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Population dynamics and reproductive success of Short-eared Owls in relation to widely fluctuating food abundance and farmland habitat degradation

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Populations of the Short-eared Owl *Asio flammeus* have declined across Europe and North America, probably in response to habitat degradation driven by agricultural intensification. However, long-term evidence linking farmland habitat change to variation in breeding density and reproductive success remains limited. We investigated these relationships in an agricultural landscape in western Finland over a 30-year period (1977–2006), focusing on owl breeding parameters and temporal changes in grassy habitats supporting their primary prey (voles). Annual breeding density ranged from 0.0 to 1.5 (mean 0.35) nests km^{-2} and increased with spring vole abundance. Mean clutch size varied between 2.5 and 8.2 eggs, and mean brood size between 0.7 and 4.4 nestlings per nest, with significantly higher values observed during years of high vole abundance. Nest failure was primarily attributed to agricultural activities and predation. To assess long-term population trends, monitoring was extended to a broader 1000-km^2 area through 2023. Over the 47-year study period, the local breeding population declined by more than 50%, corresponding to an average annual decrease of 2.8%. This decline coincided with substantial agricultural intensification, including the conversion of pasture and hay fields to cereal, potato and oilseed cultivation, as well as the reduction in open drainage systems. These changes resulted in a 46% reduction in grassy habitats suitable for voles and, consequently, for owl foraging. Our findings provide long-term empirical support for the hypothesis that farmland structural simplification associated with agricultural intensification is a primary driver of population declines in Short-eared Owls occupying grassland and farmland habitats.

Keywords: agricultural intensification, breeding density, breeding success, habitat loss, population declines, vole cycle.

Natural habitats are increasingly fragmented (Fahrig 2003). Over recent decades, agricultural intensification has led to more effective land management and increasingly homogeneous farmland environments (e.g. Gossner *et al.* 2016). This process has reduced the extent of semi-natural habitats, such as pastures, hedgerows, grassy field margins, set-aside fields and open ditches, by converting them into agricultural land, thereby decreasing habitat heterogeneity and biodiversity (Tscharntke *et al.* 2005).

Birds breeding in open grassland and farmland are among the most rapidly declining avian species in Europe and North America (e.g. Donald *et al.* 2001, Laaksonen & Lehikoinen 2013, Rosenberg *et al.* 2019, Rigal *et al.* 2023). Habitat loss and degradation caused by agricultural intensification are widely recognized as primary drivers of these declines in Europe (Donald *et al.* 2001, 2006, Newton 2004, Stanton *et al.* 2018). Population declines have been particularly pronounced among ground-nesting species (Kamp *et al.* 2021), probably because agricultural operations during

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the breeding season increase nest failure, while higher predation rates due to increasing populations of meso-predators, such as Red Fox *Vulpes vulpes* as well as invasive American Mink *Neovison vison* (Roos *et al.* 2018), increase predation pressure. Alien predators may have especially strong impacts because their effects on prey populations can considerably exceed those of native predators (Salo *et al.* 2007).

The Short-eared Owl *Asio flammeus* is widely distributed across the Holarctic and Neotropic regions (Gerber 1960, Mikkola 1983, Holt & Leasure 1993). It is a ground-breeding species that inhabits open natural and semi-natural grassland, such as pastures, agricultural fields, marshland and peatland bogs, as well as tundra (Clark 1975, Mikkola 1983). Populations of Short-eared Owls have declined across Europe and North America, with habitat loss and climate change suggested as principal drivers of these declines (Glue & Korpimäki 1997, Fernández-Bellon *et al.* 2020, Miller *et al.* 2021). However, long-term studies examining how farmland habitat degradation affects breeding density and reproductive success remain scarce.

Short-eared Owls are irruptive and nomadic predators that track fluctuations in the abundance of their main prey, small rodents (Clark 1975, Korpimäki 1984a, 1984b, 1994). They show rapid numerical responses to changes in rodent abundances and readily establish breeding territories where small rodents are abundant in suitable open habitat (Village 1987, Korpimäki & Norrdahl 1991). Voles of the genera *Microtus* and *Myodes* constitute the main prey of Short-eared Owls in both Europe and North America (Mikkola & Sulkava 1969, Clark 1975, Korpimäki & Norrdahl 1991, Holt & Leasure 1993). In northern Europe, including our study area, these vole populations undergo high-amplitude 3- to 4-year population cycles (Korpimäki *et al.* 2005, 2025a), strongly influencing the breeding performance and abundance of Short-eared Owls (Korpimäki & Norrdahl 1991).

Our study area is located in the extensive lowlands of Ostrobothnia in western Finland, a landscape characterized by agricultural fields and peatland bogs. This region was one of the main strongholds of Short-eared Owls in northern Europe from at least the 1960s through the 1980s. During peak vole years, the breeding density reached approximately one nest per km^2, and breeding pairs were regularly recorded even during years of low vole abundance (Mikkola & Sulkava 1969, Korpimäki 1984a, Korpimäki & Norrdahl 1991). However, long-term population trends since the 1990s remain poorly understood. This is partly because the nationwide raptor grid scheme, monitoring long-term population trends in Finland, has mainly been established for forest-dwelling birds of prey (Saurola 2009). Moreover, long-term data on temporal variation in clutch size and breeding success of Short-eared Owls in northern Europe, where populations experience high-amplitude 3- to 4-year vole cycles, are lacking.

In this study, we address the following questions. First, do the breeding density and reproductive success of Short-eared Owls vary in synchrony with vole abundance? Second, have clutch size and offspring production changed over the long term? Third, what are the main causes of nesting failure? Fourth, are long-term population trends associated with changes in farmland habitat structure, especially the extent of grassy habitats and open ditches that support vole populations? The information gained would be essential for the conservation of farmland bird species experiencing continent-wide declines in Europe and North America.

MATERIALS AND METHODS

The main study area was located at Alajoki, in the municipalities of Kauhava and Lapua, west-central Finland (63°00′N to 63°07′N, 22°53′E to 22°58′E), and represents one of the northernmost extensive agricultural landscapes in the world. The study area covered 47 km^2 during 1977–1987 and 24 km^2 during 1988–2006. The landscape is a flat lowland (20–30 m asl) comprising 73% arable land, 16% pine-dominated forest, 4% spruce-dominated forest, 6% peatland bogs, 1% inhabited areas and 1% river. The main cereal crops were oats and barley, but potatoes, oil plants (mostly turnip rape), and hay and silage for cattle were also cultivated. After harvest, most cereal, potato and oil plant fields were ploughed in September–October. Consequently, during winter, suitable grassy habitat for small mammals was largely restricted to narrow strips along field margins and open ditches, as well as on hay, silage and set-aside fields (Fig. 1a and 1b). Ploughed fields were harrowed and sown from late April to early May (Fig. 1c), coinciding with the onset or middle

Figure 1. Short-eared Owls usually bred in narrow strips of long grass along ditches of agricultural fields at Alajoki (a, b). Most surrounding fields were ploughed in the previous autumn (September to October) and lacked grass cover during winter and after snow-melt in late March to late April. Fields were sown with crops (mainly oats, barley, potato and oil plant) in late April to early May. Oat seedlings emerged in late May to early June (c). The late Sakari Ikola ringing a Short-eared Owl brood in early June (d). An electric perch designed by the late Sakari Ikola. Photographs (a–d) by Jalmari Lahtinen, (e) by Erkki Korpimäki.

of the breeding season of Short-eared Owls (see Korpimäki 1984a, 1987, Korpimäki & Norrdahl 1991, for further details).

Territories of diurnal Short-eared Owls were mapped by observing elaborate courtship displays of males during morning hours after sunrise and in the evening before sunset in the agricultural fields of Alajoki from late March to late May. These displays involve rapid ascent flights with rhythmic wing beats interspersed with frequent wing-clapping during which the owl loses height (Clark 1975). They are easily visible in the flat lowland landscape of the study area. From early April to June, nest locations were mapped by observing nest-guarding males that typically guard their females and nests from vantage points at sunrise and sunset (Calladine *et al.* 2010). Nests were located by systematically searching areas where displaying or nest-guarding owls had been observed. In addition, owlets were located by their begging calls, which could be heard from distances of up to 200 m. Sites where displaying owls were observed but no nests were found were subsequently examined carefully to detect territorial non-breeders. Pairs producing at least one egg were classified as 'breeders', others as 'non-breeders'. The nests were visited to record clutch and brood sizes and to ring the young during 1977–2006 (Fig. 1d). Brood size was estimated by the number of young leaving the nest, as owlets

leave the nest at the age of 12–17 days when they are still unable to fly (Gerber 1960, Glutz von Blotzheim & Bauer 1980).

A total of 75 adult Short-eared Owls were captured and ringed at Alajoki during 1977–2006. These owls were captured near nests using artificial perches (1.0–1.5 m high). After individuals became accustomed to sit on these perches, they were replaced with an 'electric perch' equipped with a 10-cm nylon loop (Fig. 1e). This trap was adapted for Short-eared Owls by local bird-ringer, the late Sakari Ikola (Fig. 1d), from a Verbail trap (Bloom *et al.* 2007; also called perch snare *sensu* Prevost & Baker 1984). Sakari Ikola designed an automatic release technique, which was based on electrical resistance powered by a motorbike battery. This capture method proved suitable for open, treeless agricultural landscapes, where natural perches are scarce. Capture and ringing of Short-eared Owls were conducted under permits issued by the Finish Museum of National History, Helsinki, Finland (ringing licence no. 524 to EK and 2664 to SI).

In addition to Alajoki, Short-eared Owl territories and nests were monitored, and data on clutch and brood sizes were collected in smaller agricultural fields east of Alajoki (Kauhava and Lapua) during 1977–2023. This work was conducted alongside long-term monitoring of nestbox occupancy and breeding performance of Eurasian Kestrels *Falco tinnunculus* and Tengmalm's Owls *Aegolius funereus*. The study area covered approximately 1000 km^2 and included 400 nest-boxes for Kestrels in open farmland (Korpimäki & Wiehn 1998, Kujala *et al.* 2024) and 450 nest-boxes for Tengmalm's Owls in forests (Korpimäki 1987, 2020, Korpimäki & Hakkarainen 2012). Within this larger area, suitable agricultural habitat for Short-eared Owl breeding accounted for 25% of the landscape, peatland bogs for 2% and the majority (69%) of the area consisted of different-aged forests and sapling and clear-cut areas (Hakkarainen *et al.* 2003). Although surveys of Short-eared Owl territories and nest searches were less intensive in this larger area than in Alajoki, survey effort remained consistent throughout the study period (1977–2023). Each year, fieldwork with Tengmalm's Owls took 4–5 weeks from early April to mid-May (Korpimäki & Hakkarainen 2012), followed by an additional 4–5 weeks of Kestrel fieldwork from mid-May to late June (Korpimäki & Wiehn 1998). This consistency enabled reliable comparisons of annual numbers of Short-eared Owl nests and territories and facilitated the detection of possible long-term population trends.

Vole abundances were estimated using snap traps in the main study area (Alajoki) and in smaller agricultural fields east of Alajoki twice a year during 1977–2023. In both study settings, four plots representing different habitat types (cultivated field, set-aside field, spruce forest and pine forest) were sampled in mid-May and late September. In each plot, 50–60 Finnish metal mouse snap traps were set at 10-m intervals in vole runways and checked once a day for three consecutive days. The area of each sample plot ranged from 0.5 to 0.6 ha. Captures from 3-night trapping periods were pooled and standardized as the number of Bank Voles *Myodes glareolus* and the combined number of *Microtus* voles (Field Vole *M. agrestis* and Sibling Vole *M. rossiaemeridionalis*) per 100 trap nights (see Korpimäki *et al.* 2005, 2025a for further details on trapping methods and vole population cycles). These standardized values are hereafter referred to as the vole abundance indices for the current spring and the previous autumn.

Winter habitat for voles and other small mammals in agricultural landscapes consists mainly of narrow strips of grassy field margins and open ditches, as well as hay, silage, pasture and set-aside fields. Long-term changes in habitat composition within the study area were quantified in two ways. First, the length of open field partition ditches was measured in five randomly selected 1 × 1-km grids within the study area using landscape maps from the National Land Survey of Finland (https://www.maanmittauslaitos.fi/en/maps-and-spatial-data/maps/view-and-download-maps). The necessary information of partition ditches was available in these maps for only five years (1971, 1986, 1997, 2006 and 2023, see Fig. S1). Second, temporal changes in crops cultivated on arable land were derived from the Official Statistics of Finland (https://stat.luke.fi/en/utilised-agricultural-area) compiled by Statistics Finland (Tike) prior to 2015, and by the Natural Resources Institute Finland (Luke) thereafter. These statistics are based on administrative register data and cover all agricultural and horticultural holdings with an economic value of at least 2000 €. Crop areas are reported for individual crop species and crop groups in thousand hectares. For this study, data from 1975, 1979, 1982, 1990, 1997, 2006, 2013, 2021 and 2023

were selected to represent key periods of change in agricultural land use within the study area (Fig. S1). For the years without data, the length of ditches and the proportion of grassy habitat were estimated using regression models that resulted in high coefficients of determination (R^2) (Fig. S1).

Statistical analyses

Depending on the response variable and study question, we used appropriate (generalized) linear (mixed) models (see Table S1) (Littell *et al.* 2006, Stroup 2013). In these models, primary explanatory variables were abundance indices of small rodent prey, *Microtus* and Bank Voles in spring, estimated by snap-trappings concurrently with the breeding of Short-eared Owls. Because preliminary analyses consistently showed that vole indices based on the previous autumn did not improve model fit, they were extracted from the final models. Explanatory variables related to changes in farmland habitat structure and agricultural intensification included the estimated proportion (%) of grassy habitat and the length of open partition ditches in the landscape. Due to collinearity, these habitat variables were never included in the same model (Table S1).

Clutch size varied between 2 and 10 eggs in 1977–2006 data and was analysed using linear mixed models (LMMs) based on individual nests (n = 287). Model residuals met assumptions of normality and homoscedasticity. Year was set as a random intercept. Long-term trend was tested using a separate linear model (LM), regressing yearly mean clutch size (n = 25) on the year (Table S1).

The number of young produced varied between 0 and 9 in individual nests (n = 422 nests observed in 1977–2006). Approximately 20% of owls that bred failed to produce any young. These count data were analysed using a generalized linear mixed model (GLMM) with a negative binomial error distribution and a log link function. Model diagnostics indicated no under- or overdispersion (variances of Pearson residuals were close to 1). Year was included as a random intercept effect. The general time trend was analysed using an LM, regressing the yearly average of the young number (n = 26 years) on the year (Table S1).

Yearly estimates (n = 30 years) of nest density (nests per km^2) and numbers of non-breeders (range 0–3, including 63% (19 years) of zeroes) during 1977–2006 were modelled by LMs and negative binomial GLMs, respectively (Table S1). Vole abundance indices and habitat variables were included as fixed effects. Time trends were analysed by including year as a fixed explanatory variable (Table S1).

For the longer dataset (1977–2023), negative binomial GLMs were also used to model the dependency of the yearly numbers of nests and territories (pooled; n = 47 years) on the vole abundance indices and habitat factors (Table S1). Also here, the temporal trend, with year as an explanatory variable, was analysed by a GLM.

In all mixed-effects models, the significance of the random intercepts was tested using the likelihood ratio test (LRT) (Littell *et al.* 2006). The Kenward–Roger method was employed to estimate denominator degrees of freedom and to adjust standard errors of the fixed effects (Kenward & Roger 2009, Stroup 2013). All the models were conducted using the GLIMMIX procedure of the SAS statistical software (v. 9.4).

RESULTS

Annual nest numbers of Short-eared Owls ranged from 0 to 49 at the Alajoki study area during 1977–2006. Most nests (73%) were located in narrow strips of long, previous-summer grass along open ditches of agricultural fields. A majority of agricultural fields had been ploughed in the previous autumn (September–October) and lacked grass cover during winter and snow-melt (late March–April), making them unsuitable habitats for overwintering small mammals and for foraging Short-eared Owls (Fig. 1a and 1b). Fields were sown with crops (mainly oats, barley, potato and oil plants) in late April to early May, and vegetation growth began in late May to early June, providing high-quality forage for voles and hunting habitat for owls (Fig. 1c). Only 12% of the nests were located on the grass-covered hay, set-aside and pasture fields that in early spring consisted of long old grass in the middle of the strip.

Marked changes in the foraging and breeding habitat composition of Short-eared Owls occurred between the 1970s and the 2020s. The proportion of arable land providing winter cover and food for voles (hay, silage, pasture and set-aside fields) decreased by 46% (Fig. S1). In contrast, the proportion of unsuitable habitats (cereal, potato and

oil plant fields) correspondingly increased. The number of open field partition ditches offering cover and food for overwintering voles and cover for owl nests decreased by 52% (Fig. S1). This was mainly due to increased subsurface drainage. In addition, reallocation of pieces of arable land where separate field plots of a single farmer were collected in one larger field plot contributed to the reduction in drainage ditches.

Annual breeding density varied from 0.0 to 1.5 nests/km^2 (mean = 0.35, sd = 0.38) in the Alajoki study area during 1977–2006. There were only four breeding seasons, when no nests of Short-eared Owls were found, while high peaks occurred in 1986 and 2005 (Fig. 2). Breeding density was largely determined by the spring abundance of both *Microtus* and Bank Voles (Table 1), but not by the proportion of grassy habitat and density of partition ditches (Table S1: models 1a–d). The number of non-breeders (0–3 annually) was negatively related to abundance of *Microtus* and Bank Voles (Table 1, Table S1: models 2a–d).

Of the 75 breeding adults captured and ringed in the vicinity of their nests, four males and four females were subsequently encountered in the study area in later breeding seasons. One male and two females were encountered at Alajoki in the following breeding season: one female was encountered 2 years later, three males were encountered 3 years later and one female was encountered 4 years later.

Short-eared Owl females laid on average 5.9 (sd = 1.5, range 2.5–8.2; Fig. 3) eggs per clutch during 1977–2006. Clutch size increased with spring abundance of *Microtus* voles but was unrelated to Bank Vole abundance, breeding density of owls, or the proportion of grassy habitat or the density of ditches in the landscape (Table 2, Table S1: models 3a–c). There was no apparent long-term trend in the clutch size (Table S1: model 3d). In years of high vole abundance, females typically laid 7–8 eggs (maximum 10), whereas in low-vole years, only 4–5 eggs (minimum 2) were laid.

Seventy-nine per cent of eggs hatched. Mean brood size (number of young leaving the nest) was 2.5 (sd = 1.1, range 0.7–4.4; Fig. 4) owlets per nest during 1977–2006, and no long-term trend

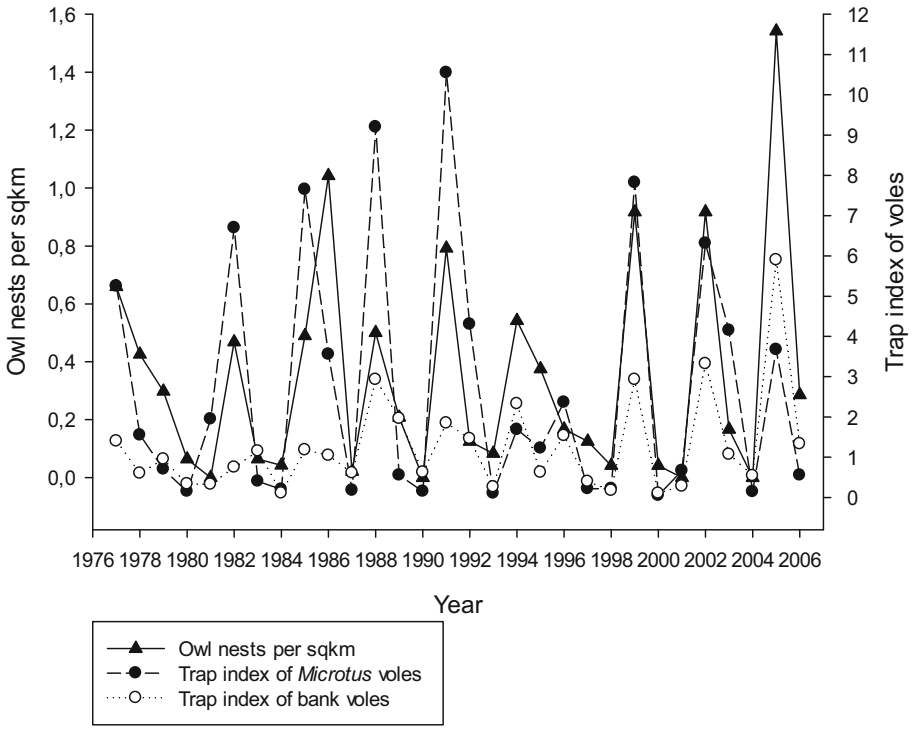

Figure 2. Number of Short-eared Owl nests per km^2 and abundance indices of *Microtus* and Bank Voles in the current spring at the Alajoki study area during 1977–2006.

Table 1. Results of the linear model (LM) for the nest density (per km^2) of the Short-eared Owl (a), and those of the generalized linear model (GLM; negative binomial error distribution with log link function) for the yearly numbers of non-breeders (b).

Response variable	Fixed explanatory factor	Test statistics	ES estimate (95% CI)[a] [exponentiated %][b]
(a) Yearly nests km^{-2}	*Microtus* spp.	$F_{1, 27} = 5.27$, $P = \mathbf{0.030}$	**0.034 (0.004–0.064)**
	Myodes spp.	$F_{1, 27} = 31.42$, $P < \mathbf{0.001}$	**0.208 (0.132–0.284)**
(b) Yearly non-breeders	*Microtus* spp. + *Myodes* spp. pooled	$F_{1, 28} = 6.85$, $P = \mathbf{0.014}$	**−0.450 (−0.803 to −0.098) [−36.2%; −55.2 to −9.3%]**

Significant effects are highlighted by bold font. Data are from the main study area of Alajoki collected during 1977–2006. [a]Model scale effect size estimate of the fixed explanatory factor with its 95% confidence interval. [b]Exponentiated effect size (with its asymmetric 95% confidence interval) as a percentage change per unit increase in the explanatory factor. This is given for the significant effect of the GLM only.

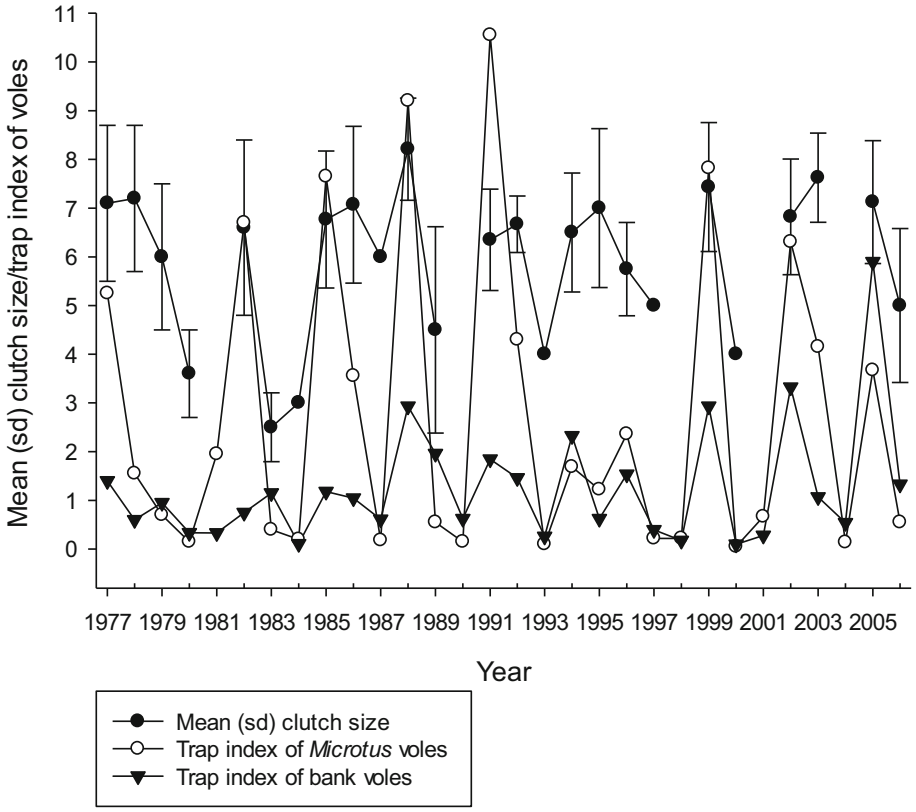

Figure 3. Yearly mean (sd) clutch size of Short-eared Owls and abundance index of *Microtus* and Bank Voles during 1977–2006 at Alajoki.

was observed (Table S1: model 4d). Brood size increased with *Microtus* vole abundance (Table 2) but showed no association with Bank Vole abundance, breeding density of owls, or with the proportion of grassy habitat or ditch density in the landscape (Table S1: models 4a–c).

Overall, 21% of nesting attempts (70 of 333 nests) failed. The main reasons for total nest failures were agricultural activities (44% of cases with known failure reasons) and nest predation (44%; Table 3). A majority of females initiate egg-laying before fields were harrowed and sown. Although

Table 2. Results of the linear mixed model (LMM) for the clutch size of the Short-eared Owl (a), and those of the generalized linear mixed model (GLMM; negative binomial error distribution with log link function) for the number of young produced (b).

Response variable	Explanatory factor (F = fixed, R = random)	Test statistics	ES estimate (95% CI)[a] [exponentiated %][b]
(a) Clutch size	*Microtus* spp. (F)	$F_{1,\ 13.2} = 7.64$, $P =$ **0.016**	**0.199 (0.044–0.354)**
	Myodes spp. (F)	$F_{1,\ 13.1} = 0.09$, $P = 0.772$	−0.072 (−0.602 to 0.457)
	Nests km^{-2} (F)	$F_{1,\ 14.1} = 2.13$, $P = 0.167$	1.311 (−0.616 to 3.237)
	Year (R)	$\chi^2_1 = 21.73$, $P <$ **0.001**	
(b) Number of young	*Microtus* spp. (F)	$F_{1,\ 11.6} = 14.26$, $P =$ **0.003**	**0.092 (0.039–0.145) [9.6%; 4.0–15.7%]**
	Myodes spp. (F)	$F_{1,\ 11.1} = 0.29$, $P = 0.604$	−0.044 (−0.226 to 0.138)
	Nests km^{-2} (F)	$F_{1,\ 12.9} = 0.98$, $P = 0.340$	0.307 (−0.363 to 0.978)
	Year (R)	$\chi^2_1 = 15.52$, $P <$ **0.001**	

Significant effects are highlighted by bold font. Nest data are from the main study area of Alajoki collected during 1977–2006. [a]Model scale effect size estimate of the fixed explanatory factor with its 95% confidence interval. [b]Exponentiated effect size (with its asymmetric 95% confidence interval) as a percentage change per unit increase in the explanatory factor. This is given for the significant effect of the GLMM only.

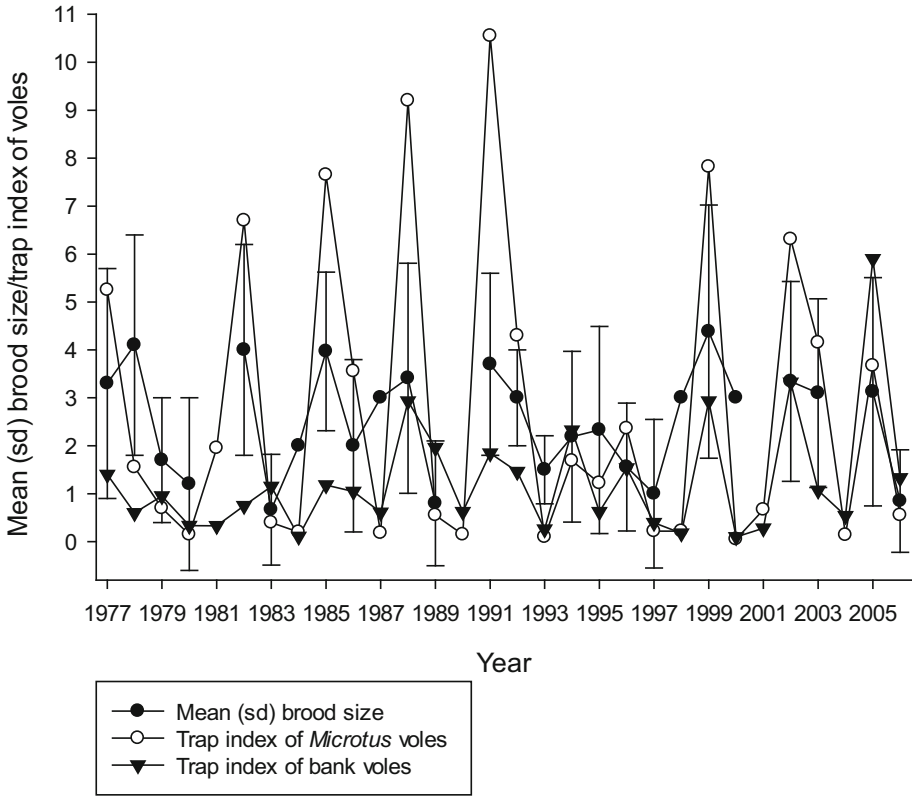

Figure 4. Yearly mean (sd) brood size of Short-eared Owls and abundance index of *Microtus* and Bank Voles during 1977–2006 at Alajoki.

Table 3. Failure reasons of Short-eared Owl nests at the Alajoki study area (pooled data from 1977 to 2006).

Reason	Total
Red Fox	2
American Mink	6
Corvid	6
Agriculture activities	14
Eggs robbed by human	1
Hatching failure	1
Starvation of nestlings	2
Unknown	38
Total	70

nests were usually located near ditches, many were destroyed by tractors and other farm machinery that became essentially larger over the 30-year study period. Native corvids (mainly Hooded Crows *Corvus corone*) and non-native American Mink were the main nest predators in cases where failure reasons were identified.

Analysis of the extended dataset (1977–2023) from the larger study area showed that, when spring abundance indices of *Microtus* and Bank Voles and either the proportion of grassy habitat or the density of partition ditches were included in the same model, all explanatory variables had significant positive effects on the number of nests and territories (Fig. 5, Table S1: models 5a, b). In addition, the number of nests and territories declined significantly over the 47-year period (Table S1: model 5c with year as an explanatory factor) corresponding with a declining proportion of grassy habitat and density of partition ditches in the landscape (Fig. 5). The mean annual decline was 2.8% (95% CI from −5.0 to −0.6%). The decline accelerated after 2011, when there were even two years (2019 and 2020) without any nests and territories and three years without nesting (2013, 2015 and 2023).

DISCUSSION

The breeding density of Short-eared Owls varied widely (0.0–1.5 nests km^{-2}, mean 0.35) and closely tracked fluctuations in vole abundance. Breeding density was positively related to vole abundance in the current spring but was not related to vole abundance in the preceding autumn, indicating a rapid numerical response with little time lag. A majority of Short-eared Owls immigrated to the study area as the vole populations began to increase and emigrated as they declined (Korpimäki & Norrdahl 1991). This rapid tracking of vole abundance was previously demonstrated using shorter (11-year) time series (Korpimäki & Norrdahl 1991, Korpimäki 1994). However, the present 47-year dataset indicates that this pattern has persisted at least into the late 2010s, despite population declines of Short-eared Owls across Europe and North America (e.g. Fernández-Bellon *et al.* 2020, Miller *et al.* 2021).

Rapid numerical responses are facilitated by the extensive natal dispersal of juvenile Short-eared Owls (mean 1500 km, 95% confidence interval 1201–1902 km) and the wide breeding dispersal of adults (mean 470 km, 255–860 km) (Calladine *et al.* 2012). Satellite tracking has revealed that individuals tagged in western Europe spend much of the non-breeding season prospecting for areas with high vole abundance, often moving thousands of kilometres (Calladine *et al.* 2024). Extensive, continent-wide movements of satellite-tracked Short-eared Owls have also been documented in North America (Johnson *et al.* 2017). These extensive movements enable owls to efficiently locate areas with high small rodent abundance.

Over the 30-year study period, Short-eared Owls were absent as breeders at Alajoki in only four breeding seasons, and non-breeders were recorded even in years of low vole abundance. This indicates more consistent occupancy compared to a long-term study area in southern Germany, where nesting was recorded in only seven of 18 breeding seasons between 1956 and 1973 (Hölzinger *et al.* 1973).

Eleven per cent (8/75) of ringed adult Short-eared Owls returned to breed at Alajoki, a proportion comparable to that reported from Scotland (14%; Village 1987). This indicates a low degree of breeding-site fidelity even in North Europe, where vole populations exhibit high-amplitude fluctuations (Korpimäki *et al.* 2005, 2025a), and suggests that not all Short-eared Owls adopt a fully nomadic lifestyle. At least in males, relatively low site fidelity may be favoured because extensive movements and the high investment for prospecting are likely to be costly. This interpretation is supported by the high mortality of year-round-tracked adult Short-eared Owls during autumn migration in North America (Johnson *et al.* 2017) and by the relatively low annual survival (45%) of satellite-tracked individuals in western Europe

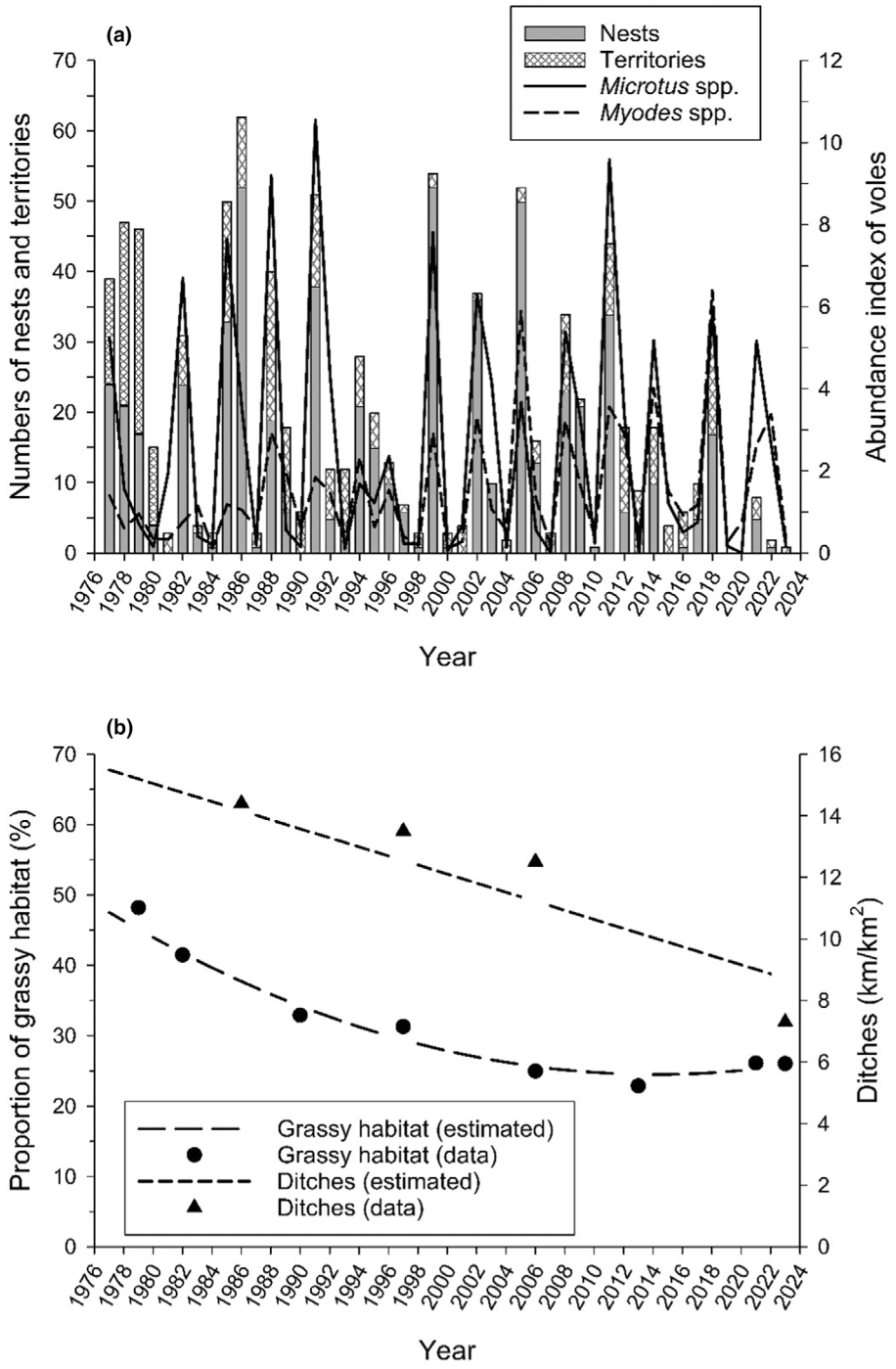

Figure 5. (a) Number of nests and territories of Short-eared Owls and spring abundance index of *Microtus* and Bank Voles during 1977–2023 in Kauhava and Lapua, western Finland. (b) The proportion (%) of grass-covered habitat in arable land and mean length of open partition ditches per km^2 regressed (by quadratic and linear regressions, respectively, see Fig. S1) on year during 1977–2023. Grass cover includes dried hay and silage, pasture, fallow and set-aside fields.

(Calladine *et al.* 2024), which is substantially lower than the survival rates of similarly sized, more site-tenacious owls and diurnal raptors (approximately 70%; Newton *et al.* 2016). In addition, the annual apparent survival of Tengmalm's Owls and Eurasian Pygmy Owls *Glaucidium*

passerinum in our study area was comparable to that of Short-eared Owls (Hakkarainen *et al.* 2002, Korpimäki *et al.* 2025b), despite their much smaller body mass. In these species, adult males tend to be site tenacious after their first successful breeding attempt (Wiesner 1992, Korpimäki 1993, Baroni *et al.* 2021), whereas juveniles and adult females disperse widely (Wiesner 1992, Lehikoinen *et al.* 2011, Korpimäki & Hakkarainen 2012). Whether similar sex-related differences in breeding dispersal occur in Short-eared Owls remains to be studied.

Clutch and brood sizes of Short-eared Owls were strongly linked to *Microtus* vole abundance. Despite the 46% reduction in grass-covered habitat for voles, which also reduced the foraging habitat available to owls, no long-term decline was detected in clutch size or offspring production. This strongly suggests that reproductive output is primarily limited by prey availability during the breeding season rather than by habitat availability. However, the loss and degradation of grass-covered winter habitat for voles probably increased the costs of prospecting for productive and safe wintering and breeding areas. In particular, subordinate juveniles may be forced to occupy low-quality habitats during their first winter (McCabe *et al.* 2022), potentially reducing their survival.

Habitat degradation may also intensify interspecific competition for prey among Short-eared Owls, Long-eared Owls *Asio otus* and Eurasian Kestrels, thereby reducing the survival of Short-eared Owl offspring during the post-fledging dependence and early independence periods. This is plausible because the food niches of these open-country birds of prey largely overlap, and their breeding densities fluctuate synchronously with vole populations (Korpimäki & Norrdahl 1991, Korpimäki 1994). When breeding densities are high, Eurasian Kestrels quite often rob prey from Short-eared Owls (Korpimäki 1984b), further intensifying interspecific competition. Probably because of the food competition, Long-eared Owls and Eurasian Kestrels breeding in close proximity (< 1 km apart) produce significantly fewer offspring than the pairs breeding farther (> 1 km) apart (Korpimäki 1987). The loss of grassy habitat supporting vole populations may further strengthen competition among birds of prey species, thereby contributing to the decline of Short-eared Owl populations.

Agricultural activities and nest predation were the two main identified causes of nest failure, each accounting for 44% of cases, although the cause remained unknown in 54% of failed nests. Detrimental effects of agricultural activities and nest predation by corvids were probably additive because ploughing, harrowing and sowing often coincided with egg-laying and incubation periods of Short-eared Owls. Even when eggs were not crushed by heavy agricultural machinery, incubating females were often flushed from their nests, allowing corvids (mainly Hooded Crows) to prey on eggs and/or small chicks. The invasive American Mink emerged as the most important mammalian nest predator, whereas native Red Foxes appeared to be less important. These findings are consistent with a global review showing that invasive vertebrate predators have twice as detrimental effects on prey populations as native ones (Salo *et al.* 2007). In contrast, Red Foxes were the main nest predators of Short-eared Owls in southern Germany (Hölzinger *et al.* 1973), whereas they were absent from the insular breeding habitat along the coast of the North Sea in northern Germany (Kämpfer *et al.* 2022). Agricultural activities were also absent from this protected nature reserve, where human access, including hiking, was strictly regulated. Under these conditions of low predation pressure and minimal human disturbance, Short-eared Owls had high offspring production (mean 2.7 young per nest at 1 month of age; Kämpfer *et al.* 2022), which was comparable to the mean number of owlets leaving the nest (2.5 per nest at 12–17 days of age) at Alajoki.

CONCLUSIONS

To our knowledge, this study provides one of the few long-term demonstrations of how temporal habitat degradation can be quantified and linked to population declines in a farmland bird of prey. Between 1977 and 2023, pasture, hay and set-aside fields were increasingly converted to cereal and other crop fields, resulting in an approximately 46% reduction in grass-covered habitats for voles, and consequently in foraging habitats for Short-eared Owls during their occupancy period. In addition, the number of open-field partition ditches, which provide cover and food resources for voles along field margins in both winter and spring, declined by 52%. This structural simplification of agricultural landscape reduced the

availability of overwintering and early-spring habitat for the primary prey, thereby decreasing foraging habitat for Short-eared Owls and possibly increasing the area required to support each breeding pair. We suggest that this substantial reduction in grass-covered habitat was the primary driver of the marked decrease (> 50%; annual decline rate of 2.8%) in the local breeding population of Short-eared Owls. Notably, habitat degradation was associated with a decline in the number of breeding pairs but not with reduced reproductive performance. Neither clutch size nor brood size showed a declining trend over the study period. Instead, both remained positively associated with annual fluctuations in *Microtus* vole abundance throughout the study, including the later years. These findings suggest that habitat degradation primarily reduced the number of breeding pairs rather than the reproductive success of pairs that successfully established territories.

Our findings are consistent with earlier studies showing that loss of habitat heterogeneity and habitat degradation due to agricultural intensification are major drivers of declines in birds breeding in grassland and farmland habitats (Donald *et al.* 2001, Newton 2004, Laaksonen & Lehikoinen 2013, Stanton *et al.* 2018, Bosco *et al.* 2024). Detrimental effects of reduced habitat heterogeneity on reproductive success have also been documented in Eurasian Kestrels (Butet *et al.* 2010, Sumasgutner *et al.* 2019, Kujala *et al.* 2024) and Montagu's Harriers *Circus pygargus* (Butet & Leroux 2001), as well as on the body condition of Barn Owl *Tyto alba* offspring (Almasi *et al.* 2015). Nevertheless, the extent to which changing weather conditions interact with habitat degradation to influence these declines remains poorly understood. The increasing frequency of extreme weather events associated with climate change may further reduce breeding success, survival and population densities in open-country birds of prey that depend primarily on small mammals, such as Short-eared Owls (Kämpfer *et al.* 2022) and Eurasian Kestrels (Kujala *et al.* 2025).

This paper is dedicated to Sakari Ikola (Fig. 1d) who suddenly passed away on 26 August 2006 at the age of 47 years, soon after the breeding season of Short-eared Owls and after finishing a unique 30-year time series on the variation in the breeding density and reproductive success of Short-eared Owls at the Alajoki study site. We would like to thank Jalmari Lahtinen, Susanna Ikola, Ossi Hemminki, Kimmo Hakola and Mikko Hänninen who continued with Sakari's field study on Short-eared Owls at Alajoki up to 2023. We acknowledge three reviewers for their valuable comments on the manuscript. Open access publishing facilitated by Turun yliopisto, as part of the Wiley - FinELib agreement.

AUTHOR CONTRIBUTIONS

Erkki Korpimäki: Conceptualization; methodology; data curation; investigation; writing – original draft; visualization; validation; funding acquisition. **Minna Koivula:** Conceptualization; writing – review and editing; data curation; methodology; investigation. **Tero Klemola:** Software; formal analysis; methodology; conceptualization; investigation; writing – review and editing; visualization.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

ETHICAL NOTE

None.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Upper panel. The proportion (%) of grass-covered habitat in arable land regressed (by a quadratic regression) on year during 1973–2023

(data from https://stat.luke.fi/en/utilised-agricultural-area). Grass cover includes dried hay and silage, pasture, fallow and set-aside fields. Lower panel. Mean length (km) of open partition ditches per km^2 at the Alajoki study area regressed (by a simple linear regression) on year during 1971–2023. Data from five randomly chosen 1 × 1-km grids in landscape maps (https://www.maanmittauslaitos.fi/en/maps-and-spatial-data/maps/view-and-download-maps). Because of very high R^2 values (0.97 and 0.85), values for the years without data can be estimated reliably.

Table S1. Design and results of (generalized, when negative binomial error distribution was used for the count data) linear (mixed, when random intercept effect was included) models for response variables of Short-eared Owls, ((1a–d) yearly nest density (per km^2), (2a–d) number of non-breeding pairs, (3a–d) clutch size and (4a–d) number of young produced), in the main study area of Alajoki during 1977–2006, and those for (5a–c) pooled number of nests and territories in a larger study area during 1977–2023. Because of high correlation coefficients (r = 0.97, n = 30 years and r = 0.88, n = 47 years) between grassy habitat (%) and the length of open partition ditches, these explanatory factors were always considered in separate models (denoted by a and b, respectively). Used error distributions and their canonical link functions are given for the models. Significant effects are highlighted by bold font.