel, Kim, William, Päivi, Jarkko, and Pepe for relaxing discussions, bowling and dinners. Even though Turku is not that distant, I met bird researches from the University of Turku mostly abroad. I have nice memories from congresses on three continents where I spent time with Päivi, Ville, Markus, Chiara, William, Suvi, and Tuomo (from Oulu).

Several colleagues and friends at Luomus made the PhD years pleasant. I had nice discussions on bird watching with Juha, Seppo, Jukka, Jarmo, Pekka P., Petteri, and Jörgen from the Ringing Centre. My special thanks to Vincenzo for all his support and sharing his knowledge on raptors and research. I joined Olof, sometimes also Pekka M., on many nice excursions to see rare birds even with just a couple of minutes of warning time, thank you! I shared relaxed coffee breaks with Katja, Timo, Anne, Pirjo, Martti, Marjatta and many others. Marjatta helped me often with library issues and Tarmo with practical problems. Lea, Hasse, Kirsi and Ville kindly assisted with printing posters and with my studies.

My friend Eeva-Maria Kyheröinen shares the office with me. Thanks for your patience when I have been quiet, introverted and concentrated on my dissertation! Our families have had nice excursions to different locations over many years, and when I have been too exhausted to organize anything, you have taken the initiative and invited us over for a visit. I also acknowledge you as my right-hand person in organizing the arrangements for the karonkka party.

I want to give a big hug to my parents and closest relatives for your support during this project in several years. My mother Irma and father Vilho, you provided indispensable help in taking care of our sons and sharing my delights and concerns. *Rakkaat kiitokset kaikesta avusta ja myötäelämisestä, äiti ja isä!* Mummu, Pirjo, Meeri, Martti, Harri, Jani Jukka ja Minna, you have always encouraged me, *lämpimät kiitokset*. My parents-in-law, Lotte and Folke, I appreciate your sympathy. Finally, my own family has kept me connected to normal, precious everyday life. My dearest sons Daniel and Mikael, you are the sunshine in my life and remind me of what is really important. My husband Tom, you may have regretted that you asked: "When will you start a PhD?" Nevertheless, you have always assisted and cheered me. Daddy the Brave of the neighbourhood, left at home with two kids when the wife travels to South America or wherever, *jag älskar dig!*

I wish to acknowledge Kone Foundation, the Doctoral Programme in Wildlife Biology Research Luova, the University of Helsinki (for the dissertation completion grant) and Luomus for funding. My congress and course trips abroad were funded by the University of Helsinki Chancellor's travel grants, Suomen Biologian Seura Vanamo ry, Kone Foundation, Luova, and the International Ornithological Congress 2014 Organizing Committee, all to whom I owe my gratitude.

Finally, my studies are based on the field work of many birds of prey ringers and enthusiasts who I hereby want to specifically acknowledge:

Aalto Matti, Aaltonen Esa, Aaltonen Arto, Ahola Antero, Ahola Pentti, Alakoski Kari, Alhainen Jouko, Aspelund Seppo, Autio Antero, Auvinen Ari-Pekka, Byholm Patrik, Degerstedt Kari, Eklund Håkan, Ekstam Bo, Elfving Roope, Erola Reijo, Ervasti

Esa, Eskelinen Olavi, Excell J., Grönlund Jukka, Haikola Juha, Hakkari Lasse, Hakkari Tomi, Halonen Jorma V.A., Halonen Jari, Halonen Markku, Hanski Ilpo K., Hartikainen Juha, Hautakorpi Hannu, Heikkilä Heikki, Heinonen Eero, Hietanen Ismo, Hietanen Timo O., Holmström Hannu, Honkalahti Pasi, Honkanen Teemu, Honkiniemi Mikko, Hostikka Jari, Huhta Esa, Hukkanen Markku, Huttunen Antti, Huttunen Seppo, Huuskonen Hannu, Hämäläinen Timo, Hölsä Ismo, Ihalempiä Petri, Immonen Timo, Jussila Silveri, Järvinen Hannu, Kaikusalo Asko, Kakko Ari, Kalenius Christer, Kallela Markku, Kananoja Pentti, Kangas Miika, Karjalainen Timo, Karjalainen Seppo, Karlin Antti, Karlin Olli-Pekka, Karlson Rolf, Karstinen Teuvo, Ketola Kari, Kevätväre Matti, Kinnunen Jukka, Kirjavainen Harri, Kivelä Jukka, Kivelä Jouko, Koivu Juhani, Koivumäki Kari, Kolari Juhani, Kontiokorpi Jari, Kontkanen Harri, Korhonen Veikko, Korpimäki Erkki, Koskela Kimmo, Koskela Tapio, Koskenkorva Raimo, Koskinen Sami, Kotilainen Risto, Kuusela Seppo, Kuusisto Tatu, Kylmänen Reijo, Laamanen Kari, Laine Timo, Laine Teppo, Lakka Johanna, Lappi Esko, Latvala Juhani, Laurila Ilpo, Lehtonen Veli-Pekka, Lehtonen Mika, Lehtoranta Hannu, Lehtoranta Jouni, Leikkonen Lauri, Leppänen Janne, Liukko Sampo, Lokki Heikki, Lukkarinen Tuomas, Makkonen Pasi, Marjakangas Arto, Martikainen Tuomo, Martiskainen Kimmo, Marttila Jouni, Marttila Jari, Matero Jukka, Miettinen Juha, Miettinen Jari, Mikala Antti, Morberg Roger, Multala Vesa, Mustakallio Pekka, Muukkonen Tomi, Mylläri Timo, Myntti Tarmo, Mäkinen Pekka, Mättö Pekka, Niemi Tapio, Nieminen Vesa, Niiranen Seppo, Niskanen Tero, Nousiainen Ismo, Nurhonen Harri, Nurmi Toni, Nyman Jan, Nyman Arto, Oittinen Kari, Ollila Mikko, Osmonen Olli, Paaer Pekka, Painilainen Ilpo, Pajunen Jyrki, Palo Kari, Peltola Martti, Peltoniemi Pekka, Perälä Harri, Pesäkivi Juhani, Pihlajamäki Kari, Pihlman Jani, Piikkilä Tapani, Piipponen Tapio, Pirkkalainen Ari, Pynssi Kai, Pöysä Silvo, Rantala Riku, Rantanen Jouko, Raudaskoski Reijo, Rautiainen Erkki, Repo Hannu, Rouhiainen Raimo, Rouhiainen Kauko, Ruti Marko, Rutonen Kalevi, Ryssy Jussi, Ryynänen Raimo, Rännänen Pia, Salo Jorma, Salo Eino, Salo Harri, Salo Rainer, Salonen Kalevi, Sarkanen Mauri, Sarlund Tapio, Sarola Vesa, Savolainen Jyrki, Siikström Kauko, Siitonen Pekka, Siltaloppi Martti, Sivonen Rauno, Sorvari Veli-Matti, Sotikov Tarmo, Suhonen Jukka, Suksi Risto, Sulkava Pertti, Sulkava Risto, Sulkava Seppo, Suopajärvi Matti, Suopajärvi Pekka, Sykkö Matti, Taivalmäki Jukka-Pekka, Tammelin Hannu, Tanner Jukka, Tanskanen Ari, Tarsa Veikko, Tenhunen Juha, Tihinen Reino, Timonen Pentti, Tittonen Jouni, Toivanen Juhani, Topp Pekka, Topp Erkki, Tunturi Kalevi, Turunen Jorma, Töytäri Olavi, Vainikka Olavi, Valkama Jari, Valkeila Väinö, Valo Matti, Valtonen Tomi, Vasko Ville, Vesanen Esko, Vikström Sten, Vilen Risto, Vilhunen Lasse, Virmajoki Olli, Virtanen Pekka, Visala Marko, Vuorenmaa Alpo, Väliaho Jouni, Vänskä Ensio, Vänskä Lassi, Ykspetäjä Tapio, Ylipekkala Jouni.

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