Habitat degradation and climate change as drivers of long-term declines of two forest-dwelling owl populations in boreal forest

Degradação do habitat e alterações climáticas enquanto causas de declínio de longo-termo de duas populações de rapinas noturnas em florestas boreais

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ABSTRACT

To understand how world-wide land-use changes interact with climate change and biotic interactions (competition and predation) to modify population dynamics of animals is particularly important in boreal forest ecosystems facing large intensification of forestry practices and fast climate change. The settlement decisions, reproductive success and food-hoarding behaviour of Eurasian Pygmy-owls (POs; *Glaucidium passerinum*) were studied during 2002-2017 in long-term (>40 yr) study area (1300 km²) of their larger competitor and intra-guild predator, Boreal Owls (BOs; *Aegolius funereus*). POs strongly avoided breeding close to conspecifics but did not avoid the vicinity of BO nests. Proportion of occupied nest-boxes by breeding POs increased with vole abundance in the previous autumn. POs had lower hatching success at high conspecific density. Even though breeding POs did not spatially avoid BOs, the increasing density of BOs reduced fledging success of POs. The results suggest that joint costs of exploitative and interference competition as well as intra-guild predation risk by BOs on reproductive success of POs were lower than those induced by intraspecific competition only. This result might be due to that BOs are only twice as large as POs. Increasing frequency of days with precipitation during the autumn generated a reduction in the total prey biomass stored, the number of bank voles (main prey) in food stores, and in the body condition of female POs during the food-hoarding season (Oct to Dec). Rainy autumns probably could decline the vulnerability of voles to predation by POs, since long-term temporal stability in local vole abundance negates the alternative hypothe-

sis that climate change drives fading of vole cycles. Breeding density of POs declined during the 15-year study period, and the long-term decline (2% per year) of BO populations was evident both locally and nation-wide. These declines are mainly attributable to the loss of mature and old-growth forests offering refuges against larger predators and better availability of main and alternative prey. The decline of POs was probably also contributed by climate change resulting in deteriorating vulnerability of small mammals during the food-storing season due to increased rainfall.

Keywords: *Aegolius funereus*, food limitation, *Glaucidium passerinum*, habitat selection, population dynamics

RESUMO

Compreender como as alterações globais nos usos do solo interagem com as alterações climáticas e as interações bióticas (competição e predação) para modificar as dinâmicas das populações animais é particularmente importante nas florestas boreais, face à grande intensificação das práticas florestais e à rapidez com que as alterações climáticas se manifestam nestes ecossistemas. A decisão de estabelecer um território, o sucesso reprodutor e o comportamento de armazenamento de alimento do mocho-anão (MAs; *Glaucidium passerinum*) foram estudados durante 2002-2017 numa área de estudo (1300 km²) de longo termo (>40 anos) do seu competidor, com maior tamanho corporal e predador intra-guilda, o mocho-funéreo (MFs; *Aegolius funereus*). Os MAs evitaram nidificar na proximidade de conspecíficos mas não evitaram a proximidade de ninhos de MF. A proporção de ninhos ocupados por MAs nidificantes aumentou com a abundância de cricetídeos no outono anterior. O sucesso da eclosão dos MAs foi inferior nos casos de elevada densidade de conspecíficos. Apesar de os MAs nidificantes não evitarem espacialmente os MFs, o aumento da densidade de MFs reduziu o sucesso da emancipação dos MAs. Os resultados sugerem que as consequências negativas da competição por exploração e interferência, assim como do risco de predação intra-guilda por MFs no sucesso reprodutor dos MAs foram inferiores às consequências negativas da competição intraespecífica. Este resultado pode dever-se ao facto de os MFs terem apenas o dobro do tamanho corporal dos MAs. O aumento da frequência de dias com precipitação durante o outono causou uma diminuição na biomassa total de presas acumuladas, no número de *Myodes glareolus* (presa principal) nos armazéns alimentares, e na condição física das fêmeas de MA durante a estação de armazenamento de alimento (outubro a dezembro). Outonos chuvosos podem reduzir a vulnerabilidade dos cricetídeos à predação por MAs, uma vez que a estabilidade temporal de longo-termo da abundância local de cricetídeos contradiz a hipótese alternativa de que as alterações climáticas determinam o desaparecimento dos ciclos de cricetídeos. A densidade de casais reprodutores de MAs diminuiu durante o período de 15 anos do estudo, e o declínio de longo-termo (2% por ano) das populações de MF foi evidente a nível local e nacional. Estes declínios devem-se sobretudo à perda de florestas maduras e longevas, que proporcionam refúgios contra predadores de maior dimensão corporal e maior disponibilidade de presas principais e alternativas. O declínio de MAs poderá também ter sido agravado pelas alterações climáticas, resultando num aumento da vulnerabilidade à deterioração dos micromamíferos acumulados durante a estação de armazenamento de alimento, devido ao aumento da precipitação.

Palavras-chave: *Aegolius funereus*, dinâmica populacional, *Glaucidium passerinum*, limitação do alimento, seleção de habitat

Introduction

To understand how world-wide land-use changes interact with climate change to modify dynamics and persistence of animal populations is a primary goal in present-day ecological research. This is particularly important in boreal forest ecosystems facing fast climate change (Ruckstuhl et al. 2008) and intensification in forestry practices (Kuuluvainen 2009). In addition, biotic interactions, such as competition and predation, may complicate our understanding of the effects of climate change on animal populations under changing forest habitat composition. Large predators impose a mortality risk for small predators, and habitat degradation and climate change may reduce availability of primary prey, which together will lead to population declines and possibly to local extinction. How changes in the forest habitat composition and climate interact to modify trophic interactions and demography of avian predators has yet to be studied, particularly in altering boreal forests.

Our team has studied the nest-site occupancy, habitat selection, reproductive success, survival, dispersal and food-hoarding behaviour of Eurasian Pygmy-owls (*Glaucidium passerinum*; hereafter Pygmy Owl) in the same long-term study area where we have also installed a wide nest-box network for Boreal Owls (*Aegolius funereus*). Boreal and Pygmy Owls subsist on the same main foods (i.e. voles of the genera *Microtus* and *Myodes*) in North European boreal forests (Korpimäki & Hakkarainen 2012). In Finland, where this study was conducted, these voles fluctuate in 3-year high-amplitude (100 to 200-fold) population cycles (Korpimäki et al. 2005). Boreal Owls are approximately twice as large as Pygmy Owls, and therefore, they can intimidate and even kill smaller allo-specifics (i.e. intra-guild predation; Morosinotto et al. 2017).

In this paper, my first intention is to review studies on nest-site occupancy, habitat selection and reproductive success of Pygmy Owls under varying levels of food competition and predation risk imposed by Boreal Owls. The second aim is to review how food-store contents and body condition indices of Pygmy Owls in the food-hoarding season are associated with varying autumn climate conditions and forest composition. The final intention is to examine long-term trends of Pygmy and Boreal Owl populations in our study area.

Material and methods

The study area covered approximately 1300 km² in the Kauhava region, western Finland (63° N, 23° E). The landscape consisted of commercially managed pine- and spruce-dominated forests with some birch-dominated patches, interspersed with clear-cut areas, agricultural land and peatland bogs (Korpimäki 1987, Korpimäki & Hakkarainen 1991, 2012, Hakkarainen et al. 2003). The proportion of old-growth forest in our study area was low as a consequence of forestry practices (i.e. clear-cutting and thinning; Hakkarainen et al. 2003), and thus suitable natural cavities for Boreal and Pygmy Owls were scarce. Therefore, nest-boxes for Boreal Owls were provided from 1966 onwards, and for Pygmy Owls during 2001-17. The diameter of the entrance hole of Boreal Owl boxes was 80 to 100 mm, and that of Pygmy Owl boxes was 45 mm. The total number of Boreal Owl nest-boxes was approx. 420 during 1983-1987 and 470 from 1988 onwards, and these nest-boxes and known natural cavities (approx. 30) made by Black Woodpeckers (*Dryocopus martius*), were inspected each spring (Korpimäki 1987, Korpimäki & Hakkarainen 1991, 2012).

The nest-box project for Pygmy Owls was initiated in 56 forest patches in autumn 2001. From 2004 onwards the number of forest

patches was 150 and reached a maximum of 285 patches in 2015 (mean no. of patches 211 per year during 2002-17). In each forest patch (hereafter called as box-site), two nest-boxes for Pygmy Owls were provided during 2002-2017. Two boxes were placed per site 80-100 m apart because Siberian flying squirrels (*Pteromys volans*) also use nest-boxes for roosting and reproduction throughout the year and this ensured availability of the nest-site and food-storing site for Pygmy Owls. Approximately 80 natural cavities, excavated by Great Spotted Woodpeckers (*Dendrocopos major*), are also available for breeding Pygmy Owls in the study area. The two owl species do not compete for available cavities; Pygmy Owls do not breed in cavities with large entrance-holes and Boreal Owls cannot enter the cavities used by Pygmy Owls (Korpimäki & Hakkarainen 2012, Morosinotto et al. 2017).

The density of Boreal Owl nest-boxes in our study area (approximately 1 nest-box per 2 km²) does not substantially differ from natural conditions: the density of suitable natural cavities in pristine coniferous forests of southern Finland is 0.5-1.5 per km² (Virkkala et al. 1994). In addition, in coniferous forests managed for forestry in Central Sweden, the density of natural cavities made by Black Woodpeckers, the size of which also is suitable for Boreal Owls, is 0.3-0.4 per km² (Johnsson et al. 1993). The two owl populations in our study area were not constrained by the availability of nesting sites, because even in good vole years characterized by highest numbers of owls, only 33% of Boreal Owl and 31% of Pygmy Owl boxes were occupied. Nest boxes were also homogeneously distributed across the landscape (average distance between available Pygmy Owl nest-box sites 1429 m; and between available Boreal Owls boxes 760 m).

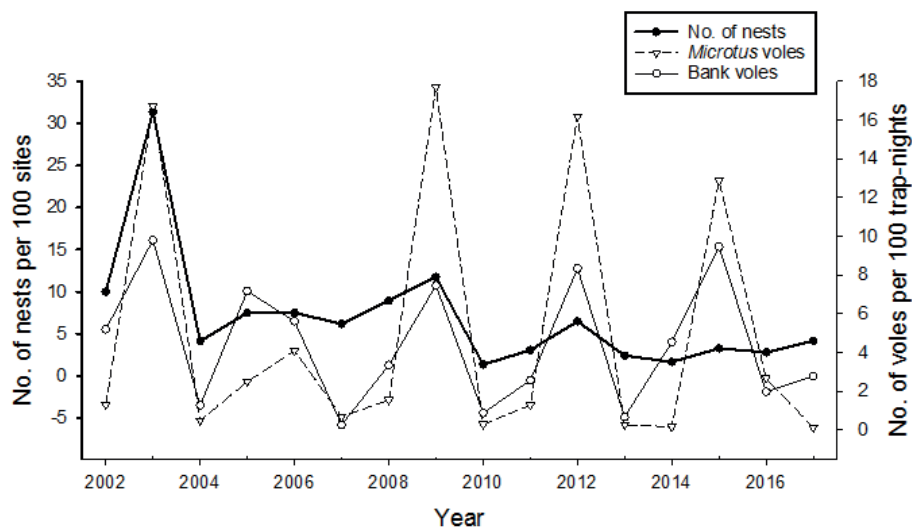All owl boxes, and known natural cavities, were inspected twice every spring (in April and again in late May to early June) to detect breeding attempts. In all nests of both owl species, clutch size, hatching date, and number of hatchlings and fledglings were recorded, as well as fledglings were ringed and a majority of the parent owls were ringed and/or re-captured (see Korpimäki & Hakkarainen 1991, 2012, Morosinotto et al. 2017).

The nest-boxes of Pygmy Owls were inspected to find stored prey items twice during the autumn, from late October to mid-December during 2002-2017. Prey items were usually stored as whole, and thus species identification, sexing, ageing and weighing was possible in most cases. Prey items in food stores were also marked by toe-clipping (birds) or tail-clipping (mammals) to avoid double counting. The total number and mass of prey items, as well as for the five main groups of prey (i.e. bank voles, *Microtus* voles, shrews, mice and birds), were calculated by summing up the fresh prey items counted in the two visits (see Terraube et al. 2017, Masoero et al. 2018). During the food-hoarding season in 2002-2017, Pygmy Owls were captured, measured and ringed for individual identification (a total of 327 individuals during 2002-2016). The vast majority of owls was captured with nest-box traps (a copy of the food store-box equipped with swing door). The captured Pygmy Owls were sexed and aged, their wing and tail lengths were measured and body mass taken. To estimate the body condition of Pygmy Owls, the Scaled Mass Index was calculated (see Peig & Green 2009). Sexing was based on wing length, tail length and body mass (females larger and heavier than males; E. Korpimäki unpublished data, Masoero et al. 2018).

Abundances of voles have been estimated by snap-trappings each year in mid-May and in late September in four sample plots (i.e. cultivated field, abandoned field, spruce for-

Figure 1 - Number of nests of Eurasian Pygmy Owls per 100 box-sites inspected (solid line and dots; left y-axis) and number of *Microtus* voles (the field vole *M. agrestis* and the sibling vole *M. rossiaemeridionalis*; triangles) and bank voles (*Myodes glareolus*; circles) trapped per 100 trap-nights (right y-axis) in the previous autumn during 2002-2017. Spearman rank correlation between breeding density and *Microtus* voles $r_s=0.64$, $p=0.007$, $n=16$ and bank voles $r_s=0.60$, $p=0.015$, $n=16$.

Figura 1 - Número de ninhos de Mocho-anão por 100 parcelas com caixas-ninho inspecionadas (linha contínua e pontos; eixo vertical da esquerda) e número de *Microtus* (*M. agrestis* e *M. rossiaemeridionalis*; triângulos), e *Myodes glareolus* (círculos) armadilhados por 100 noites de amostragem (eixo vertical da direita) no outono anterior durante 2002-2017. Correlação de Spearman entre a densidade de casais reprodutores e de *Microtus* $r_s=0.64$, $p=0.007$, $n=16$ e de *Myodes glareolus* $r_s=0.60$, $p=0.015$, $n=16$.

Results

Nest-site occupancy, habitat selection and reproductive success of Pygmy Owls

The proportion of occupied nest-sites by Pygmy Owls varied between years, from 1 nest per 100 sites (in 2010) to 31 nests per est, pine forest; see Korpimäki et al. 2005 for more details on trapping methods and vole cycles). Fifty to one hundred Finnish metal mouse snap traps were set at 10 m intervals in vole runways in each plot and were checked once a day for three-four days. Thus, the area of a sample plot ranged from 0.5 to 1.0 ha. The results from 3-4-night trapping periods were pooled and standardized to the number of animals caught per 100 trap nights.

100 sites (in 2003) during 2002-2017 (Fig.1). The proportion of nest-boxes occupied by breeding Pygmy Owls augmented with increasing abundance of voles in the previous autumn (Fig. 1), whereas there was no similar relationship to vole abundance index in the current spring. Nest-site occupancy of Pygmy Owls also amplified with increasing proportions of spruce forests, mature and old pine forests and farmlands (see Fig. 2 in Morosinotto et al. 2017).

Habitat selection of breeding Pygmy Owls varied in relation to the distance to breeding conspecifics, main food abundance, and food competitors and intra-guild predators, Boreal Owls (Morosinotto et al. 2017). The proportion of nest-site occupancy of Pygmy Owls increased with the augmenting distance to the conspecific nest, but when vole abundance was high, avoidance among conspecific Pygmy Owls decreased (Fig. 1 in Morosinotto et al. 2017). This relationship was, however,

partly modified by the distance to the nearest nest of Boreal Owls. Nest-site occupancy of Pygmy Owls increased closer to a nest of Boreal Owls, but only as the distance to the nearest Pygmy Owl nest also increased (Fig.1 in Morosinotto et al. 2017).

Pygmy Owls bred earlier in sites with a large proportion of agricultural lands within 1000 m-radius of the nest-box. Despite that increasing proportion of agricultural land advanced start of egg-laying in the early phase of the breeding season, a large proportion of agricultural land within 1000 m from the nest decreased both hatching and fledging success of Pygmy Owls (Fig. 5 in Morosinotto et al. 2017). The high proportion of mature spruce forest at a local scale (300 m) around the nest increased the hatching success of Pygmy Owls (Morosinotto et al. 2017).

Food-stores and body condition of Pygmy Owls

There appeared to happen marked changes in the autumn climate (October to December) during the food storing season of Pygmy Owls and in habitat composition around nest-box sites of Pygmy Owls during the study period. The number of days with rainfall in autumn significantly increased (0.15 ± 0.006 d per year), whereas the number of days with frost (minimum temperature <0°C) significantly decreased (-0.24 ± 0.006 d per year) during the 12 year study period (2001-2012; Fig. S2 in Terraube et al. 2017). The proportion of clear-cuts within a radius of 1500 m around the food stores of Pygmy Owls significantly increased during the 12-year study period (Fig. S3 in Terraube et al. 2017).

Overall, 15850 prey items from a total of 436 nest-boxes distributed on 218 box-sites were identified and weighted during 2001-2012. Pygmy Owls stored mainly bank voles (*Myodes glareolus*; 47% of prey items and 47% of prey biomass) and *Microtus* (*M. agrestis* and *M. rossiaemeridionalis*) voles (33% of prey items and 43 % of prey bio-

mass). Alternative prey groups included mainly small passerine birds (6% of prey biomass) and shrews (3%; Terraube et al. 2017). The total biomass of prey items cached per nest-box increased in relation to pooled vole abundance in the current autumn. The total biomass of prey items decreased with the increasing number of days with rainfall and the number of days with frost during October to December (Fig. 1 in Terraube et al. 2017).

The number of bank voles found per food-store decreased during the study period and was positively related to the abundance index of bank voles. The number of bank voles declined with augmenting number of days with rainfall and with the increasing number of frost days during October to December (Fig. 2 in Terraube et al. 2017). When the proportion of clear-cuts around the nest-box was low, the number of bank voles found in food-stores increased with augmenting local abundance of voles (Terraube et al. 2017).

The body condition index (as estimated by the scaled mass index) of female Pygmy Owls decreased with increasing number of frost days, whereas it remained relatively stable for males independently of the number of days with frost (Fig. 5 in Terraube et al. 2017). Males had a lower body condition index than females.

Long-term trends of owl populations

Linear regression between year and density estimate of Pygmy Owls (the number of nests per 100 box-sites) revealed that breeding Pygmy Owl population in our study area significantly declined during 2002-2016 (Fig. 2, r=0.580, R²=0.336, p<0.05). The similar trend was not significant for Boreal Owls during 2002-2016 (Fig. 2), but earlier analyses showed that Boreal Owl population in our study area declined 2% per year during 1973-2009 (Fig. 13.7. in Korpimäki & Hakkarainen 2012).

Discussion

Determinants of nest-site occupancy, habitat selection and reproductive success of Pygmy Owls

The probability of nest-site occupancy of Pygmy Owls increased with abundance of main prey (voles) in the previous autumn, whereas there was no obvious relationship to vole abundance in the current spring. The importance of vole abundance in the previous autumn rather than in the current spring is probably attributable to the fact that Pygmy Owls store larger number and biomass of prey items in their food stores in autumns with abundant voles (Masoero et al. 2018; see also Solheim 1984). These food stores are then consumed during forthcoming winter (Järvi 1986), and more Pygmy Owls are probably in high body condition in the next spring and can thus initiate a breeding attempt which results in their increasing breeding densities. This interpretation is supported by the fact that in Boreal Owls breeding in the same study area, the abundance of voles in the current spring rather than in the previous autumn determines the breeding density (Korpimäki & Hakkarainen 1991, 2012). Boreal Owls do not collect large food stores in nest-boxes and natural cavities in autumn, probably because these boxes and cavities with a large entrance hole are accessible to robbers and enemies including, for example, pine martens (*Martes martes;* Korpimäki 1987). Pine martens also roost and reproduce in boxes and cavities of Boreal Owls so that they could easily find food-stores of Boreal Owls in tree-holes. Nest-boxes and natural cavities in which Pygmy Owls breed and store food are not accessible to pine martens, but can be entered by smaller mustelids, such as stoats (*Mustela erminea*) and weasels (*M. nivalis*). However, these smaller predators hunt mainly on the open ground (Klemola et al. 1999) and do not often climb on trees.

The proportion of nest-site occupancy of Pygmy Owls increased with the augmenting distance to the conspecific nest, but when vole abundance was high, avoidance among conspecific Pygmy Owls decreased. Therefore, Pygmy Owls largely avoided their conspecifics when selecting a breeding site, probably as a consequence of food and interference competition. The fact that avoidance in settlement decreased with abundant food suggests that high vole availability led to weaker intraspecific competition for food and probably also to reduced territory size. The degree of intraspecific competition for high-quality territories among Pygmy Owls is probably also increased by the fact that suitable habitat for Pygmy Owls (mature and old-growth forest) has substantially declined in our study area during the study period. However, the number of nest-sites did not limit the breeding density of Pygmy Owls in this case, because even at the highest breeding densities only 31% of nest-boxes were occupied by Pygmy Owls.

Boreal Owls are twice as large as Pygmy Owls. This small size difference probably led to a reduced number of lethal interactions among two owl species, although there are at least three recorded cases where Boreal Owls have killed Pygmy Owls (review in Korpimäki & Hakkarainen 2012). In addition, the non-lethal costs of presence of Boreal Owls may still persist in Pygmy Owl populations. Nevertheless, the joint costs of interspecific competition and intra-guild predation risk imposed by Boreal Owls on Pygmy Owls appeared to be lower than those induced by competition by conspecifics only. In earlier intra-guild predation studies on birds of prey, the intra-guild predators were considerably larger (>3-times) than the intra-guild prey (review in Sergio and Hiraldo 2008).

Pygmy Owls had delayed start of breeding and lowered hatching success when breeding at high conspecific density, probably due to the exploitative competition for food and interference competition for high-quality territories (Morosinotto et al. 2017). Unex-

pectedly for a small (approx. 55 to 80 g) owl species, the detrimental effects of conspecific neighbours on reproductive success were evident at relatively large radius (500 to 3000 m) of the nest (Morosinotto et al. 2017). The main reason probably is the overall scarcity of small mammal and bird prey in boreal forests compared to more southern temperate environments. In addition, it might be necessary to ensure a sufficiently large hunting territory to reduce interference competition with other neighbours during the breeding season, because small birds are efficient at warning and mobbing against Pygmy Owls (Dutour et al. 2016).

Unexpectedly, occupancy of nest-boxes by Pygmy Owls increased closer to Boreal Owl nests, but only when conspecific nests were farther away (Morosinotto et al. 2017). This tendency of attraction of Pygmy Owls to the vicinity of Boreal Owls is probably due to a conjunction in habitat preference for the two owl species. There is ample evidence that Boreal and Pygmy Owls prefer mature and old-growth coniferous forest habitats both in North and Central Europe (reviews in Schönn 1980, Korpimäki & Hakkarainen 2012; see also Santangeli et al. 2012 for Boreal Owls; Strøm & Sonerud 2001, Barbaro et al. 2012, Morosinotto et al. 2017 for Pygmy Owls). Mature and old-growth spruce- and pine-dominated forests offer rich patches of main (bank voles) and alternative (shrews and small birds) prey and refuges against larger avian predators including e.g. Ural Owls (*Strix uralensis*), Northern Goshawks (*Accipiter gentilis*) and Eurasian Sparrowhawks (*A. nisus*).

Despite that Pygmy Owls were attracted close to Boreal Owls during the nest-site selection period, proximity of Boreal Owls induced lowered hatching and fledging success of Pygmy Owls (Morosinotto et al. 2017). This detrimental effect of hetero-specific density on reproductive success of Pygmy Owls probably arises from both the exploitative and interference competition,

since these species have largely overlapping diets (mostly small rodents and small passerines birds; Korpimäki & Hakkarainen 2012. Owls and other predators have been shown to reduce high density patches of cyclic voles in North Europe (Korpimäki et al. 2002, 2005). Vole patches and densities of small birds in the vicinity of these breeding owl species are probably rapidly depleted, which in turn would lead to lower hatching and reproductive success of the smaller Pygmy Owl.

The probability of nest-site occupancy of Pygmy Owls was higher if nesting happened in the box-site of the previous year (Morosinotto et al. 2017). The high-quality of the habitat in the surrounding of these frequently-used nest-box sites probably explains why the same individuals tend to occupy the same box-sites year after year or why newcomers are attracted to these high-quality sites (Newton and Marquiss 1986, Korpimäki 1987). Yet, nest-site fidelity of adult Pygmy Owls appeared to be an unlikely explanation, because >80% of the females and >70% of the males trapped and ringed in the study area during the breeding season were one-time breeders (E. Korpimäki unpublished data). Therefore, the occupancy pattern of box-sites found is probably due to the preference of immigrant Pygmy Owls for these high-quality forest patches.

Habitat change, climate change and long-term decrease of owl populations

Total prey biomass in food-stores of Pygmy Owls decreased over the study period .The number of days with rainfall and of frost days were negatively related to the total biomass of prey in stores, numbers of main prey (bank vole) in stores and individual body condition of Pygmy Owls. Unexpectedly, we did not find any close relationship between the biomass of stored prey and the proportion of clear-cut areas (or the proportion of old spruce forests) around the food-stores

Figure 1 - Number of nests of Eurasian Pygmy Owls per 100 box-sites (solid line and dots), and number of nests of Boreal Owls per 100 nest-boxes (dashed line and triangles) during 2002-2016 in the Kauhava region, western Finland.

Figura 1 - Número de ninhos de Mocho-anão por 100 parcelas com caixas-ninho amostradas (linha contínua e pontos), e número de ninhos de Mocho-funéreo por 100 caixas-ninho (linha tracejada e triângulos) durante 2002-2016 na região de Kauhava, oeste da Finlândia.
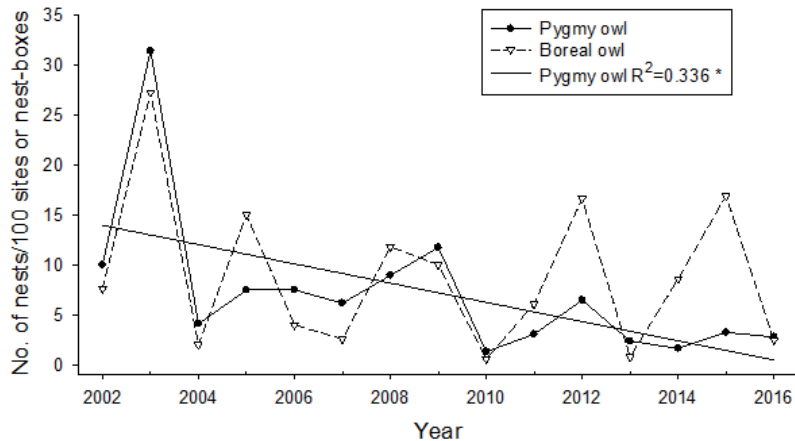
(Terraube et al. 2017). The most intensive food-hoarding period of Pygmy Owls happens before the permanent snow layer (Järvi 1986), as >70% of prey items were hoarded during this period (Halonen et al. 2007). Cold autumns are generally associated with early snowfalls and permanent snow cover from November to April in the study area. Small Pygmy Owls are too light to penetrate the deep snow layer and catch small rodents below the snow layer, which explains why Pygmy Owls store more small mammals in warm and snowless autumns. However, autumns are getting warmer in Finland, and therefore variation in autumn temperatures cannot be associated with the decrease in prey biomass in food stores of Pygmy Owls.

The prey biomass stored by Pygmy Owls decreased with the increasing number of days with rainfall in late autumn. Densities of voles did not show any marked long-term trend in our study area but fluctuated in regular 3-year cycles during 2002-2017 (Korpimäki et al. 2005, Korpimäki & Hakkarainen 2012; see also Fig. 1). This shows that climate-driven long-term decreases in abundances of vole populations are not the likely explanation for the declining prey biomass in food-stores of Pygmy Owls. Rainfall could impose a direct detrimental effect on the foraging activity and success of Pygmy Owls, but this decline of prey items in stores emerged only for small mammal prey, whereas the number of passerine birds in stores did not show any temporal trend over the study period (Terraube et al. 2017). Increasing rainfall likely decreases activity of small mammals, because energetic costs of thermoregulation of small mammals due wet fur in cold environments are substantial (e.g. Conley & Porter 1986). These costs can limit their above-ground activity and reduce the vulnerability of small mammals to avian predators. In addition, the noise of rainfall makes small mammals more difficult to hear to avian predators and moist leaf and needle litter makes less noise than dry one. All in all, precipitation may reduce mobility and prey detectability of small mammals to avian predators thus decreasing their foraging success.

Female Pygmy Owls captured during the food-storing season were in poorer body condition during cold and rainy autumns than during warm and less-rainy ones, whereas body condition indices of males remained stable over the years (Terraube et al. 2017). This indicates that ongoing increase in autumn rainfall may have detrimental consequences for fitness of female Pygmy Owls. Male owls are smaller than females and larger aerial agility may make them more efficient hunters in dense mature and old-growth forests (Hakkarainen & Korpimäki 1991), particularly for prey with higher escape ability like birds. Indeed, the proportion of small birds was higher in food stores of males than in those of females (Terraube et al. 2017, Masoero et al. 2018). Therefore, males have probably been able to better respond to the climate-driven reduction in capture success of small mammals by catching more birds. On the contrary, larger females probably are less agile in capturing birds. Further research is badly needed to find out whether these different trends in body condition indices between male and female pygmy owls may have carry-over effects on over-winter survival and future reproductive success at the population-level.

The present results indicate that there was no apparent decrease of breeding Boreal Owl population in our study area during 2002-2016 (Fig. 2). However, a divergent trend emerged when putting our results in more long-term viewpoint. Owl monitoring schemes of 20 local ornithological societies in Finland revealed that there was a 2% annual decline of nation-wide Boreal Owl population during 1973-2009 (Korpimäki & Hakkarainen 2012), and the nation-wide raptor grid monitoring also showed similar (2%) annual decline of Boreal Owl population during 1982-2016 (Meller et al. 2017). Therefore, our present results should be interpreted with caution, especially because wide cyclic among-year fluctuations due to the 3-year vole cycle happen in northern Boreal Owl populations.

The most probable reason for remarkable long-term decline of Boreal Owl population in Finland is degradation and loss of forest habitat due to clear-cutting, because over-winter survival of Boreal Owls is higher in home ranges including >10% of old-growth forests (Hakkarainen et al. 2008). In addition, the lifetime reproductive success of owl males is higher in home ranges including an increasing proportion of old-growth and middle-aged forests (Laaksonen et al. 2004). Middle-aged and old-growth forests offer more refuges against larger avian predators, such as Ural owls (see Hakkarainen & Korpimäki 1996), and there also are less main (bank voles) and alternative (shrews and small birds) prey items in sapling areas and young forests.

The results showed a local decline of breeding Pygmy Owl population during 2002-2016 (Fig. 2), and a weak declining trend also emerged in the Pygmy Owl population breeding in Finland during 2000s on the basis of nation-wide raptor grid monitoring (Meller et al. 2017). The similar declining trend of Pygmy Owl is also apparent during the food storing season in autumn during 2002-2016 in our study population (E. Korpimäki & G. Masoero, unpublished data). Because abundances of main prey (voles) did not show any apparent long-term trends (Fig, 1), this long-term decline is probably associated with the degradation and loss of forest habitat and climate change. During the 15-year study period, the coverage of middle-aged, mature and old-growth forests (main habitat for Pygmy Owls) in our study area has reduced by approx. 20% (E. Korpimäki, unpublished data). Currently, our study area is mostly a mosaic of agricultural fields, clear-cut and sapling areas, as well as young thinned forest plantations with very small coverage of middle-aged, mature and old-growth forests. Therefore, forest management resulted in a habitat degradation, which probably induced a decline of breeding and wintering population of Pygmy Owls. This decline was proba-

bly also contributed by climate change resulting in increased rainfall in late autumn to early winter, which has declined the number and biomass of prey items in the food stores and body condition of female Pygmy Owls (Terraube et al. 2017). During 2000s, warmer temperatures in late autumn to early winter have also often induced decay of food-stores of Pygmy Owls (E. Korpimäki unpublished data), which may even steepen the decline of Pygmy Owl populations in the future. In an another food-storing bird species (the Grey Jay *Perisoreus canadensis*) in boreal forest of Canada, warming autumn temperatures also induced food store spoilage with detrimental consequences for reproductive success in the next spring (Waite & Strickland 2006, Sechley et al. 2015).

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