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Research article

Benefit or ecological trap? Monitoring the effects of small clear-cuts on capercaillie *Tetrao urogallus* and its mammalian predators

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The shift to 'close to nature forestry' as the dominating forestry regime in western-European forests has resulted in increasing timber volume and denser forests with negative effects on photophilic species. Hence, there is an increasing focus on active habitat management measures to support these species. To guarantee that the measures prove beneficial to the target species, it is essential to evaluate both their benefits as well as possible negative effects. However, while species' population trends are often well-studied, rigorous monitoring schemes for management interventions are often lacking. Here we applied a before-after-control-intervention (BACI) study design over multiple years to study the effects of actively creating small clear-cuts of up to 1 ha on the occurrence of western capercaillie *Tetrao urogallus* and its mammalian predators. While habitat management measures had immediate positive effects on the probability of capercaillie presence that remained constant during the five years after the intervention, predator presence did not increase in the years after clear-cutting. Assuming that predator activity density is related to predation risk, this would refute the hypothesis that the intervention created an ecological trap.
Our study confirms correlative studies indicating that the creation of small clear-cuts in a closed forest matrix represents an effective measure for improving capercaillie habitats in Western-European lower mountain forests, and contributes to a solid basis for science-based, large-scale management strategies to comply with international species conservation legislation.

Keywords: ecological trap, forest management, gap, management intervention, nature conservation, predators

Introduction

The human induced biodiversity crisis has globally led to species extinction rates that are 1000 times higher than the likely background rate of extinction (Pimm et al.

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2014), with habitat loss and degradation being key drivers (Brook et al. 2008, Cardinale et al. 2012). In European forest ecosystems, habitat degradation is mainly caused by timber-oriented management which reduces the structural complexity of forests and leads to a decline in forest specialist species, especially those associated with old forest structures and natural disturbances (European Commission 2021, Muys et al. 2022). To counteract this trend, various national and international conservation policies and agreements are being implemented to save species from (local) extinction (López-Bao et al. 2018) e.g. by prohibiting killing and disturbance, or restoring their habitats to support viable populations (Newmark et al. 2017, Banks-Leite et al. 2020). Forest habitat restoration can involve a large variety of measures, ranging from passive approaches such as cessation of management and strict protection to active management interventions to improve habitat conditions for target species or communities (Banks-Leite et al. 2020). However, although various measures are regularly implemented in practical forest management, their effectiveness is rarely systematically monitored over sufficiently long periods of time (Gram et al. 2003) and there is a lack of knowledge on possible negative side effects.

In western-European forests, 'close-to-nature silviculture' (CNS) is widely applied (Mason et al. 2022), which is characterized by continuous cover forestry with selective felling and natural regeneration (Brang et al. 2014). CNS, introduced to replace even-aged forestry and enhance structural complexity in managed forests (Bauhus et al. 2013), resulted in vertically well-structured but dense forests, with high timber volume and closed canopy (Lieser 2009, Kändler and Cullmann 2014). In addition, as managed for stability, these forests lack early and late successional stages, which are typically characterised by gaps and open forest structures (Hilmers et al. 2018). Active conservation management interventions in these forests therefore often aim at creating open structures, such as gaps or small clear-cuts, to support photophilic species. In contrast to the large clear-cuts in even-aged forestry systems, these structures can support forest biodiversity, as they provide islands of favourable microclimate and light conditions within a dense forest matrix, locally boosting the development of ground vegetation and insects (Eckerter et al. 2022) which in turn benefits various species at higher trophic levels.

While these effects are positive for the forest ecosystem in general, there is, however, a risk that management interferences may have undesirable side-effects in addition to the intended benefits for the target species. For instance, if gaps or small clear-cuts created to support a target species also attract its predators, the conservation measure can lead to an ecological trap (Robertson and Hutto 2006). Open, grass-dominated areas support a high abundance of small mammals (Ecke et al. 2002, Greenberg et al. 2006, Sollmann et al. 2015) and therefore attract a variety of mesopredators. Especially when these areas are scarce and embedded in a closed forest matrix, predation risk may be considerably increased, not only due to 'concentration effects' leading to a locally high abundance of predators (Angelstam 1992, Hansson 1994, Kurki et al. 1998, Šálek et al. 2010, Savola et al. 2013), but also because their search efficiency is particularly high in small and isolated habitats (Angelstam 1992, Seymour et al. 2004). To ensure that the habitat management measures do not result in an increased predation risk for the target species, it is essential to monitor the impact of the measures on potential predators over multiple years.

One indicator species for open coniferous mixed forests is the capercaillie *Tetrao urogallus*. Due to its specific habitat requirements and extensive spatial needs, this forest grouse is considered an umbrella species for light demanding forest species (Suter et al. 2002, Pakkala et al. 2003) and is therefore frequently selected as a target species for conservation programs. The capercaillie is widely distributed across the boreal zone of Eurasia. The western-European populations, however, are restricted to mountain regions (Klaus et al. 1989, Coppes et al. 2015), strongly fragmented and declining across large parts of its range (Storch 2007a). Therefore, despite not globally threatened with extinction (BirdLife International 2016), the capercaillie is listed in Annex 1 of the EU Birds Directive, which obliges EU Member States to designate special protected areas for the species. In addition, several countries (France, Germany, Scotland, Spain and Switzerland) have developed regional management schemes (Moss 1994, Espinosa et al. 2004, Mollet et al. 2008, Suchant and Braunisch 2008, Ministère de la transition écologique/DGALN and LPO 2012). The main causes for population declines comprise habitat deterioration (Čas and Adamič 1998, Storch 2002, Miettinen et al. 2010, Kämmerle et al. 2020), increased predator populations (Chautan et al. 2000), anthropogenic disturbance (Summers et al. 2007, Coppes et al. 2017, Coppes et al. 2018) as well as climate change (Braunisch et al. 2013), although their relative impact differs between populations.

In western Europe, capercaillie historically profited from forestry practices with intensive management, resulting in acidification of soils and low production forest with many gaps in the forest canopy, open areas and a rich ground vegetation with high cover of dwarf shrubs such as bilberry *Vaccinium myrtillus* (Braunisch and Suchant 2008), a key food resource (Klaus et al. 1989, Picozzi et al. 1992, Storch 2002). The shift to CNS has drastically reduced capercaillie habitat suitability in recent decades (Suchant and Braunisch 2004). Therefore, most capercaillie conservation programmes focus on habitat improvement through silvicultural measures, i.e. by reducing canopy cover and creating gaps and small clear-cuts in the forest matrix (Storch 2007b). The amount of these open-forest structures at a landscape scale has been shown to be positively related to capercaillie population persistence (Kämmerle et al. 2020) and – in combination with suitable ground vegetation – can buffer negative effects of climate change (Braunisch et al. 2014). However, the direct effects of creating such structures on capercaillie occurrence, as well as possible undesirable side effects on predator presence, have not yet been tested experimentally.

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Capercaillie population dynamics is less dependent on adult survival than on reproductive success (Kurki et al. 1997), which can be negatively affected by predator abundance (Kurki et al. 1997, Kauhala et al. 2000, Baines et al. 2004, Moreno-Opo et al. 2015, Baines et al. 2016). Effects of predation are particularly strong in highly fragmented forest areas (Storaas and Wegge 1997, Kurki et al. 1998, Storch et al. 2005), while under favourable habitat conditions (e.g. open forest structures with ground vegetation cover providing hiding opportunities, little anthropogenic disturbance), the species could possibly cope with high predation pressure (Baines 1991, Kämmerle et al. 2017). The main predators of capercaillie in the Black Forest are red fox *Vulpes vulpes* and pine marten *Martes martes* (Kämmerle et al. 2019). Due to widespread rabies vaccination campaigns, a lack of top-down control by top predators and high environmental productivity, red fox densities in Europe have increased in recent decades (Chautan et al. 2000, Pasanen-Mortensen et al. 2013, Pasanen-Mortensen and Elmhagen 2015, MLR 2022), and are considered a key factor for the decline of many endangered species (Elmhagen et al. 2010, Salo et al. 2010, Smith et al. 2010). The red fox, as a generalist, can flexibly adapt to a wide variety of habitats, preferring mosaic-like rural landscapes that offer a large variety of food and cover (Cavallini and Lovari 1994, Schnaitl and Stürzer 2009). Within forests, open areas are strongly preferred (Schnaitl and Stürzer 2009) and repeatedly visited (McKeown et al. 2020). Capercaillie nest particularly frequently at the edges between grass- and shrub-dominated clearings adjacent to forest (Storch 1991), where many mesopredator species prefer to move in search of food (Bider 1968, Šálek et al. 2010). Such locally increased predator densities could negatively affect breeding success.

Here, we applied an experimental before-after-control -intervention (BACI) (Eberhardt 1976, Green 1979) design to study the effects of active habitat management through the creation of small clear-cuts on the probability of capercaillie presence, while in parallel testing for potential effects on the presence frequency of their main mammalian predators. In addition to the red fox, we also included the badger *Meles meles*, pine marten, stone marten *Martes foina* and wild boar *Sus scrofa* as potential nest predators (Saniga 2002, Jahren et al. 2016, Palencia and Barroso 2024) and monitored their activity density on the study sites over four of the six years of the study.

Material and methods

Study area

We conducted our study in the Black Forest mountain range in south-west Germany (max. elevation 1493 m a.s.l.). This low-altitude mountain range is characterized by mixed forests, dominated by Norway spruce *Picea abies*, European silver fir *Abies alba*, and beech *Fagus sylvatica* (Kändler and Cullmann 2014) and is largely managed for timber production. After decades of even-aged forestry, the forestry regime progressively shifted to 'close-to-nature silviculture' (CNS), which has been officially introduced in 1990 (Weidenbach and Kohnle 2011). Capercaillie used to be a common resident bird in the study region, but population size and range extent have been declining significantly, and today it is critically endangered (Coppes et al. 2019). The capercaillie is protected under both the European Birds Directive and the German Nature Conservation Act. Furthermore, the federal state of Baden–Württemberg has launched an Action Plan in 2008, in which specific target values for habitat management are defined, including gaps and clearings on at least 10%, and open forest on at least 20% of the forested area (Suchant and Braunisch 2008). The main predator of capercaillie in the region is the red fox (Kämmerle et al. 2019), whose abundance has doubled in the last 50 years according to hunting bag statistics (MLR 2022). Other mammal species that prey on capercaillie nests include badger, pine marten, stone marten and wild boar (Kämmerle et al. 2019, Palencia and Barroso 2024).

Study design

To study the effects of small clear-cuts on capercaillie and predator presence, we used a pairwise experimental BACI study design with multiple study sites. We collected data from 2018 to 2023 on 30 square study sites of 9 ha (300 × 300 m), distributed across the entire Black Forest study region (Fig. 1) and arranged these sites in 15 pairs, with the paired sites being similar in altitude, aspect, soil type, tree species composition and site conditions. The site information was extracted from a digital elevation model (25 m resolution), the forest site mapping (Michiels 2014) and the forest inventory data provided by the forestry administration of the Federal State of Baden-Württemberg and subsequently verified in the field. Paired sites were located in spatial proximity to each other (min. 584 m and max. 5119 m distance, mean: 1576 m, SD: 1051 m), with the minimum distance roughly corresponding to the radius of a small capercaillie home range in the study area (100 ha, r = 564 m, Coppes et al. 2017). For each pair, a small clear-cut of 0.7–1.0 ha was experimentally created in the centre of one study site (intervention, I), while the other served as control (control, C), with the treatment (control or intervention) randomly assigned. Study sites were oriented parallel to the slope, surrounded by forest and located in areas with a high landscape habitat potential for capercaillie (Braunisch and Suchant 2008), which are also the focal areas of the local capercaillie management scheme (Suchant and Braunisch 2008).

Clear-cuts were created in autumn 2018 after the first sampling and cleared of all trees and woody debris to promote the development of ground vegetation, especially bilberry, the main capercaillie diet in summer (Klaus et al. 1989, Picozzi et al. 1992, Storch 2002). The remaining forest on the study sites was continuously managed during the study following the principles of close-to-nature silviculture.

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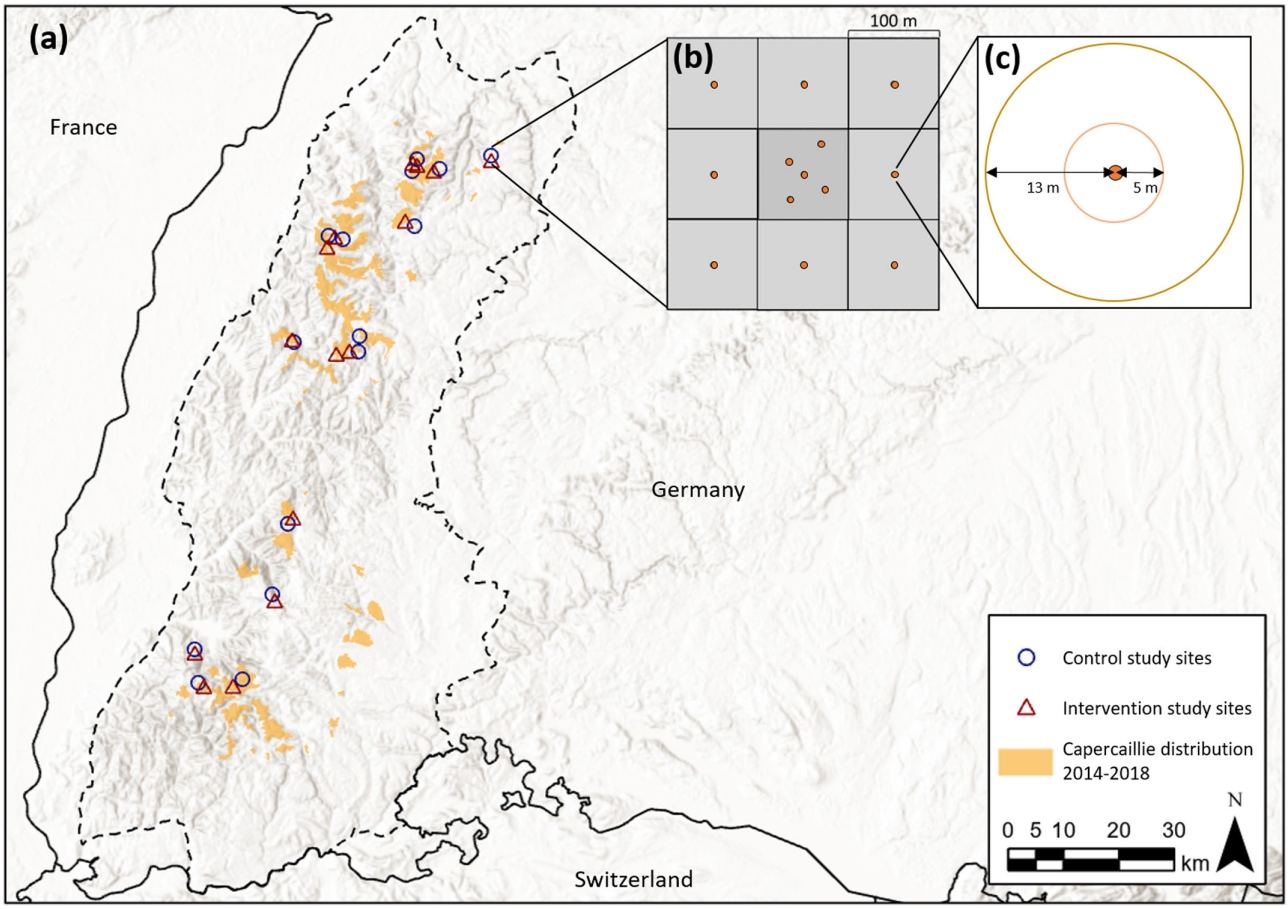


Figure 1. (a) Location of the study sites (9 ha) to assess the effects of habitat management (blue circles = study sites with experimental clear-cuts of 0.7–1.0 ha in the centre (intervention, I), red triangles = control sites (control, C) in the Black Forest (dashed line), Germany, in relation to the capercaillie distribution (light orange). Note that the size of the symbols is not to scale and that therefore not all locations can entirely be seen, as the symbols partially overlap at this scale; (b) The arrangement of the sampling plots within the study sites, and (c) the different radii used for sampling capercaillie signs (5 m) and habitat variables (13 m). Predator activity was recorded for the central hectare (b, dark grey).

To sample capercaillie occurrence and habitat, we systematically placed 13 sampling plots (from here on referred to as 'plots') in each of the 30 study sites (Fig. 1). In addition to the nine plots located in the centre of each of the nine hectare squares of the site, we added four additional plots in the four corners of the central hectare, two of them (in opposite corners) at 25 m, the other two at 40 m from the centre (Fig. 1), to better capture the different microclimatic and vegetation conditions within and at the edges of the clear-cut and the control site (Fig. 1).

Sampling

Capercaillie

We assessed capercaillie occurrence during six consecutive years (2018–2023) by applying an established, non-invasive method (Storch 2002), searching for direct (sightings) and indirect (e.g. feathers, faeces, dust baths) capercaillie signs for 10 min within circular plots of 5 m radius around each plot centre. Using indirect signs is a widely applied method in capercaillie monitoring and to study capercaillie habitat use (Storch 2002, Summers et al. 2007, Zohmann et al. 2014, Coppes et al. 2020), which allows for integration and even differentiation between summer and winter habitat use, as more than 90% of the winter faecal samples persist long enough to still be found in summer surveys (Poggenburg et al. 2018). To minimize effects of disturbance, we conducted the fieldwork between 15 July and 15 September, i.e. outside the reproductive period. Capercaillie signs were removed after each survey event, to prevent signs from the previous year being included.

Habitat variables

To account for the initial habitat suitability before the creation of the clear-cuts, we recorded habitat variables (Table 1) within a 13 m radius around each plot centre, simultaneously to the capercaillie sampling in 2018. We reduced the original radius of 20 m proposed by Storch (2002) to 13 m based on the protocol for forest structure inventories in the forest reserves of the study region (Wevell von Krüger et al.

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Table 1. Habitat variables to assess the initial habitat suitability in the year before management intervention (2018). The vegetation data (tree and ground layer) were assessed according to Storch (2002) but within a 13 m radius, the geospatial data was derived by the federal state's geoinformation department (Landesamt für Geoinformation und Landentwicklung (LGL) Baden–Württemberg).

Variable category	Definition	Unit
Tree layer (> 5 m)	Canopy cover	Percentage (%)
	Cover of silver fir *Abies alba*	Percentage (%)
	Cover of Scots pine *Pinus sylvestris*	Percentage (%)
	Cover of European larch *Larix decidua*	Percentage (%)
	Presence of gaps (gaps in the tree layer with a diameter exceeding the stand height)	Yes/No (0/1)
Ground layer (< 1 m)	Cover of ground vegetation	Percentage (%)
	Height of the dominant ground vegetation type	Centimetre (cm)
	Cover of bilberry *Vaccinium myrtillus*	Percentage (%)
	Cover of other berry species (e.g. blackberry *Rubus fruticosus*, raspberry *Rubus idaeus*, cranberry *Vaccinium vitis-idaea*)	Percentage (%)
Geospatial data	Slope	Degree (°)
	Distance to hiking trails	Meter (m)

2016) to avoid a spatial overlap of the sampling plots in the central hectare. Recorded variables included canopy cover, composition of the tree layer and whether there was a gap in the tree layer, as well as cover, height and composition of the ground layer. Additionally, we assigned slope and distance to hiking trails based on geospatial data to each plot. These variables have been shown to be related to capercaillie habitat suitability in previous studies (Storch 2002, Suchant and Braunisch 2004, Coppes et al. 2020, Table 1).

Predators

To assess the effect of clear-cutting on the frequency of predator presence, we installed a camera trap in the central hectare of each study site. We used motion-triggered Reconyx PC 900 Professional HF2X (Reconyx Inc.) with an infrared flash, which we set to take three consecutive images, one per second, and a period of one second between two triggers. Cameras were attached to a tree at 50–90 cm height and oriented towards structures favouring the potential presence of predators, e.g. game trails, forced crossings or open areas. We installed a camera trap on each study site during the first four years of the study (2018–2021) between mid April and mid June depending on local phenology with sites at lower altitudes equipped first, and dismantled them between late August and the beginning of October. We checked each camera at least once per month and changed its location within the central hectare once per year.

For picture classification we used the program FFM2 (Kluth et al. 2011), which automatically groups images taken in a time interval of 5 min into an event. For each event, we visually identified the animal species and counted the number of individuals. Red fox, badger and wild boar were identified to species level, while stone marten and pine marten were grouped together in the class 'marten' as it was not always possible to distinguish the species on the images. Finally, we calculated trapping rates per species, season and site as the number of trapping events (accounting for the number of individuals, e.g. counting a trapping event with two individuals twice) divided by the number of days the camera was active (Rovero and Marshall 2009).

Statistical analysis

Capercaillie presence

To study the effect of the management intervention (clear-cut) on the probability of capercaillie presence at each plot, we used generalized linear mixed models (GLMM) in the R package 'lme4' (Bates et al. 2015), with a logit link and including 'site' nested within the 'pair' (consisting of one I and one C study site) as nested random intercept. In addition, we accounted for inter-annual variation using the 'study year' as a second random intercept, but discarded it in the final model, as it did not improve the model as suggested by AIC-based model selection (AIC of 898.4 versus 898.15). However, we included 'study year' as a fixed effect in the model to test for temporal effects during the study period. We classified the sites with two binary variables 'time period', with 'B' and 'A' standing for 'before' and 'after' clear-cutting (i.e. 2018 versus 2019–2023); and 'treatment' with 'C' and 'I' for 'control' (C) and 'intervention' (I) according to the BACI design, and used both, as well as their interaction as predictors as in Coppes et al. (2020). In intervention sites, we classified all plots as 'I', irrespective of their location within or outside the clearing, as we expected the presence of a clearing to affect also the probability of capercaillie presence in the immediate surrounding. Furthermore, to account for differences in the probability of capercaillie presence due to differences in the initial habitat suitability, i.e. before the management intervention, we included the habitat suitability in 2018 as a predictor. We modelled habitat suitability as the probability of finding capercaillie signs at a plot as a function of the habitat variables using the model of Coppes et al. (2020) (Supporting information), which had been calibrated with data collected with the same sampling method from different European capercaillie populations and therefore provides a robust estimate (Coppes et al. 2020). All numerical variables were scaled for the analysis using z-score standardisation and back-transformed for the response curves. We used the 'bobyqa' optimizer and assessed statistical significance of fixed effects, using Wald Z-test, as implemented in the 'lme4' package (Bates et al. 2015). We tested for violations of model assumptions via residual diagnostics using

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the DHARMa-package (Hartig 2022). Finally, from the predicted probability of capercaillie presence per plot, we calculated the probability that capercaillie was present in at least one plot of a study site as 1-∏(1-predicted probability$_{(plot)}$) across the 13 sampling plots per site. All statistical analysis were conducted with R Statistical Software, ver. 4.3.1 (www.r-project.org).

Frequency of predator presence

We modelled the effect of management intervention on trapping rates of the predator species using GLMMs with a negative binomial error distribution and a log link function. We used the 'bobyqa' optimizer and included the study site pair as a random intercept. Statistical significance of fixed effects was assessed using Wald Z-test, as implemented in the 'lme4' package (Bates et al. 2015). As for capercaillie, we accounted for inter-annual variation by including 'study year' as a second random intercept, which was discarded in the final models as it did not significantly improve the model as suggested by AIC-based model selection, and tested for an interaction of the two binary variables: 'time period' (before-after) and 'treatment' (control-intervention). As a second predictor, we included 'study year' in the model to account for trends over the study period.

Results

Capercaillie presence

Throughout the six study years we found 161 signs of capercaillie presence on the sampling plots (control sites (C) = 39, intervention sites (I) = 122). The majority of signs were faeces followed by feathers (Supporting information). No signs indicating predation (i.e. dead capercaillie, large numbers of feathers in one location or feathers with bite marks) were found. The number of sites with capercaillie presence varied between the years, and increased in the intervention sites compared to the control sites after establishing the clear-cuts in 2018 (Fig. 2).

Generally, the probability of capercaillie presence at sampling plot level was low (Fig. 3), increased slightly over the study period and was strongly related to the initial habitat suitability (Table 2, Fig. 3b). Across all sites, occurrence probability was significantly lower in the post-intervention period than before (Table 2). This decrease, however, was dependent on the treatment, as shown by the significant BA × CI interaction: While the probability of capercaillie presence decreased in the plots of the control sites (C) after the intervention, it remained stable in the intervention sites (I) (Table 2, Fig. 3a). This effect remained stable across the intervention years, both at plot and at site-level (Fig. 4).

Predator frequency

We did not find a significant effect of clear-cutting on the trapping rates of fox, badger and marten (Table 3), neither directly after, nor within three years after the intervention. While the overall trapping rates of fox and badger trapping rates were higher in the period after the intervention, this increase did not differ between the treatments. Wild boar activity was generally higher in intervention sites but decreased in these sites after clear-cutting (i.e. 2019–2021). We did not find an influence of study year on predator trapping rates, except for badgers, where a decline in trapping rates was observed over time.

Discussion

Applying an experimental BACI design, we demonstrate that creating small-scale clear-cuts in a closed forest matrix is an effective tool in capercaillie conservation, as it mitigated the decrease in capercaillie presence compared to untreated stands with close to nature forestry in a declining capercaillie population. This result is consistent with

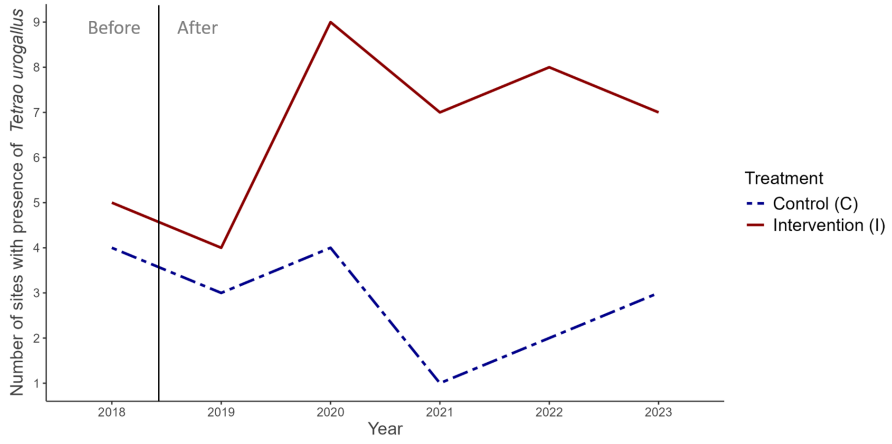


Figure 2. Number of study sites with capercaillie presence on at least one of the 13 sampling plots per year: clear-cut sites (Intervention (I)): solid red line; control sites (Control (C)): dashed blue line. The clear-cuts were created in the centre of the intervention study sites between the sampling in 2018 and 2019.

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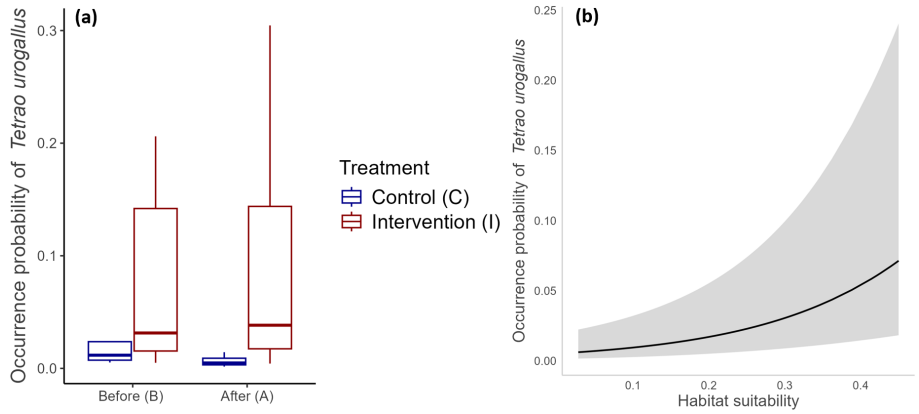


Figure 3. Effect plots showing the probability of capercaillie presence as a function of the BA × CI interaction term (a) and the initial habitat suitability in 2018 (b).

previous studies on capercaillie habitat selection (Storch 1993, 1994, 2002, Braunisch et al. 2014, Coppes et al. 2021, Taubmann et al. 2021), which report a positive effect of clear-cuts up to 1 ha in size on capercaillie occurrence, reflecting the general preference of capercaillie for gaps and open forests (Suchant and Braunisch 2004, Bollmann et al. 2005, Graf et al. 2007). Other studies, indicating negative impacts of clear-cutting on the occurrence of capercaillie refer to larger clear-cuts (> 1 ha to < 226 ha) (Kurki et al. 2000, Storch 2007b, Mikoláš et al. 2015), which are still part of silvicultural systems in parts of eastern Europe and Scandinavia. Large clear-cuts can increase predation risk due to reduced cover opportunities and, at a landscape scale, lead to fragmentation and destruction of the actual habitat (Kvasnes and Storaas 2007). In contrast, clear-cuts with a maximum size of 1 ha were created in our study, which is indicated in the literature as the largest clear-cut area suitable for capercaillie (Storch 2002).

These smaller clear-cuts can promote bilberry growth (Nybakken et al. 2013, Eckerter et al. 2019), increase insect biomass (Grämiger et al. 2015) and provide dry and warm microclimate for chick rearing (Klaus et al. 1989). At the population level, open forest structures (gaps and clear-cuts) have been shown to reduce local extinction risk (Kämmerle et al. 2020) and to buffer negative effects of climate change on capercaillie (Braunisch et al. 2014), especially in the lower mountain ranges of central Europe, where range restrictions are predicted (Braunisch et al. 2013)

Despite the positive effects of creating gaps and small clear-cuts on capercaillie, the associated risk of attracting predators by improving prey availability and hunting conditions is often discussed (Angelstam 1986, Rudnicky and Hunter 1993, Steventon et al. 1999, Flaspohler et al. 2001, Robertson and Hutto 2006). Locally high production of plant and insect biomass in clear-cuts (Eckerter et al. 2022) can lead to increased densities of small mammals (Hansson 1994), which in turn can attract mesopredators and promote their reproduction, potentially leading to increased predation rates on species targeted for conservation efforts.

Predator activity has frequently been linked to reproductive success in birds (Cooper and Ginnett 2000, Zanette and Jenkins 2000, Rodewald et al. 2011) and has been confirmed as a valid proxy for nest predation risk (Laux et al. 2024). In our study, the creation of small clear-cuts did not increase the trapping rates of any of the potential predator species compared to the control sites, neither directly nor in the three years after the intervention. Assuming that predator activity is related to predation risk in capercaillie, this would refute the ecological trap hypothesis. This result is supported by earlier studies, in which clear-cutting was not identified as a factor increasing the predation rates on bird nests (Rudnicky and Hunter 1993, Darveau et al. 1997, Kvasnes and Storaas 2007), while others report a positive effect on the predator abundance, including red fox and wild boar (Eom et al. 2020), one of the most influential capercaillie nest predators (Klaus and Bergmann 1994). One explanation for the

Table 2. Results of the Generalized Linear Mixed Model predicting capercaillie presence at the sampling plot level of intervention (Treatment: I) and control (Treatment: C) sites, before (Period: B) and after (Period: A) the management intervention (clear-cutting). Significant fixed effects are highlighted. Site, nested in the site-pair was used as random intercept in the capercaillie model.

Fixed effects	Estimate	SE	Z-value	p-value	Random effects	SD (intercept)
Tetrao urogallus						
(Intercept)	−3.825	0.688	−5.561	< 0.001	Pair	0.851
Period: A	−1.357	0.466	−2.912	**0.004****	Pair:Site	1.418
Treatment: I	0.929	0.770	1.207	0.227		
Study year	0.289	0.124	2.342	**0.019***		
Habitat suitability 2018	0.472	0.114	4.155	< 0.001***		
Period: A × Treatment: I	1.033	0.500	2.065	**0.039***		

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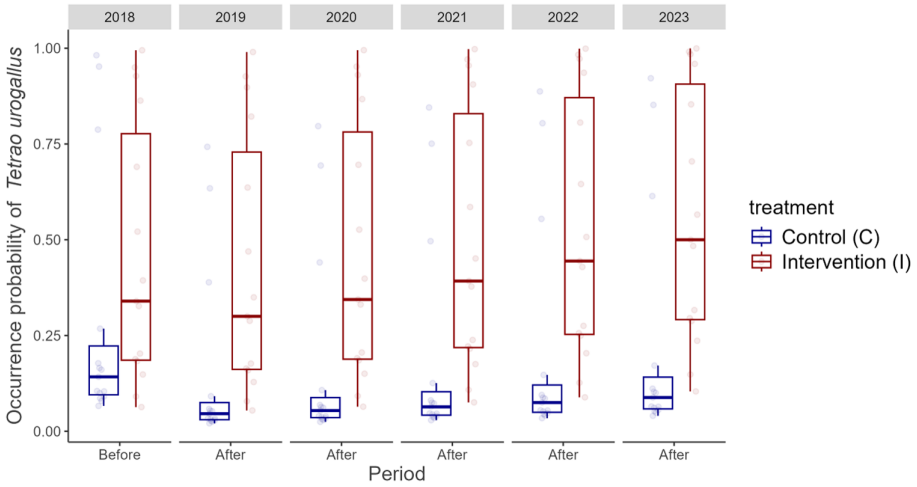


Figure 4. Probability of capercaillie presence in at least one of the 13 plots of a study site, as a function of the treatment (C = control, I = Intervention) and the study year, with 2018 representing the year before and 2019–2023 the years after the intervention.

absence of increased predator occurrence on the intervention sites is that the clear-cuts were relatively small and located in a closed forest matrix. Most studies report increased predator activity along forest edges bordering to agricultural areas (Björklund 1990, Sandström 1991, Donovan et al. 1997), where a higher primary productivity results in a greater food supply (Angelstam 1986, Andrén 1995). At inner forest edges, i.e. between two successional stages, the primary productivity gradient is considerably smaller, which has been shown to reduce their attractiveness to predators (Lahti 2001). Yet, as the cameras were set up between April and October, our results apply only to the capercaillie breeding season, while effects on predator presence during the winter months cannot be ruled out. In addition, using camera traps, our study only covers mammalian predators and neglects potential effects by avian predators such as corvids Corvidae (Baines et al. 2004, Summers et al. 2004) or goshawk *Accipiter gentilis* (Tornberg 2001), which is recommended as a subject for future studies.

While the creation of small clear-cut areas increased the probability of capercaillie occurrence, also initial habitat suitability, i.e. habitat suitability prior to clear-cutting, which mainly depends on tree species composition, slope

Table 3. Results of generalized linear mixed models predicting predator trapping rates in the central hectare of intervention (Treatment: I) and control (Treatment: C) sites, before (Period: B) and after (Period: A) the management intervention (clear-cutting). Significant fixed effects are highlighted. The site-pair was used as random intercept in the predator models.

Fixed effects	Estimate	SE	Z-value	p-value	Random effects	SD (intercept)
a. *Vulpes vulpes*						
(Intercept)	0.819	0.344	2.380	0.017	Pair	0.196
Period: A	1.012	0.432	2.342	**0.019***		
Treatment: I	0.535	0.434	1.233	0.218		
Study year	−0.201	0.128	−1.565	0.118		
Period: A × Treatment: I	−0.352	0.477	−0.738	0.461		
b. *Meles meles*						
(Intercept)	−0.789	0.568	−1.390	0.164	Pair	1.077
Period: A	1.270	0.636	1.996	**0.046***		
Treatment: I	0.181	0.601	0.302	0.763		
Study year	−0.514	0.233	−2.204	**0.028***		
Period: A × Treatment: I	−0.788	0.712	−1.107	0.268		
c. *Martes* sp.						
(Intercept)	0.507	0.280	1.807	0.071	Pair	0.280
Period: A	0.149	0.384	0.389	0.697		
Treatment: I	−0.735	0.432	−1.704	0.089		
Study year	0.208	0.117	1.777	0.076		
Period: A × Treatment: I	0.754	0.473	1.594	0.111		
d. *Sus scrofa*						
(Intercept)	0.213	0.479	0.444	0.657	Pair	1.038
Period: A	0.608	0.564	1.078	0.281		
Treatment: I	1.222	0.530	2.307	**0.021***		
Study year	0.323	0.172	1.872	0.061		
Period: A × Treatment: I	−1.490	0.605	−2.463	**0.014***		

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and distance from hiking trails, had an influence. Previous studies showed that the 'landscape habitat potential', i.e. the conditions defining the development and usability of suitable habitat, must be taken into account when defining priority areas for habitat management (Graf et al. 2007, Braunisch and Suchant 2008). We show, that also the actual, local-scale habitat conditions play a role as they define the probability of capercaillie being already present in the area which are then attracted to the newly created habitat. In addition, given that brood and chick loss is higher in fragmented forests compared to large old forests (Wegge et al. 1990, Kurki et al. 2000), it is essential to consider the forest matrix when implementing habitat management measures such as clear-cutting to avoid the creation of ecological traps. In order to make the most effective use of limited financial resources, measures should therefore be concentrated on areas with suitable landscape configuration and close to areas with capercaillie occurrence and a high habitat suitability.

In our analysis the BA (before–after) predictor had a negative influence on the probability of capercaillie presence on the control sites (Table 2), indicating that the overall probability of capercaillie presence on the control plots was higher in 2018 than in the following years (2019–2023). This result is further supported by the number of study sites with capercaillie presence per year (Fig. 2), which decreased in the control sites reflecting the overall decline of the capercaillie population in the Black Forest, as measured by annual lek counts (Coppes et al. 2019, MLR 2022). While long-term monitoring of the population size and distribution is essential to identify population trends and their drivers at the landscape-scale, rigorously monitoring the effectiveness of local-scale management interventions to counteract these trends, as well as evaluating their possible negative effects is equally important for optimizing the effectiveness of management plans. As effects can occur with a delay or weaken rapidly under the influence of natural succession, such studies should cover several years after the intervention, in order to enable the derivation of intervention intervals. Using an experimental set up in a BACI design, we demonstrate that the implemented measures have a beneficial effect on the probability of capercaillie presence, even in a declining population, without increasing the potential risk of predation. In combination with studies showing the importance of habitat management for long-term population persistence (Kämmerle et al. 2020) and for mitigating climate change effects (Braunisch et al. 2013, 2014), our results provide a solid basis for science-based habitat management to support the central-European capercaillie populations and comply with international legislation.

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.k0p2ngfjw (Kochs et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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