Česká zemědělská univerzita v Praze

Fakulta lesnická a dřevařská

Katedra myslivosti a lesnické zoologie

Populační a akustická variabilita tetřívka obecného (*Lyrurus tetrix*): implikace pro efektivní ochranu a monitoring druhu

Population and acoustic variability of the Black grouse (*Lyrurus tetrix*): implications for effective conservation and monitoring of the species

Disertační práce

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2024

"Prohlašuji, že jsem disertační práci na téma Akustická identifikace jedinců tetřívka obecného vypracovala samostatně s použitím uvedené literatury a na základě konzultací a doporučení školitele.

Souhlasím se zveřejněním disertační práce dle zákona č. 111/1998 Sb. o vysokých školách v platném znění, a to bez ohledu na výsledek její obhajoby."

V Praze dne Lucie Brožová

Poděkování

Tímto bych ráda poděkovala všem spoluautorům odborných článků, z nichž je tato práce sestavena. Bez jejich neocenitelné spolupráce a obětavosti by její dokončení nebylo možné. Velmi si vážím času, který do společného výzkumu investovali, a odborného přínosu, který do této práce vložili.

Poděkování patří mému školiteli Ing. Vlastimilu Hartovi, Ph.D. a konzultantovi Mgr. Richardu Polichtovi, Ph.D., kteří mě odborně vedli a poskytovali mi cenné rady a zpětnou vazbu, konzultovali průběh výzkumu a jeho metodiku, pomáhali mi realizovat analýzy a publikaci výstupů. Velkou pomocí mi byl také doc. Ing. Tomáš Kušta, Ph.D., jenž dohlédl na zdárné dokončení této práce.

Ráda bych také vyjádřila vděk svým kolegům z práce, jmenovitě Ing. Janu Cukorovi, Ph.D., Ing. Richardu Ševčíkovi, Ph.D. a Ing. Kateřině Brynychové, Ph.D., jejichž pomoc po odborné stránce a pozitivní motivace mě během doktorandského studia povzbuzovaly a pomáhaly mi pokračovat. Vaše podpora a zájem mi významně pomohly překonat náročné okamžiky a setrvat na cestě k úspěšnému dokončení této práce.

V neposlední řadě bych chtěla srdečně poděkovat své rodině. Mým rodičům, kteří ve mně po celou dobu věřili a podporovali mě nejen finančně v počátcích, ale také emočně po celou dobu studia, a rodičům mého manžela za poskytnutí prostoru a času na klidné dokončení práce. Zvláštní poděkování patří mému manželovi, který mi byl neustálou oporou, zejména v momentech, kdy věci nešly podle představ. Tuto práci s láskou věnuji jemu a naší dceři Štěpánce, která mi dodávala sílu a radost v těžkých chvílích.

Abstrakt

Tetřívek obecný (*Lyrurus tetrix*) patří mezi druhy lesních kurů, jejichž populace je zejména ve střední a východní Evropě na ústupu. Tento dlouhodobý trend je způsoben mnoha vlivy, které se liší v závislosti na oblasti. Přestože globálně není označován za ohroženého, jako významný druh si zaslouží pozornost a péči. Cílem tohoto výzkumu bylo sumarizovat dostupné údaje o populační dynamice tetřívka obecného a důvodech jeho poklesu a analyzovat akustické projevy jako potenciální podklad pro efektivní monitoring.

Na základě rozboru 228 zdrojů literatury z let 1955 až 2024 bylo zjištěno, že ve střední Evropě jsou hlavními důvody úbytku populace ztráta biotopů, fragmentace lesů a negativní vliv rekreačních aktivit. V severských zemích je za pokles početnosti zodpovědná především nízká úspěšnost reprodukce a rostoucí mortalita kuřátek. I když jsou tyto faktory regionálně rozdílné, jejich významná část má původ v lidské činnosti, a proto je třeba zaměřit se na ochranná opatření, která zahrnují obnovu stanovišť pomocí vhodných lesnických postupů, management predátorů a spárkaté zvěře, a efektivní metody monitoringu.

Právě monitoring tetřívka obecného lze podpořit pomocí analýzy zvukových projevů jedinců. Akustická individualita v hlasových projevech hraje u mnoha druhů ptáků klíčovou roli v období páření. U tetřívka obecného jsou důležité dva hlavní typy volání, bublání a syčivé pšoukání, signál, který není produkován syringem. Analýza pšoukání 24 jedinců ve Finsku a Skotsku prokázala vysokou míru akustické individuality s přesností klasifikace až 78 % pomocí diskriminační analýzy. Výsledky ukázaly, že pšoukání nese informace o jedinečné identitě kohoutků, což může hrát roli v jejich vzájemném rozpoznávání během lekování.

Geografická variabilita v akustickém projevu tetřívků byla zkoumána na 82 jedincích ze čtyř zemí (Česká republika, Skotsko, Finsko a Rusko). Analýza pšoukání odhalila rozdíly mezi populacemi, přičemž populace ze Skotska a Ruska vykazovaly větší vnitřní variabilitu ve srovnání s těmi z České republiky a Finska. Ačkoli nebyly identifikovány jasné dialekty, zjištěné rozdíly poukazují na to, že geografická variabilita v akustických projevech může figurovat v evolučních procesech a diferenciaci populací. Tato data mají potenciál obohatit naše znalosti o dynamice populací a přispět k ochraně tohoto ohroženého druhu.

Klíčová slova: Tetraonidae, populační dynamika, akustická individualita, geografická variabilita

Abstract

The Black grouse (*Lyrurus tetrix*) is one of the woodland species whose population is on the decline, especially in Central and Eastern Europe. This long-term trend is due to many influences that vary by region. Although it is not globally classified as endangered, as an important species it deserves attention and care. The aim of this research was to summarize the available data on the population dynamics of the Black grouse and the reasons for its decline, and to analyse the acoustic performance as a potential basis for effective monitoring.

Based on an analysis of 228 sources of literature from 1955 to 2024, it was found that in Central Europe the main reasons for the population decline are habitat loss, forest fragmentation and the negative impact of recreational activities. In the Nordic countries, the decrease in numbers is mainly due to the low success rate of reproduction and the increasing mortality of chicks. Although these factors vary regionally, a significant part of them originates from human activities, and therefore conservation measures that include habitat restoration through appropriate forestry practices, predator and ungulate management, and effective monitoring methods must be targeted.

It is precisely the monitoring of the common grouse that can be supported by analysing the sound performances of individuals. Acoustic individuality in vocalizations plays a key role in the mating season in many bird species. Two main types of calls are important in the Black grouse, rookooing and hissing call, a signal that is not produced by a syrinx. Analysis of hissing calls from 24 individuals in Finland and Scotland demonstrated a high degree of acoustic individuality with classification accuracy of up to 78% using discriminant analysis. The results showed that hissing calls carries information about the unique identity of the males, which may play a role in their mutual recognition during lekking.

Geographical variability in the acoustic expression of grouse was investigated on 82 individuals from four countries (Czech Republic, Scotland, Finland and Russia). Hissing call analysis revealed differences between populations, with populations from Scotland and Russia showing greater internal variability compared to those from the Czech Republic and Finland. Although clear dialects have not been identified, the differences found indicate that geographic variability in acoustic performance may figure in evolutionary processes and differentiation of populations. These data have the potential to enrich our knowledge of population dynamics and contribute to the conservation of this endangered species.

Key words: Tetraonidae, populations dynamics, acoustic individuality, geographic variability

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II. **Hambálková, L.**, Policht, R., Horak, J., Hart, V., 2021. Acoustic individuality in the hissing calls of the male black grouse (*Lyrurus tetrix*). *PeerJ* 9. https://doi.org/10.7717/peerj.11837

III. **Hambálková, L.**, Policht, R., Cukor, J., Hart, V., Ševčík, R., 2023. Black Grouse Hissing Calls Show Geographic Variability across the Distribution Area. *Animals*. https://doi.org/10.3390/ani13111844

1. Úvod

Tetřívek obecný (*Lyrurus tetrix*) je pozoruhodný zástupce čeledi tetřevovitých (Tetraonidae) z řádu hrabaví (Galliformes), jehož areál rozšíření sahá od Britských ostrovů přes střední a severní Evropu a Asii až po Severní Koreu (BirdLife International, 2022). Osídluje širokou škálu prostředí, od rozsáhlých vřesovišť až po horské lesy (Červený, 2009; White et al., 2015; Hora et al., 2018), a je známý pro svůj výrazný pohlavní dichromatismus. Zatímco kohoutci se vyznačují kovově černým zbarvením v kontrastu s bílými ocasními krovkami, doplněnými v době páření o výrazně červené poušky, slepičky oplývají jednoduchým krycím zbarvením v hnědých odstínech (Červený, 2009). Jedinečnost tohoto lesního kura navíc podtrhuje akustický projev kohoutků, který je součástí namlouvacího rituálu. Specifické pohyby, roztahování ocasních per a zvedání křídel, které zdůrazňuje dominanci kohoutků, doprovází zpěv složený z několika různých signálů (Cramp, 1983). Ty hrají roli v komunikaci jak mezi jedinci stejného pohlaví, tak opačného (Tibbetts and Dale, 2007; Bradbury and Vehrencamp, 2011). Charakteristické jsou dva hlavní hlasy, pšoukání a bublání, které jsou nejčastěji slyšet z lesů a vřesovišť, a to i na velké vzdálenosti. Díky tomu se na tokaniště slétá více kohoutků, kteří chtějí soupeřit o nejlepší místo leku, i slepiček, které si vyhlíží toho nejlepšího partnera k páření (Hovi et al., 1997).

V posledních letech však přibývá tokanišť, na kterých své souboje a zpěv předvádí stále méně kohoutků. Zaznamenáváme nárůst solitérního lekování, kohoutci se drží více v krytu vegetace a je obtížné je vysledovat, někteří jedinci se pak neozývají vůbec (Zeitler, 2000; Svobodová et al., 2011b; Chamberlain et al., 2012). Tento trend je alarmující a stojí za ním pokles početnosti populací a izolace jednotlivých skupinek tetřívků (Storch, 2000; Caizergues et al., 2001; Segelbacher et al., 2003; White et al., 2013). K tomu dochází v důsledku mnoha faktorů: od ztráty přirozeného prostředí, přes predaci vajíček i dospělců, až po změnu klimatu a disturbanci lidskými aktivitami.

Tetřívek obecný vyžaduje pro život klidná otevřená stanoviště s bohatým bylinným a keřovým patrem, která volně navazují na hustší porost sloužící jako úkryt před predátory (Rolstad et al., 2009; White et al., 2015; Cukor et al., 2022). Odklon od tzv. extenzivního hospodaření však způsobil zarůstání volných ploch a odvodnění mokřadů drasticky změnilo složení vegetace (Doenecke and Niethammer, 1970; Loneux and Ruwet, 1997; MacDonald et al., 2000; Storch, 2007; Northrup et al., 2013). Důsledkem je nejen úbytek vhodných tokanišť, ale i omezení dostupnosti potravy, což má dopad na reprodukční úspěšnost druhu. Člověk si stále více ukrajuje z přírody pro své stavby a rekreační vyžití a ruší tetřívky v důležitých obdobích jejich života (Ingold, 2005; Zeiler and Grünschachner-Berger, 2009; Storch, 2013). Měnící se podnebí má za následek neobvyklé podmínky pro vylíhnutá kuřátka, ale i pro dospělce v zimním období, kdy místo klidného odpočinku ve sněhových závějích obtížně shánějí obživu. To vše je činí zranitelnějšími pro predátory a náchylnější k nemocem (Prellwitz, 2002; Ludwig et al., 2006; Bocca et al., 2014; Canonne et al., 2021).

Ačkoli je tetřívek obecný celosvětově zařazen do skupiny druhů označené „nejmenší obavy“ (BirdLife International, 2022), je nezbytné věnovat pozornost trendům jednotlivých populací, příčinám, které vedou k poklesu jejich počtů, a podpořit snahy o zachování vhodného prostředí pro tento druh. Monitoring populace patří mezi klíčové strategie péče o ohrožené druhy (Goldsmith, 2012). Přesnost výsledků sčítání je zásadní, zvláště jedná-li se o roztříštěné populace, jaké pozorujeme u tetřívka obecného. Akustická individualita, tedy schopnost rozeznat jedince na základě jejich zvukového projevu, by mohla hrát významnou roli při takovémto monitoringu. Použití akustických senzorů a analýzy zvukových záznamů umožňuje kontinuální sledování i v těžko přístupných oblastech, čímž se zvyšuje přesnost dat a zlepšuje ochrana druhu. Taková metoda není ohrožena chybami v důsledku vizuálního sčítání a může poskytnout cenné informace i v těžko přístupných a nepřehledných lokalitách, kde hustý porost znemožňuje přímé sledování jedinců.

2. Cíle práce

I. Provést rozbor dostupných zdrojů na téma populační dynamika tetřívka obecného, důvody poklesu početnosti populace tetřívka obecného, možnosti ochranných opatření v rámci lesnictví a myslivosti

Tetřívek obecný je vzácným druhem řádu hrabavých a na většině lokalit jeho výskytu se projevuje snaha o zachování a dlouhodobou podporu jeho populace. Ačkoli není celosvětově zařazen mezi ohrožené druhy, dochází v mnoha státech Evropy k významnému a znepokojivému poklesu jeho početnosti. Údaje o vývojových trendech však nejsou sjednocené, proto bylo snahou první části této práce sumarizovat dostupná data týkající se tetřívka obecného napříč areálem jeho výskytu se zaměřením na hlavní důvody poklesu početnosti. Spolu s doporučením konkrétních vhodných postupů pro ochranu tetřívka mohou výstupy této práce významně pomoci při vytvoření účinného plánu pro podporu jeho populace jak na lokální, tak i mezinárodní úrovni.

II. Analyzovat akustické projevy kohoutků tetřívka obecného se zaměřením na individualitu v hlase jedinců

a

III. Identifikovat individuálně specifické parametry v hlasech kohoutků tetřívka obecného

Pšoukání (hissing call) je řazeno mezi tzv. nevokální akustické signály, jelikož není vyluzováno pomocí zpěvného ústrojí syringu. I přesto však překvapivě může být nositelem akustické variability, která je často klíčová během různých interakcí jedinců. U tetřívka obecného se jedná konkrétně o setkávání protivníků na tokaništích v období páření a výběr partnerů k páření prováděný slepičkami. Akustická individualita může navíc sloužit jako efektivní podklad během monitoringu tetřívka obecného. Zejména na nepřehledných lokalitách by metoda založená na analýze hlasového projevu tetřívků mohla významně snížit riziko potenciální chybovosti při sčítání jedinců.

IV. Analyzovat akustické projevy kohoutků tetřívka obecného se zaměřením na geografickou variabilitu na úrovni populací v České republice a zahraničí

Tetřívek obecný má poměrně rozsáhlý areál výskytu, proto je pravděpodobné, že se u jednotlivých subpopulací mohou projevovat geografické odlišnosti v jeho akustickém projevu. V současné době, kdy jsou jedním z hlavních ohrožujících faktorů populace její fragmentace a následné izolování jednotlivých skupinek, může být důkladná znalost původu jedinců klíčová pro zajištění dlouhodobé stability a opětovného růstu početnosti tetřívků. V rámci plánované reintrodukce by pak mohlo být účinně předcházeno nebo naopak cíleně podpořeno vysazování jedinců z různých oblastí, jelikož akustický projev je významnou součástí reprodukčního procesu tetřívka obecného.

3. Literární rešerše

3.1 Populace tetřívka obecného

Evropská populace tetřívka obecného je odhadována na 2.45 – 4.08 milionů dospělých jedinců (BirdLife International, 2022; IUCN, 2023). Tyto počty zahrnují populace nacházející se od Fenoskandie po Alpy a od Velké Británie po Severní Koreu (Perrins, 1978; BirdLife International, 2022), a konkrétní údaje jednotlivých oblastí se liší stát od státu.

3.1.1 Tetřívek obecný v České republice – historie a současnost

Tetřívek jako druh obývající území České republiky je v literatuře zmiňován v roce 1884 (Černý, 1884) a podle statistických údajů zde byla jeho populace na vrcholu pravděpodobně kolem roku 1910 (Sekera, 1938). V letech 1933 – 1935 bylo odloveno v průměru 6182 kusů a ještě v roce 1950 se tetřívek nacházel téměř na celé rozloze České republiky (Kostroň, 1953; Hudec et al., 1966). V následujících desetiletích zaznamenala česká populace dynamický vývoj, kdy klesající trend krátkodobě několikrát převážil lokální nárůst početnosti např. v souvislosti se vznikem velkých ploch bezlesí po mniškové kalamitě v 50. letech 20. století a imisemi vzniklými holinami v letech sedmdesátých (Komárek, 1945; Hanuš et al., 1979; Šťastný et al., 1987, 1997; Flousek and Gramsz, 1999). Celkový pokles populace však již zvrácen nebyl a tetřívek obecný byl v českém Červeném seznamu zařazen do kategorie ohrožené druhy s kritériem C1 (Chobot and Němec, 2017). Druh, jenž se v minulosti počítal na tisíce, se na začátku nového tisíciletí propadl na počty kolem 710 kusů (Hora et al., 2018).

V současnosti se většina zbytkových populací nachází na lokalitách pohraničních pohoří (Jizerské hory, Krkonoše, Novodomské rašeliniště – Kovářská, Šumava, Východní Krušné hory) a v řádech jednotek je tetřívek obecný monitorován v nižších polohách na územích vojenských újezdů Boletice a Doupovské hory), které si díky vojenským aktivitám udržely ráz své krajiny, jenž tetřívkovi vyhovuje (Hora et al., 2018). Ještě v roce 2019 byl tetřívek zaznamenán také na Libavé, odkud však poté vymizel. Klesající trend početnosti, který konkrétně v letech 2000 - 2011 zaznamenal snížení hodnot o třetinu, pokračuje i v současnosti. Záznamy, které vede Ústav pro hospodářskou úpravu lesa pro území České republiky mimo národní parky a vojenských prostorů, udávají počet 388 jedinců tetřívka obecného v roce 2022, Český statistický úřad pak pro sezónu 2023 – 2024 uvádí celkem 436 tetřívků (Český statistický úřad, 2024).

3.1.2 Tetřívek obecný ve světě

Areál výskytu tetřívka obecného je poměrně rozsáhlý. Tetřívky lze nalézt od Albánie přes země severní a střední Evropy, Ruskou federaci, až po Spojené Království Velké Británie na západě a Severní Koreu na východě. Tetřívek byl také introdukován v Kanadě a Spojených Státech Amerických. Celkové početní odhady tohoto druhu se pohybují v rozmezí 8 – 14 milionů dospělých jedinců, přičemž pro Evropskou populaci je uváděno 2,45 – 4,08 milionů dospělců (BirdLife International, 2022) a z toho 0,79 – 1,03 milionů lekujících kohoutků (European Environment Agency, 2023). Populační trend vykazuje klesání, avšak vývoj není ve všech zemích stejný. Zatímco v oblasti Fenoskandie je jeho populace více méně stabilní, ve státech západní, střední a východní Evropy je tetřívek považován za ohrožený druh a v některých zemích je již považován za vyhynulý (Danko et al., 2002; Sim et al., 2008; Elts et al., 2013; Ķerus et al., 2021; Statistisk Sentralbyra, 2022; European Environment Agency, 2023; Statistics Austria. Federal Institution under Public Law, 2023; Statistics Finland, 2023; Svenska Jägareförbundet, 2023; The Forest Management Institute Brandýs nad Labem, 2024).

3.2 Důvody poklesu populace tetřívka obecného napříč areálem rozšíření

3.2.1 Ztráta habitatu a změna vegetační struktury

Faktory, které negativně ovlivňují vývoj početnosti, se liší napříč výskytem tetřívka obecného a působí jak na úrovni populací, tak lokálně na izolované skupinky jedinců. Jedním z nejčastějších důvodů poklesu početnosti je ztráta habitatu (Doenecke and Niethammer, 1970; Loneux and Ruwet, 1997; Ludwig et al., 2009a; Gimmi et al., 2011; Strauß et al., 2018). Tetřívkům vyhovují stanoviště, na kterých převládají otevřené plochy s bohatým bylinným patrem, které volně navazují na křoviny a lesíky poskytující úkryt před predátory (e.g. Scherzinger, 1976; Koch, 1978; Müller, 1979; Porkert, 1982; Klaus, 1991; Baines, 1994; Calladine et al., 2002; Baines et al., 2007; Wegge and Kastdalen, 2008; Ludwig et al., 2008; Patthey et al., 2012; Immitzer et al., 2014; Nelli et al., 2016; Tost et al., 2022). Takový biotop byl v minulosti udržován prostřednictvím extenzivního hospodaření, kdy díky pasení dobytka nedocházelo k zarůstání luk a pastvin (Doenecke and Niethammer, 1970; Loneux and Ruwet, 1997; MacDonald et al., 2000; Storch, 2007; Ludwig et al., 2009b; Northrup et al., 2013; Lešo et al., 2023). Sukcesní stadia porostů, jejichž složení je obvykle hospodářsky směřováno k monokulturám, tetřívkům nevyhovuje, jelikož neposkytují dostatečně pestrou potravu (Storch, 2007; Kurhinen et al., 2009; White et al., 2013; Roos et al., 2016; Tost et al., 2022). Tetřívci v minulosti obývaly také zemědělskou krajinu v okolí lidských obydlí, přechod k velkoplošnému hospodaření s intenzivním zapojením prostředků na ochranu rostlin však vedl k jejich odsunutí do horských oblastí (Angelstam et al., 2000; Kurki et al., 2000). Zalesňování cílené na monokulturní porosty, intenzifikace zemědělství a umělé vysoušení mokřadů jsou nejčastější procesy vedoucí ke změnám vegetační struktury, s níž souvisí i složení živočišných druhů, konkrétně hmyzu, který je zejména pro první týdny života tetřívků nepostradatelný (Helminen and Viramo, 1962; Hudec and Šťastný, 2005; Červený, 2009).

3.2.2 Hnízdní úspěšnost a mortalita jedinců

Zdárná reprodukce tetřívka je ohrožena sníženou úspěšností hnízdění a narůstající mortalitou jak kuřat, tak dospělých jedinců (Spidsø et al., 1997; Storch, 2000, 2007; Merta et al., 2009; Pekkola et al., 2014; Viterbi et al., 2015; Jahren et al., 2016; Cukor et al., 2021), a následná struktura populace zpětně ovlivňuje reprodukční procesy, kdy může dojít k vymizení lekování a neúspěchům v páření (Höglund and Stohr, 1997; Geary et al., 2012; Nelli et al., 2016). Pokles počtu úspěšně vyvedených hnízd byl pozorován ve Fenoskandii a střední Evropě (Jahren et al., 2016) a studie byla provedena také ve Švýcarsku, kde byl zjištěn dlouhodobý průměr 2 kuřátka na slepičku (Zbinden et al., 2022). Toto číslo není vysoké vzhledem k tomu, že snůška tetřívka obecného obvykle činí alespoň 6 vajíček (Červený, 2009). Následné vyvedení mláďat je ovlivněno potravní nabídkou, jelikož pro kuřátka je v prvních týdnech života klíčová živočišná složka a její nedostatek může zvýšit mortalitu jedinců (Ludwig et al., 2010; Wegge et al., 2022). Kondice mladých jedinců a jejich přežití závisí také na příznivosti povětrnostních podmínek; náhlé změny teplot nebo dešťové či sněhové srážky mají negativní dopad zejména v období po vylíhnutí (Viterbi et al., 2015; Rotelli et al., 2021).

Od snesení vajíček po dospělý život ohrožuje tetřívky predace. Slepičky hnízdí na zemi, snůšky jsou tedy ohroženy mnoha predátory, a to již v prvních dnech po založení hnízda (Merta et al., 2009). Mezi hlavní druhy predátorů patří kuny, lišky a krkavcovití, ale také prase divoké, ačkoli pro většinu z nich jsou vajíčka pouze alternativní kořistí v případě, že nemají k dispozici dostatek jiné potravy (Šálek et al., 2004; Svobodová et al., 2004; Cukor et al., 2021). Velmi častým predátorem ve Walesu a ve Finsku je jestřáb lesní (Charnov et al., 1976; Widen et al., 1987; Korpimaki et al., 1996; Tornberg et al., 2013), ve Skotsku pak nejvíce tetřívkům škodí vrány a lišky (Summers et al., 2004). Predace je hlavním důvodem mortality mladých tetřívků zejména v jejich prvním roce života (Hannon and Martin, 2006; Park et al., 2008) s nejkritičtějším prvním měsícem po vylíhnutí (Johnstone and Lindley, 2003), ohrožuje však i dospělé jedince (Tornberg et al., 2006; Pekkola et al., 2014), jejichž mortalita následně ovlivňuje reprodukční proces (Summers et al., 2004).

Vliv na dynamiku tetřívčí populace mohou mít také onemocnění včetně parazitických (Isomursu et al., 2017), která způsobují zvýšené hladiny stresových hormonů a snižují odolnost organismu vůči dalším činitelům (Berto and Lopes, 2020). Konkrétní skupiny parazitů u tetřívka obecného jsou kokcidie (genus *Eimera*), hlístice (*Trichostrongylus tenuis*, *Capillaria caudinflata*, *Syngamus trachea*), tasemnice (*Hymenolepis* spp.), roztoči (*Pterolichus obtusus*) a ploštěnci (e.g. Jankovska et al., 2012; Tizzani et al., 2021; Sokól and Pluta, 2022; Strauß et al., 2022).

3.2.3 Změna klimatu

Měnící se klimatické podmínky, které sebou stále častěji nesou nepředvídatelné a náhle změny počasí, se nevyhýbají ani populaci tetřívka obecného. Zvyšování teplot může způsobit posun období páření, a ne vždy je výsledek pozitivní, jako v jižním Norsku, kde se díky němu úspěšnost reprodukce celkově zvýšila (Wegge and Rolstad, 2017). Právě na datum snůšky, úspěšnost páření, přežití kuřátek, ale i na velikost tetřívčí populace mohou mít neobvyklé povětrností podmínky škodlivý dopad (Prellwitz, 2002; Ludwig et al., 2006; Bocca et al., 2014; European Commission et al., 2020; Canonne et al., 2021).

Pro tetřívka, jenž přežívá kruté zimy díky vyhloubeným dutinám v silné sněhové pokrývce, je nedostatek sněhu nebo vytváření ledové krusty, znemožňující odpočinek a úkryt, faktorem vedoucím k jeho úbytkům (Marjakangas, 1992; Bocca et al., 2014; Canonne et al., 2021). Ty souvisejí také s větší početností predátorů v důsledku kratších a mírnějších zimních období (Bartoń and Zalewski, 2007). Silné deště, návrat zimního počasí nebo rychlé teplotní změny v období hnízdění a vyvádění kuřátek se také podílejí na snižování početnosti tetřívků (Ludwig et al., 2006, 2010; Viterbi et al., 2015). Nepřízeň podnebí mohou jedinci zažívat také během léta, kdy vysoké teploty snižují ostražitost ptáků, jelikož věnují více energie na ochlazení organismu, a zejména kuřátka mohou trpět dehydratací (Prellwitz, 2002).

3.2.4 Lidské aktivity

Narušování života tetřevovitých lidskými rekreačními, turistickými, ale také průmyslovými aktivitami se stává velkou překážkou ve snaze chránit jejich populace (Storch, 2013). Disturbance mohou mít krátkodobé následky, které ovlivňují chování jedinců v daném období, ale také způsobují dlouhodobé změny ve využití životního prostředí, pokles úspěšnosti reprodukčního procesu a snižování početnosti populací (Ingold, 2005). Této problematice je přisuzován význam poměrně krátkou dobu. Výzkum se soustředí na vyhodnocení rozdílů ve využití prostředí tetřevovitými v oblastech s různou intenzitou lidské přítomnosti a experimentální studie modelující interakce s lidmi s následnou analýzou fyziologických a behaviorálních reakcí zvěře. Významnými tématy studií jsou předávání vědomostí, anti-predační chování, adaptace na události podstatně zasahující do života lesních kurů, jakými je např. lov, či hladina stresových hormonů v organismech tetřevovitých (Thiel et al., 2008, 2011; Formenti et al., 2012; Storch, 2013).

Často skloňovanou problematikou v souvislosti s tetřívčími lokalitami je výstavba větrných elektráren. Dva roky po konstrukci těchto staveb v Rakouských Alpách byl zaznamenán pokles lekujících kohoutků tetřívka obecného z 12 jedinců na nulu (Zeiler and Grünschachner-Berger, 2009), podobná situace nastala také ve Skotsku, kde po stejné dlouhé době monitorovali pouze čtyři slepičky a žádného lekujícího kohoutka (Percival et al., 2018). V jiné Skotské oblasti došlo k posunutí tokanišť dále od větrných farem (Zwart et al., 2015). Vliv těchto staveb na distribuci a početnost tetřívků je nepopiratelný, zjištěny byly i případy úmrtí jedinců pravděpodobně po nárazu do věží elektráren (Wöss and Zeiler, 2003; Zeiler and Grünschachner-Berger, 2009; Coppes et al., 2020).

Podoba a složení krajin je často formováno lidskou činností. Odklon od extenzivního hospodaření vedl k zalesňování lokalit, vysoušení mokřadů zcela změnilo vegetační strukturu daných stanovišť, intenzifikace zemědělství drasticky snižuje biodiverzitu polí, luk a jejich okolí. Mezi další významné změny v přírodě patří zakládání lyžařských areálů, které poškozují horská prostředí a ruší zvěř (Patthey et al., 2012; Storch, 2013). Outdoorové aktivity, mezi něž patří lyžování, cyklistika, pěší turistika, ale také fotografování nebo sběr plodů mohou vést ke zvýšeným energetickým výdajům a hladinám stresových hormonů a tím k oslabení kondice tetřívků vedoucí i k jejich úmrtí (Storch, 2000, 2013; Baltić et al., 2004; Ingold, 2005; Arlettaz et al., 2007, 2013; Immitzer et al., 2014; Formenti et al., 2015; Rutkowski et al., 2018; Tost et al., 2020; Adamowicz et al., 2023). Vyrušení jedinci opouštějí svá stanoviště, kohoutci mohou přecházet k solitérnímu toku, v horších případech přestanou lekovat úplně, po vyplašení mohou tetřívci narazit do lesnických oplocenek i dalších překážek (Zeitler, 2000; Baines and Andrew, 2003). V době, kdy stoupá obliba rekreace ve volné přírodě, je potřeba chránit populace tetřívků před vyrušováním a předcházet tak negativním dopadům vedoucím k poklesu početnosti.

3.3 Potrava a biotop tetřívka obecného

Tetřívek obecný vyžaduje pro svůj život a úspěšný vývoj populace specifické podmínky prostředí a je velmi citlivý na jejich změny (Rolstad et al., 2009). Ideální lokalita má podobu mozaiky ploch, na kterých se střídá nízký bylinný porost s křovinami a lesíky, poskytující pestrou škálu potravních zdrojů. Rostlinná strava, která začíná u tetřívků převládat přibližně po třetím týdnu života, zahrnuje jehličí, pupeny, výhonky, listy či nevyvinuté šišky dřevin (smrk, modřín, borovice, bříza, jeřáb, olše, vrba), dále kočičky a jehnědy břízy, olše, topolu či vrby, vegetativní a generativní části bylin a keřů (trávy, šťovík a další), bobule, plody, semena, bukvice a žaludy, přičemž složení se mění dle sezóny (Hudec and Černý, 1977; Stubbe, 1987). Z živočišné složky, která je zásadní především pro kuřátka v prvních týdnech života, vyhledávají tetřívci na jaře zejména brouky a mravence, na podzim se v jejich potravě objevují v malé míře měkkýši, pavouci a další hmyz (Helminen and Viramo, 1962; Ivanter, 1963; Červený, 2009). Složení potravy se může jednotlivých stanovištích různě lišit (Baines et al., 1996), přičemž Patthey et al. (2012) uvádí, že vhodnou lokalitu lze indikovat na základě přítomnosti kobylek a mravenců.

V ideálním případě je centrem tetřívčího stanoviště otevřená plocha, která slouží kohoutkům v době reprodukce jako tokaniště. Na tuto plochu volně navazuje pásmo keřů a solitérních stromů, sloužících k hřadování, které následně přechází do stále více zapojeného lesního porostu s bohatým podrostem křovinného a bylinného patra. Tato struktura poskytuje tetřívkům klid na tokaništích a zároveň dostatek zdrojů potravy a úkrytu před predátory (Cukor et al., 2022). Volné plochy využívají také slepičky, které si zde vybírají partnery a následně hnízdí zpravidla v okruhu 0,5 km od tokanišť (Warren and Baines, 2002), kde je dostatečně hustý porost chránící vylíhlá kuřátka před predátory (Cukor et al., 2022). Jednotlivá stanoviště, která jsou vhodně propojená biokoridory, pak vytvářejí biotop, který poskytuje tetřívkům podmínky zajišťující prosperující život (Ludwig et al., 2009b; Rolstad et al., 2009; White et al., 2015; Cukor et al., 2022).

V České republice se tetřívek nejčastěji vyskytuje na lokalitách, kde se střídají listnaté a smíšené lesy s pasekami, loukami a mlazinami, rašeliništi a vřesovišti. Zde hledá potravu v podobě bobulovitých a oříškových plodů, obilek a semínek, pupenů, mladých listů a letorostů. Z živočišné složky, důležité především pro kuřátka v prvních týdnech života, vybírají tetřívci zejména vývojová stadia brouků, plže, žížaly a další bezobratlé (Červený, 2009). Populace Velké Británie dává přednost vřesovištím s navazujícími lesy, přičemž dle studie kohoutci preferují lesy listnaté, zatímco slepičky obývají okrajové části původních borových, případně hospodářských jehličnatých lesů (White et al., 2015). Charakter prostředí se velmi dobře odráží ve velikosti domovských okrsků; v České republice se jejich výměra pohybuje mezi 71,0 – 276,5 ha v závislosti na ročním období (Svobodová et al., 2011a), ve Švýcarsku v oblasti subalpínského lesa stanovili rozmezí 4,0 – 80,0 ha s odlišnostmi mezi pohlavími tetřívků a mezi slepičkami dle úspěšnosti vyvedení kuřátek (Patthey et al., 2012).

3.4 Reprodukční proces tetřívka obecného

Vhodné podmínky prostředí podporují úspěšnou reprodukci, na níž stojí stabilita populace. Výsledek reprodukčního procesu však významně ovlivňuje samotný průběh páření (Jahren et al., 2016). Tetřívek obecný je polygamním druhem a páření u něj probíhá prostřednictvím lekování. Tato aktivita zahrnuje setkání dvou a více kohoutků na tokaništi, kde od dubna do května předvádí namlouvací tanec. Ten je doprovázen akustickým projevem a spolu se vzájemnými souboji tak kohoutci bojují o možnost spářit se se slepičkami (Červený, 2009), přičemž v jejich přítomnosti omezují repertoár chování na vzájemné souboje a namlouvací tanec doprovázený akustickým projevem zvaným bublání (Höglund et al., 1997). Bublání (rookooing) připomíná vrkání hrdličky a během toku má velký význam, jelikož je slyšet na velké vzdálenosti a díky tomu se na tokaniště slétá více kohoutků a následně i slepiček (Hovi et al., 1997). Za tokaniště slouží obvykle louky, mýtiny a paseky se solitérními stromy, bezlesá cvičiště ve vojenských újezdech, holé plochy na vřesovištích a rašeliništích, případně pole či zamrzlá jezera (Koivisto, 1965; Alatalo et al., 1991; Červený, 2009; Rolstad et al., 2009).

Lekování ovšem neprobíhá na všech tokaništích. Stále častěji se objevují populace, v nichž tetřívci nevytvářejí společné leky a kohoutci se vystavují samostatně. Takové případy byly sledovány například ve Švédsku, Itálii, Německu a Česku (Höglund and Stohr, 1997; Zeitler, 2000; Angelstam, 2004; Svobodová et al., 2011b; Chamberlain et al., 2012; Rutkowski et al., 2018). Příčinou tohoto chování je disturbance během období reprodukce, pokles efektivní velikosti populace, či v ojedinělých případech nárůst početnosti dominantních kohoutků na tokaništi, vedoucí k oddělení slabších jedinců, kteří následně tokají solitérně (Zeitler, 2000; Svobodová et al., 2011b; Chamberlain et al., 2012). Populace s nelekujícími kohoutky následně trpí sníženou genetickou variabilitou, která vede k dalšímu poklesu početnosti (Svobodová et al., 2011b).

Výběr partnerů provádějí slepičky na základě morfologických, behaviorálních a prostorových charakteristik (Alatalo et al., 1992; Höglund et al., 1997; Kokko et al., 1998; Rintamäki et al., 2001). Vitalita samotných slepiček přitom může výběr ovlivnit; ty, které mají dobrou fyzickou kondici, navštěvují více tokanišť a páří se s těmi nejlepšími samečky (Rintamäki et al., 1998). Pokud mají možnost, navštěvují slepičky větší tokaniště, na kterých se nachází více kohoutků, z nichž preferují ty dominantní, obhajující větší teritoria blíže středu, a nejvíce bojovné (Kervinen et al., 2012; Lebigre et al., 2013). Tím je zajištěno, že pouze několik samců má možnost se pářit (Höglund and Alatalo, 1955; Rintamäki et al., 1995; Lebigre et al., 2007). Ve výběru partnera pak hraje roli atraktivita související s jejich fyzickou kondicí a schopností krátkodobě během doby páření, ale také dlouhodobě v následujících letech si udržet pozici na tokaništi (Alatalo et al., 1991; Rintamäki et al., 1995; Kokko et al., 1998; Kervinen et al., 2012), přičemž starší slepičky mají tendenci pářit se stejným jedincem jako v minulých letech, i když samec již není nejvitálnější (Rintamäki et al., 1995). Při soubojích mimo další zranění dochází také k vytrhávání peří z podtatrčí, které vypovídá o šikovnosti kohoutků a podílí se na jejich přitažlivosti (Alatalo et al., 1991) podobně jako velikost poušek (Rintamäki et al., 2000) či skvrny na bílém peří podtatrčí (Soulsbury et al., 2016).

Následný výběr stanoviště pro hnízdění hraje významnou roli a souvisí jednak s fidelitou samiček, jednak s povahou prostředí (Ludwig et al., 2010; Warren et al., 2012). Například na severu Anglie preferují slepičky lokality s vyšší a hustší vegetací (Warren et al., 2012), zatímco v nejsevernějších oblastech Skotska upřednostňují stanoviště v porostech vřesu (PARR and WATSON, 1988) a ve Švédsku pak lesní houštiny (Brittas and Willebrand, 1991). Mladší slepičky snášejí méně vajec, zahajují inkubaci později a mají nižší úspěšnost při vychovávání potomků, což je mimo jiné způsobeno jejich vyšší mortalitou (Caizergues and Ellison, 2000). V případě ztráty první snůšky vyhledají slepičky sekundární stanoviště ve větší vzdálenosti od původního (Marjakangas et al., 1997). V mělkém hnízdě ukrytém ve vegetaci snáší slepičky 6 – 12 vajíček, z nichž se kuřátka líhnou po 24 – 27 dnech (Červený, 2009). Již druhý den jsou schopná hledat si potravu a během dvou týdnů se naučí létat na větší vzdálenosti (Červený, 2009). Sociální chování se vyvíjí od hravých forem interakcí po stupňující se agresivní jednání, kdy si jedinci pomocí soubojů utvářejí hierarchii v rámci svých skupin pro obhajobu popelišť a pastevních míst (Gwinnerhanke, 1991). Pohlavní dospělosti dosahují tetřívci ve dvou letech. Kromě období páření se jedinci shlukují do smíšených skupin (Červený, 2009; Ciach et al., 2010).

3.5 Zpěvné ústrojí a akustické signály tetřívků

Vokální signály zprostředkovává zpěvné ústrojí syrinx, jehož morfologií se zabývá několik studií (Greenewalt, 1968; Stein, 1968; King and McLelland, 1984), v rámci řádu Galliformes se však jeho výzkum soustřeďuje na vzorový druh, jímž je kur domácí (*Gallus gallus*) (Gaunt et al., 1976; Gaunt and Gaunt, 1977; Araya-Salas et al., 2019). Výzkum byl proveden také u koroptve polní (*Perdix perdix*) a tetřívka pelyňkového (*Centrocercus urophasianus*), u nějž byl odhalen tzv. dvou-hvizd, odlišnosti v morfologii syringu mezi pohlavími a také odchylky oproti kuru domácímu (Beani et al., 1995; Krakauer et al., 2009). Zpěvné ústrojí tetřívka obecného nebylo doposud z hlediska morfologie zkoumáno.

První zvukové signály, které se objevují u kuřátek, jsou děleny do dvou typů, a to čisté tóny, kam patří hlasy stoupající, klesající, trylek, hlas bědování a naříkání, a bohatší přechodné tóny. S postupem času a přibýváním váhy klesá frekvenční rozsah těchto signálů z rozmezí 3,5 – 4 kHz až k hodnotám těsně nad 2 kHz, přičemž právě díky změnám přechodných tónů hlasu v rámci fyzického vývoje se u kuřátek projevuje intra i inter-individualita v rámci jedinců (Meinert and Bergmann, 1983). Mladí jedinci dále projevují zvuky při hledání matky, když se ztratí, když jsou spokojení a během spánku, dospělé slepičky se ozývají kokrhavým zvoláním, zvuky doprovázejícími let a další signály sloužící k interakci s kuřátky, dalšími jedinci nebo jako varování (Cramp, 1983).

Akustický projev, jenž je součástí reprodukčního chování dospělých kohoutků, se skládá ze čtyř základních druhů signálů (Cramp, 1983). Patří mezi ně rezonanční bublání, zvuky agrese, varovná zvolání a syčivé signály (hissing call), které se dále dělí na kvílivé syčení (pšoukání), poměrně dlouhé syčivé volání, sykot doprovázející let a nerytmický sykot vyluzovaný během soubojů (Cramp, 1983). Tyto syčivé zvuky patří mezi tzv. nevokální signály, jelikož nejsou vyluzovány prostřednictvím syringu, nýbrž zúženími, kterými prochází vzduch z plic do zobáku (Fitch and Hauser, 2001). Spolu s bubláním patří pšoukání k nejvýraznějším akustickým projevům tetřívků, jelikož jsou slyšet na velké vzdálenosti a překonají i hustý porost zapojených lesů či křovin. Bublání lze popsat jako opakující se signál o nízkých frekvencích s hodnotami v rozmezí 200 – 1000 kHz, který se právě díky tomuto rozsahu často překrývá s hlukem v pozadí. Oproti tomu pšoukání dosahuje frekvencí 350 – 4500 kHz, což umožňuje odfiltrování rušivého hluku a snadnější měření pomocí akustických softwarů (Hambálková et al., 2021).

3.6 Akustická individualita v hlase kohoutků

Akustický projev je prvkem sloužícím mimo jiné při rozpoznávání interagujících jedinců a jako takový je nositelem individuální identity (Tibbetts and Dale, 2007; Bradbury and Vehrencamp, 2011; Linhart et al., 2019). Tato individualita je kódována v konkrétních parametrech měřících frekvenční a časové údaje signálu a jeho intenzitu. Jedinečnost akustického projevu byla prokázána např. u severoafrického dropa obojkového (*Chlamydotis undulata undulata*) zejména v rozmezí frekvenčních hodnot, které však v rámci jedinců nezůstávaly během jedné sezony konstantní (Cornec et al., 2014). Časové parametry se jako potenciální nositel akustické individuality projevily u křepelky japonské (*Coturnix coturnix japonica*) (Sezer and Tekelioglu, 2010). Podle studie ze Švýcarska se jeřábek lesní (*Bonasa bonasia*) projevuje během toku 6 až 11 elementy vokalizace vyznačující se individualitou, která zůstává stabilní déle než jedno období/sezónu (Mulhauser and Zimmermann, 2003). U křepelky polní byla odhalena individualita v projevech používaných během utváření partnerských párů. U kohoutka se jedná konkrétně o specifity vrčivého vibrata, druhou slabiku signálu a nejvyššího energetického komponentu základního projevu, u slepiček pak individualitu projevují parametry svolávacího signálu, a to frekvence maximální amplitudy ve druhé sloce svolávání, interval mezi body nejnižší frekvence a interval mezi první a druhou slabikou (Guyomarc'h et al., 1998). Pravděpodobná individualita se projevuje také v poplachovém zvolání samců orebice rudé (*Alectoris rufa*), kteří v přítomnosti svých partnerek snižují frekvenci signálu za účelem snížení rizika predace (Morton, 1975; Zaccaroni et al., 2013). Potenciál individuality mají také nevokální zvuky vydávané např. pohyby těla během projevů na tokaništi, jak bylo zjištěno u tetřívka pelyňkového (*Centrocercus urophasianus),* u nějž se projevili odlišnosti mezi jedinci v šustění vydávané tlukotem křídel (Koch et al., 2015).

3.7 Geografická variabilita v akustickém projevu kohoutků

Variabilita akustického projevu ptáků na úrovni populací vzniká z různých důvodů. Jedním z nich je různorodost konkrétních habitatů, ve kterém se jednotlivé skupiny ptáků nacházejí, a které utvářejí podobu produkovaných signálů (Luttrell and Lohr, 2018; Salinas-Melgoza and Renton, 2021). Dalším činitelem může být segregace skupin na velké vzdálenosti, lišící se morfologické znaky či celkový vliv životního prostředí a přispět může také pohlaví nebo sociální výběr (Yandell et al., 2018; Kirschel et al., 2019). K variabilitě může docházet i procesem vytěsňování znaků akustických projevů prostřednictvím hybridizace nebo konkurence, případně naopak jejich sjednocováním podporujícím klidné soužití jedinců (Kirschel et al., 2019). Mohou však nastat také případy, kdy se geografická variabilita neprojevuje (Wright, 1996; Baker, 2000; Bradbury et al., 2001; Guerra et al., 2008). Areál rozšíření tetřívka obecného je poměrně rozsáhlý a v důsledku mnoha faktorů v něm vznikají fragmentované a izolované populace (Storch, 2000; Caizergues et al., 2001; Segelbacher et al., 2003; White et al., 2013) což vytváří situaci, jež by mohla vést ke vzniku odlišností mimo jiné v akustickém projevu jedinců.

Tématu geografické variability v akustickém projevu ptáků se věnují studie jak u druhů, u nichž je zpěv výsledkem učení (Langin et al., 2017; Luttrell and Lohr, 2018; Sementili-Cardoso et al., 2018; Yandell et al., 2018; Araya-Salas et al., 2019; Kirschel et al., 2019), tak u druhů s vrozenou vokalizací, mezi něž patří řády Gruiformes, Psittaciformes a Sphenisciformes (Budka and Osiejuk, 2017; Lynch and Lynch, 2017; Wright and Dahlin, 2018; Salinas-Melgoza and Renton, 2021). Ačkoli byly u hrabavých zaznamenány případy naznačující, že vývoj akustického projevu u této skupiny druhů může být ovlivněn i interakcemi jedinců (Sparling, 1979), převládá názor, že tetřívek obecný nepatří do skupiny ptáků, kteří se vokální signály učí. Syčivé pšoukání tetřívčích kohoutků navíc nelze charakterizovat jako zpěv, jelikož se nejedná o zvuky produkované syringem, avšak vzduchem procházejícím konstrikcemi v dýchacích cestách ptáků. O to více je překvapivé, že i nevokální signály mohou nést prvky individuality jedinců.

4. Metodika

4.1 Vyhledávání zdrojů

Sumarizace dostupných údajů o populačním vývoji tetřívka obecného se zaměřením na faktory ovlivňující jeho početnost probíhala pomocí vyhledávání zdrojů na online webových vyhledávačích Web of Science, Scopus, Google Scholar a ResearchGate, statistické údaje o početnosti, respektive o výši lovu tetřívka obecného byly vyhledány na oficiálních stránkách myslivecké správy daných zemí. Mezi zdroje byly zařazeny články, knihy, sborníky z konferencí, dále internetové zdroje, statistiky a další, datované v rozmezí let 1955 - 2024. Z pramenů byly vyřazeny nerecenzované příspěvky. Zdroje byly rozděleny do kategorií podle toho, zda je možné uvedený negativní dopad na populaci tetřívka obecného snížit či eliminovat prostřednictvím lidského managementu.

4.2 Studijní oblast a sběr dat

Akustická individualita (II.) a geografická variabilita (III.) byla zkoumána na nahrávkách pšoukání, tedy nevokálních signálech kohoutků tetřívka obecného. Pokud není uvedeno jinak, probíhaly postupy stejně pro analýzu akustické individuality a geografické variability. Nahrávání probíhalo vždy v období páření, tedy v měsících dubnu a květnu. V letech 2012 - 2014 bylo uskutečněno nahrávání ve Finsku (II., III.), Rusku a České republice (III.) a v roce 2019 ve Skotsku (II., III.), celkem na šesti lokalitách. Všichni jedinci byli nahráváni ve volné přírodě. Příjezd na tokaniště byl načasován vždy alespoň dvě hodiny před východem slunce, respektive před sletem kohoutků a zahájením toku, a nahrávání probíhalo z přenosné zástěny nebo přirozeného úkrytu, aby nedocházelo k vyrušování tetřívků. Nahrávací relace trvaly přibližně hodinu a průměrná vzdálenost od kohoutků byla 10 m. Na každé lokalitě bylo navštíveno více stanovišť s tokaništi, pro účely nahrávání vždy pouze jednou. Relace na daném stanovišti byly vždy zaměřeny na jednoho, maximálně na dva tokající kohoutky, které šlo od sebe jednoznačně vizuálně i akusticky odlišit, aby bylo zabráněno riziku opakovaného nahrání stejného jedince. Vzhledem k silné fidelitě kohoutků vůči svému tokaništi (Borecha et al., 2017) je riziko záznamu stejného jedince na více stanovištích velmi nízké. Akustické záznamy byly pořízeny pomocí audiorekordéru Olympus LP-100 v kombinaci se směrovým mikrofonem Sennheiser ME 66 (fr. odezva 20 Hz–20 kHz ± 2,5 dB), který byl doplněn o napájecí modul K6. Nahrávky byly uloženy ve formátu .wav (vzorkovací frekvence 48 kHz, velikost vzorku 16 bitů).

4.3 Akustické analýzy

Pro akustické analýzy byly z nahrávek vybrány pouze kvalitní záznamy, na kterých se jednotlivé hlasy nepřekrývaly a nebyly rušeny šumem a dalšími zvuky v pozadí. Analýzy byly provedeny v softwaru Raven Pro 1.5. Analyzované signály byly ručně ohraničeny rámcem definovaným začátkem a koncem signálu a jeho nejnižší a nejvyšší frekvencí. Pomocí softwaru byly poté automaticky měřeny frekvenční a časové parametry signálů, které byly následně zpracovány statistickými analýzami. Spektrogramy signálů byly generovány v softwaru Avisoft-SASLab Pro s délkou FFT, velikostí vzorku 1024, Hammingovým oknem, a překryvem 87.5 %.

4.4 Statistické analýzy

4.4.1 Akustická individualita

Do statistického zpracování vstoupilo celkem 426 kvalitních hlasů od 31 jedinců, přičemž každý jedinec byl zastoupen alespoň 10 hlasy. Celkem bylo hodnoceno 29 parametrů. Pro otestování individuální variability byla v programu IBM SPSS Statistics 24.0 provedena diskriminační analýza (DFA) s validací výsledků. Potenciál parametrů pro individuální variabilitu (Potential of Individual Coding) byl testován porovnáním koeficientem variace v rámci jedinců a mezi nimi pomocí vypočtení poměru (Robisson, 1992).

4.4.2 Geografická variabilita

Celkem 853 hlasů od 82 kohoutků ze čtyř zemí vstoupilo do statistické analýzy. Každý jedinec byl zastoupen minimálně pěti hlasy, v průměru pak jedenácti. Po vyloučení parametrů s nulovou nebo velmi nízkou variancí bylo testováno 30 proměnných. Opět byl testován potenciál parametrů pro individuální variabilitu, který odhalil, že všechny proměnné mohou být podrobeny dalším analýzám. Dále byla provedena diskriminační analýza (DFA) a analýza hlavních komponent (PCA).

5. Výsledky

Výsledky se skládají ze tří vědeckých článků, které byly napsány jako prvoautorské, a které byly publikovány v odborných periodikách. První kapitola výsledků pojednává o etologii a aktuálním stavu populace tetřívka obecného od západní a střední Evropy po Fenoskandii, se zaměřením na faktory, které negativně ovlivňují početnost tohoto lesního kura, a s doporučením pro podpůrná opatření v lesnickém a mysliveckém managementu. Druhá část práce je cílena na poznatky o akustické individualitě v hlase kohoutků tetřívka obecného, konkrétně v signálech zvaných pšoukání. Monitoring tetřívka obecného je důležitou součástí jeho ochrany a akustická individualita v hlase jedinců má potenciál podpořit efektivitu metod sčítání. Informace získávané na lokální úrovni je dále potřeba doplňovat o údaje na úrovni globální. Proto se třetí část disertační práce zabývá tématem geografické variability opět v akustických signálech kohoutků tetřívka obecného.

5.1 Stav populace tetřívka obecného (*Lyrurus tetrix*), důvody úbytku a potenciální ochranná opatření od západní a střední Evropy po Fenoskandii: přehled literatury

První kapitola výsledků dle zadaných cílů práce (I.) obsáhla daná témata, která jsou zásadní pro ochranu tetřívka obecného. Na základě rozboru dostupných dat byly informace o populační dynamice a důvodech poklesu početnosti tetřívka obecného sestaveny tak, aby byly přehledné a mohly sloužit jako podklad pro tvorbu strategických opatření na podporu a stabilizaci tetřívčí populace. Výsledky této kapitoly obsahují údaje o výskytu a současných populačních trendech tetřívka obecného v západní, střední a severní Evropě, dále popisují reprodukční proces tetřívků, detailně se zabývají příčinami poklesu jeho početnosti a navrhují opatření, která mohou podpořit snahy o zachování a stabilizaci fragmentovaných a izolovaných tetřívčích populací.

Znalosti životních aktivit tetřívka obecného a vnějších procesů, které do nich zasahují, jsou klíčové pro tvorbu ochranných plánů. Ty mohou na straně jedné cílit na mitigaci zmiňovaných negativních faktorů, ať se již jedná o zpomalení ztráty životního prostředí, omezení lidských aktivit rušících tetřívky v průběhu roku, či o snížení predace, na straně druhé prosazovat kroky vedoucí ke zlepšení životních podmínek tetřívků, od zakládání vhodných lokalit s ideálním složením vegetace, přes potlačení vlivu klimatických změn pomocí stabilizace ekosystémů, po případné reintrodukce jedinců.

Publikováno jako:

Hambalková, L., Cukor, J., Brynychová, K., Ševčík, R., Vacek, Z., Vacek, S., Skoták, V., Andersen, O. 2024. Black grouse (*Lyrurus tetrix*) population status, reasons for decline and potential conservation measures from Western and Central Europe to Fennoscandia: a literature review. Frontiers in Ecology and Evolution. 12:1452317. doi: 10.3389/fevo.2024.1452317

Příspěvek autorů:

Jan Cukor vytvořil koncept studie a navrhl metodiku.
Na správě dat se podíleli Kateřina Brynychová, **Lucie Hambálková** a Richard Ševčík.
Původní návrh vypracovali Kateřina Brynychová, **Lucie Hambálková**, Jan Cukor, Richard Ševčík, Vlastimil Skoták, Stanislav Vacek a Zdeněk Vacek.
Supervizi studie měli na starosti Jan Cukor a Oddgeir Andersen.
Kurátorem dat a autorem vizualizace výsledků byl Rostislav Linda.

Kateřina Brynychová, **Lucie Hambálková**, Jan Cukor, Richard Ševčík, Vlastimil Skoták, Rostislav Linda, Odgeir Andersen, Stanislav Vacek a Zdeněk Vacek provedli recenze a úpravy textu.

Frontiers in Ecology and Evolution

TYPE Review
PUBLISHED 30 September 2024
DOI 10.3389/fevo.2024.1452317

OPEN ACCESS

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RECEIVED 20 June 2024
ACCEPTED 13 September 2024
PUBLISHED 30 September 2024

CITATION
Hambálková L, Cukor J, Brynychová K, Ševčík R, Vacek Z, Vacek S, Skoták V, Linda R and Andersen O (2024) Black grouse (*Lyrurus tetrix*) population status, reasons for decline and potential conservation measures from Western and Central Europe to Fennoscandia: a literature review. *Front. Ecol. Evol.* 12:1452317. doi: 10.3389/fevo.2024.1452317

Black grouse (*Lyrurus tetrix*) population status, reasons for decline and potential conservation measures from Western and Central Europe to Fennoscandia: a literature review

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The long-term decline of the black grouse population throughout Europe is influenced by many factors that affect populations differently depending on the distribution range, from Central Europe to the Scandinavian countries. Therefore, we analyzed available literature sources to describe the main reasons for the population decline of this species and to suggest conservation measures. In total, 228 pieces of literature from 1955 to 2024 were analyzed for this study. Based on the literature analysis, it is clear that the drivers of population decline differ across the distributional range. In Central Europe, where the population is declining rapidly, habitat loss and forest fragmentation are crucial factors, as is the negative impact of tourism. In Scandinavia, where the population is gradually declining, decreasing breeding success and increasing chick mortality rates are generally considered the main negative factors. However, these factors also affect black grouse populations in Central Europe. It is crucial to acknowledge that a significant proportion of the contributing factors, such as predation and habitat loss, can be attributed to human activities. Therefore, it is necessary to emphasize that environmental protection should work hand in hand with wildlife managers to improve the situation.

KEYWORDS

Tetraonidae, predation, nest success, climate change, habitat loss, biodiversity conservation

1 Introduction

The black grouse (*Lyrurus tetrix*) is one of the forest grouses classified as a "least-concern species." The European population is estimated at 2.45–4.08 million adult individuals (BirdLife International, 2022; IUCN, 2023). The native range extends from Great Britain through Russia to North Korea and from Fennoscandia to the Alps, with scattered populations in Central Europe (Cramp and Simmons, 1977; BirdLife International, 2022). Black grouse were also introduced to Canada and the United States of America, with the global population of adult individuals between 8–14 million (BirdLife International, 2022). However, the abundance varies considerably across the extension range worldwide. The black grouse is facing a population decline, especially in the countries of Western, Central and Eastern Europe, which have experienced a significant decrease in numbers over recent decades (Tomiałojć, 1990; Murin et al., 1994; Ludwig et al., 2009b; Merta et al., 2009; Chobot and Němec, 2017). In some countries, individuals are barely surviving (Höglund et al., 2007; Larsson et al., 2008; Watson and Moss, 2008; Segelbacher et al., 2014; Rutkowski et al., 2018). In Fennoscandia, the center of the European distribution range, the black grouse remains a hunted species despite a moderate long-term population decline (Spidsø et al., 1997; Storch, 2000, 2007; Jahren et al., 2016; Zhang et al., 2024).

The reasons for population declines vary throughout the distribution range, often differing on the local scale, due to the influence of many factors. The black grouse is a species with specific environmental requirements and is highly sensitive to its changes (Rolstad et al., 2009). Habitat loss, among other things, is considered one of the most important reasons for population decline, primarily in Central Europe (Doenecke and Niethammer, 1970; Loneux and Ruwet, 1997; Ludwig et al., 2009b; Gimmi et al., 2011; Strauß et al., 2018). Changes in population density lead to an alternative way of reproduction, where solitary lekking occurs, and mating success decreases (Höglund and Stohr, 1997; Geary et al., 2012; Nelli et al., 2016). Furthermore, there is a confirmed decrease in nesting success and an increase in the mortality of both chicks and adults (Spidsø et al., 1997; Storch, 2000, 2007; Merta et al., 2009; Pekkola et al., 2014; Viterbi et al., 2015; Jahren et al., 2016; Cukor et al., 2021). In general, habitat changes, predation, and changes in climatic conditions appear to be the main negative factors affecting black grouse. A considerable threat is also caused by tourism, recreation pressure, and other human activities, including forest management practices, which negatively affect both the reproduction period and the survival of individuals during the winter due to increased energy expenditures and much higher visibility to predators during the disturbances (Storch, 2000; Baltić et al., 2004; Arlettaz et al., 2007, 2013; Ludwig et al., 2008; Zeiler and Grünschachner-Berger, 2009; Immitzer et al., 2014; Formenti et al., 2015; Coppes et al., 2020; Tost et al., 2020). This review summarizes existing studies on the status of black grouse populations from Western and Central Europe to Fennoscandia. It identifies the current primary causes of the population decline. The partial aims of this study are (i) to summarize the available published studies dealing with the decline of the black grouse population, (ii) to point out the main reasons for the decline based on the literature, and (iii) to suggest options for the fundamental principles of population support.

2 Methods

This article focuses on the literature review of previously published sources on black grouse population dynamics and reasons for population decline. Online web search engines, including Web of Science, Scopus, Google Scholar, and ResearchGate, were used to gather information on the subject under study. Non-peer-reviewed sources (popular articles, media reports, unverified sources, etc.) were excluded from the study. The literature related to black grouse topic was searched based on a combination of the following keywords: black grouse, population dynamics, climate change, decline, land use change, mortality, survival rate, chick mortality, nest success, and predation. Document types were restricted to articles, books, conference proceedings, internet sources, statistics and other sources (including dissertations, technical reports, research reports, etc.), and the time period included years 1955-2024.

Based on the main issues addressed in the literature, we further divided the evaluated literature into three categories according to whether the negative impact on the black grouse population referenced in the articles can be reduced or eliminated by human management intervention. The literature in the first category indicates that an improvement can be observed in a relatively short period of time, potentially within a few years after the implementation of the measures ("short-term influence possible"). We have included topics related to human disturbance, tourism and habitat change in the first category because human disturbance and tourism can be reduced to a minimum in a relatively short period of time and habitat change is also feasible (of course, depending on the scale). The second category includes publications which consider reduction or elimination of the negative effects by management intervention within a short time-scale of a few years impossible ("short-term influence not possible"). In the second category, we have included topics related to population dynamics, reproduction, predation, parasites and climate change, because we believe they are impossible to solve and eliminate in the short time frame of a few years. The third category consists of publications, which do not directly address the negative impacts to black grouse populations. The third category includes behavioral topics, methodology, general information websites, genetics and acoustics studies and habitat catalogues (Figure 1). Our search returned 228 references included in this review, of which 176 were scientific articles from the Web of Science or Scopus databases, 22 were chapters from scientific books, eight were conference proceedings, four were internet sources, 11 were other sources (dissertations, technical reports, research reports, etc.) and seven sources were statistics on population dynamics. All sources found are listed in the references. The number of publications per year (Figure 2A) and the overview of the different types of sources are shown in Figure 2B.

For European countries where black grouse is still a hunted species, hunting bag counts have been collected. The hunting bags

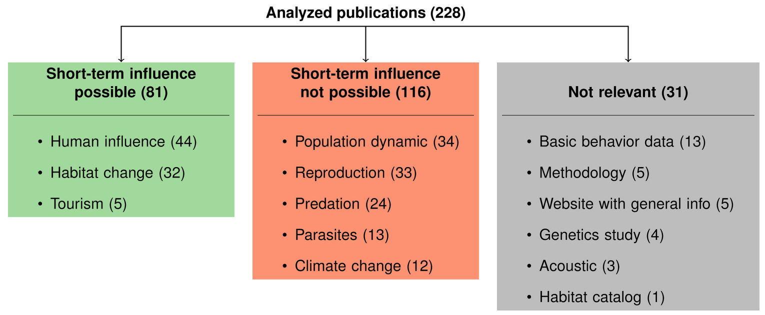

FIGURE 1
Division of article topics into three categories according to the possibility of human influence.

data are considered as the most reliable data source from hunting statistics compared to the number of counted individuals (Kahlert et al., 2015). Hunting trends for black grouse in Sweden, Finland, Norway, Austria, and the Czechia alongside with particular linear regression results are shown in Figure 3. Each subplot contains p-value for hypothesis of slope equal to zero and R^2 value. Computations were performed in R software (R Core Team, 2023), plot was created using its package ggplot2 (Wickham, 2016).

3 Occurrence and population trends

In Europe, the breeding population of the black grouse is estimated to range between 792,000 and 1,030,000 calling/lekking males. However, there is a long-term population decline (European Environment Agency, 2016). European countries, where the black grouse is still present, can be roughly divided into three separate areas according to the population density. In the countries of Western, Central and Eastern Europe, the black grouse population is considered to be threatened. These countries include Austria, Italy, Czechia, Germany, Estonia, France, Belgium, Lithuania, Latvia, Poland, Belarus, Slovenia, Slovakia, and Great Britain (Ruwet et al., 1997; Danko et al., 2002; Sim et al., 2008; European Environment Agency, 2016; Dos Santos et al., 2021; Ķerus et al., 2021; Statistik Austria-Federal Institution under Public Law, 2023; The Forest Management Institute Brandýs nad Labem, 2022; Delcourt et al., 2023; Tomášek et al., 2023). Countries with few individuals or even zero population are Denmark, the Netherlands, and Romania (European Environment Agency, 2016; Elts et al., 2013).

On the other hand, stable populations with only moderate declines are reported from Finland, Sweden, and Norway (Statistics Finland, 2023; Svenska Jägareförbundet, 2023; Statistisk Sentralbyra, 2023). Although black grouse are still hunted there and population densities are sufficiently high, declines have been reported also in these Fennoscandian countries, mainly due to nest predation and an increase in mortality of chicks and subadults (Spidsø et al., 1997; Storch, 2000, 2007; Jahren et al., 2016).

There are also countries with only scattered information about their black grouse population, e.g., the history of records from Lithuania contains considerable data from 1948–2017, when the initial population size was more than 10 thousand black grouse, while the last record indicates only 1750 individuals (BirdLife International, 2023); available records in Ukraine cover the period

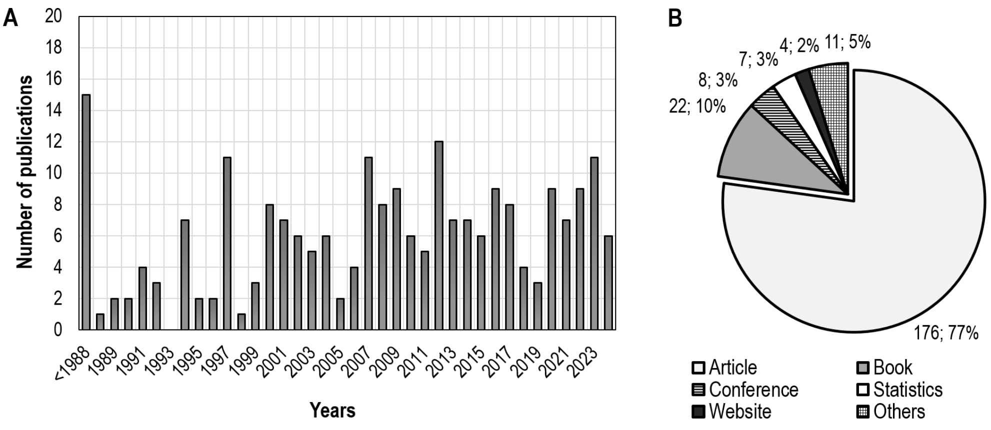

FIGURE 2
Temporal distribution of 228 literature sources from 1955 to 2024 on the black grouse population dynamics and reasons for population decline **(A)**, and the proportion of references by source [scientific articles, professional books, conference proceedings, and other sources; **(B)**].

between 1999 and 2007 when around 13,000 individuals were hunted (Ukrainian Nature Conservation Group, 2009). In Hungary, black grouse were hunted until the 19th century but also became extinct. The last record comes from 1966 (Pluhar et al., 2010). The same fate also befell the black grouse in Bulgaria, where, like in many other countries, it is registered on the Red List (Boev, 1997; Michev et al., 2011). Positive long-term growth of the black grouse population is taking place only in Latvia and Slovenia (except Fennoscandia). In other countries, the grouse is either stable or declining over the long term (European Environment Agency, 2016). Whether lesser or greater attention is paid to the black grouse in the countries mentioned above, the return, stabilization, or even an increase in its population is not easy, as it is a species that requires specific conditions to flourish.

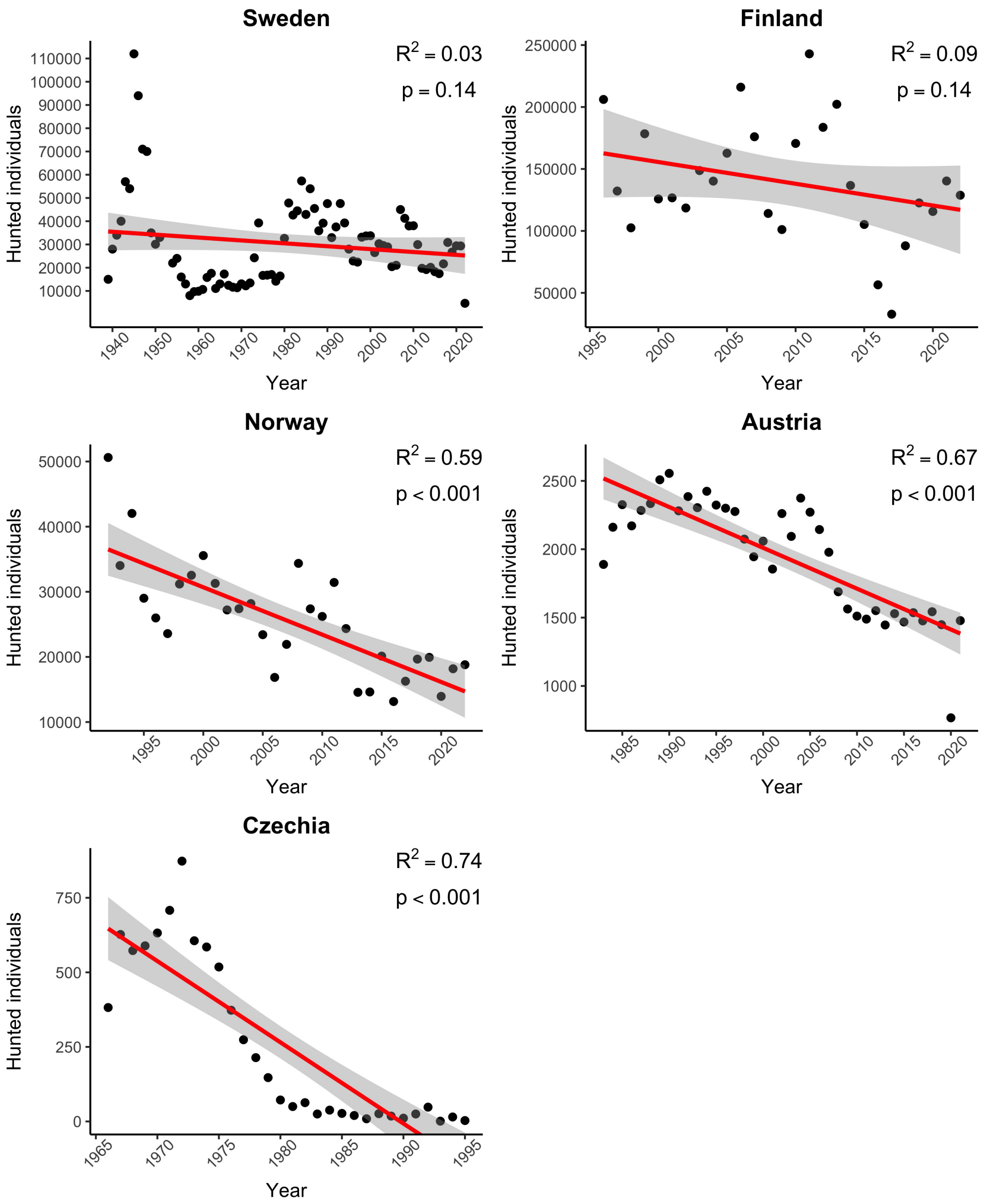

FIGURE 3
Declining trends in the number of black grouse hunted in Sweden, Finland, Norway, Austria, and Czechia (Statistik Austria-Federal Institution under Public Law, 2023; Statistics Finland, 2023; Svenska Jägareförbundet, 2023; Statistisk Sentralbyra, 2023; The Forest Management Institute Brandýs nad Labem, 2022).

4 Reproduction process

The stability of the black grouse population is directly dependent upon the reproduction process, which is influenced by the course of the mating performance itself (Jahren et al., 2016). At the beginning of the breeding season (March), but sometimes also in the autumn, promiscuous or polygamous males maintain typical leks (Baines, 1996; Rintamäki et al., 1999). Leks are usually found in open swamps, clearings, fields, or frozen lakes but never far from the forest (Koivisto, 1965; Alatalo et al., 1991; Rolstad et al., 2009). However, habitat selection is related to population density (Nelli et al., 2016). On the leks, females select males based on morphological, behavioral, or spatial characteristics (Alatalo et al., 1992; Höglund et al., 1997; Kokko et al., 1998; Rintamäki et al., 2001).

Female grouse choose the largest leks, and on them, the most dominant and vital males who fight the most (Alatalo et al., 1991, 1992, 1996; Hovi et al., 1994). As a result, only a few dominant males from the entire lek have the opportunity to mate, while most do not mate at all (Höglund and Alatalo, 1955; Lebigre et al., 2007). An interesting finding is that older females tend to mate with the same male as in previous years, even though the male is no longer the most vital (Rintamäki et al., 1995). Apparently, attractiveness also seems to play a role, related to the plucking of feathers from undertows during fights. Fewer plucked feathers indicate greater dexterity in the male, increasing its chances of success (Alatalo et al., 1991). On the other hand, ornaments of males, e.g., the length of their lyre-shaped tail and color of plumage, probably have only a complementary effect on the female's choice (Höglund et al., 1992, 1994; Rintamäki et al., 1997, 2002; Siitari et al., 2007; Hämäläinen et al., 2012; Kervinen et al., 2016).

An essential part of the mating performance is the male acoustic manifestation. For male grouse, four types of vocalizations are typical (Cramp, 1983). These are resonant "rookooing," similar to the cooing of a dove, a "hissing call," further subdivided into four types (a wailing hiss, a hiss accompanying flight, a relatively long hissing call, and an arrhythmic hiss during fights), as well as tones of aggression and warning calls. Females emit cooing calls, tones during flight, and other sounds, which are divided into five types according to the situation (they relate to social contacts between individuals, with chicks, and, last but not least, warning calls). Rookooing is probably the most important during the mating performance, as females prefer leks with more than one male, and weaker male individuals may sometimes benefit from the presence of other rookooing males according to hotshot hypothesis (Hovi et al., 1997).

The lekking behavior is typical for well-established populations with high densities of birds. Males that move closer to the center of the lek become more successful (Kervinen et al., 2012). The selection of a place during the mating performance then depends on two factors: the position of the male on the imaginary social hierarchy and their patient waiting for a place to become available. High-ranking males maintain their territories for several years, but random shifts of weaker individuals are not excluded, as the stronger ones do not need to change their position to be closer to the center of the lek (Kokko et al., 1998). On the contrary, less preferred males take advantage of the eventual release of territorial positions, caused by mortality between seasons, to move closer to the center of the lek (Rintamäki et al., 1995). In Sweden, they noted a 15% probability of movement of males between leks, more so in younger individuals. It can be said, therefore, that grouse males show habitat fidelity during the mating season, but also across seasons. Thus, annual home ranges represent enlarged territories used during the mating season (Borecha et al., 2017). Leks are distributed irregularly at shorter distances of 1–2 km, according to habitat characteristics and the black grouse population density (Rolstad et al., 2009). The size of the lek can then affect its lifespan and resistance (Geary et al., 2012).

In the past, the leks were visited by large groups of males, but nowadays, the number is lower, and solitary males also appear (Höglund and Stohr, 1997). In recent years, there have been studies describing non-lekking populations in which males attract females with solitary displays (Höglund and Stohr, 1997). Non-lekking populations can be found, for example, in Sweden, Italy, Germany, and the Czechia (Höglund and Stohr, 1997; Zeitler, 2000; Angelstam, 2004; Svobodová et al., 2011b; Chamberlain et al., 2012; Rutkowski et al., 2018). Populations with solitary leks have lower genetic diversity than sites where birds aggregate at leks and may experience a reduction in effective population size and an overall decline in abundance (Svobodová et al., 2011b). Thus, the fragmented black grouse population in Central Europe seems to have lost genetic variation compared to those incomparably larger populations in Fennoscandia (Caizergues et al., 2003; Höglund et al., 2007; Svobodová et al., 2011b). Therefore, it seems that the low population density with non-lekking behavior represents an alarming risk for the black grouse population, not only from the point of lower and ineffective reproduction rate but also the risk for population sustainability from the perspective of genetic variability and black grouse conservation.

5 Factors affecting black grouse populations

5.1 Habitat loss

One of the crucial factors affecting black grouse populations is undisputably the loss of suitable habitat (Pearce-Higgins et al., 2007; Geary et al., 2015; Strauß et al., 2018; Tomášek et al., 2023). The authors agree that black grouse, like many other protected wildlife species, must deal with anthropogenic changes in habitats (Storch, 2000; Tost et al., 2020). For example, the abandonment of traditional extensive management (e.g. mowing or cattle grazing) of mountain meadows and pastures leads to the loss of suitable habitats through succession (MacDonald et al., 2000; Lešo et al., 2024). Habitat selection is a fundamental aspect of animal ecology, the understanding of which is essential for wildlife management and conservation (Northrup et al., 2013). Loss of suitable habitats can be a leading factor in time-delayed extinctions, as the current occurrence of species may instead reflect historical wetland cover and habitat configuration (Gimmi et al., 2011; Pearce-Higgins et al., 2016). In the past, grouse populations were dependent on extensive farming. As a result, most native subpopulations became extinct due to habitat loss caused by the large-scale conversion of heathland and peatland to forest, farmland, and pasture (Ludwig et al., 2009b). These phenomena began to occur most intensively around the 1950s and are considered the foremost causes of the loss of numerous grouse habitats from the Central European cultural landscape (Doenecke and Niethammer, 1970; Loneux and Ruwet, 1997). Until then, extensive land use with heathland and sheep farming provided optimal habitat conditions (Storch, 2007). Studies in Finland have shown that black grouse breeding success deteriorates as the proportion of agricultural land increases (Kurki et al., 2000) and the conditions for predators improve (Angelstam et al., 2000). Consequently, the renaturation of wet habitats not only within existing grouse habitats but also within dispersal distance is probably one of the most important measures to strengthen and increase black grouse metapopulations (Roos et al., 2016; Tost et al., 2022). Regarding forest habitat, when a new stand is established, it is possible to create new grouse sites, but, as the stand eventually closes, grouse leave it (Kurhinen et al., 2009). Therefore, it is recommended to produce smaller and more permanent forests, to focus on the protection of peatlands, and to carry out small-plot harvesting (White et al., 2013).

5.2 Changes in vegetation composition and structure

The demands on the structure and diversity of black grouse habitats are the subject of a long-term and multifaceted study (e.g., Müller, 1974, 1979; Scherzinger, 1976; Eiberle, 1976; Koch, 1978; Glänzer, 1980; Porkert, 1982; Klaus, 1991; Andrén, 1994; Baines, 1994; Glutz von Blotzheim et al., 1994; Calladine et al., 2002; Angelstam, 2004; Baines et al., 2007; Ludwig et al., 2008, 2009a, 2009b; Wegge and Kastdalen, 2008; Signorell et al., 2010; Patthey et al., 2012; Schweiger et al., 2012; Immitzer et al., 2014; White et al., 2015; Nelli et al., 2016; Strauß et al., 2018; Tost et al., 2020, 2022). These works show that a structural mosaic of both tree, shrub, and herb layers, as well as the relief of the soil, is crucial for the black grouse stability or even population increase. This structure allows grouse to use different properties of stands and soil in terms of microclimate, food opportunities, and shelter supply (Porkert, 1973; Šálek et al., 2004; Svobodová et al., 2004; Patthey et al., 2012). In the herb layer, the ratio of different age structures of Vacciniaceae (especially *Vaccinium myrtillus*, *Vaccinium vitis-idaea*, *Vaccinium uliginosum*) or Ericales (*Calluna vulgaris, Erica tetralix, E. carnea*) is of great importance (Porkert, 1982; Ludwig et al., 2010). Furthermore, interspersed areas covered with bryophytes and ferns, including some Cyperales and Juncales, or only with sedge, are crucial in the biotope structure (Porkert, 1973, 1976, 1980). From the point of forest stand management, small-scale management methods with natural renewal are preferred, which create a mosaic structure of stands (Poleno et al., 2009) and offer an optimal food and shelter in a suitable microclimate (Porkert, 1982, 1991).

The mosaic forest stands with a high proportion of open areas without tree vegetation are critically important, especially in the intensively managed forests of Central Europe (Klaus, 1991; Ludwig et al., 2009b; Wegge and Rolstad, 2011). Open places in forest ecosystems were related to peat bogs, moorlands, or other stands with high groundwater levels. Unfortunately, most of them were drained off in the 20th century (Paavilainen and Päivänen, 1995; Sjöberg and Ericson, 1997; Skaggs et al., 2016). Therefore, many habitats were destroyed by spontaneous succession after drying up and became unsuitable for black grouse, especially in the lekking season (Ludwig et al., 2010). Contrarily, another large-scale habitat change, which was positive from the black grouse point of view, was caused by the immission calamity in Central Europe between 1970 and 1995. There was a temporary creation of favorable habitats for the growth of grouse populations because of Norway spruce diebacks in mountain areas and the opening of forest stands (Porkert, 1982; Flousek, 1989; Vacek et al., 2007). As a result of the involvement of these stands in their artificial restoration, this effect waned at the beginning of the 21st century (Svobodová et al., 2011a). Moreover, open habitats with solitary trees or stands with a loose canopy (pine, spruce, larch, birch, and rowan) are suitable for grouse to use as lookouts during mating season, as a source of food in winter and spring (Porkert, 1982; Patthey et al., 2012; Strauß et al., 2018; Tost et al., 2022). Loose conifer forests also support the occurrence of anthills as a staple food for grouse chicks (Signorell et al., 2010; Schweiger et al., 2012).

Maintaining or restoring high-quality habitats in semi-natural and anthropogenic landscapes is a fundamental issue in conservation biology, as habitat quality is one of the main determinants of reproductive performance and survival (Pärt, 2001; Vickery et al., 2001; Hirzel and Le Lay, 2008; Patthey et al., 2012; Schweiger et al., 2012; Northrup et al., 2013; Immitzer et al., 2014; White et al., 2015; Tost et al., 2022; IUCN, 2023). Suitable habitats within Europe are relatively diverse for the given dwelling and vegetation conditions (Patthey et al., 2012). This is mainly a mosaic of shrubby stands, peat bogs, wetlands, meadows, extensive pastures, and loose forest stands, which closely follow each other in such a way as to ensure the availability of all essential environmental parameters for the grouse (Ludwig et al., 2009a; Rolstad et al., 2009; White et al., 2015; Tost et al., 2022). Considering the landscape characteristics, type of forest management, and acreage of protected areas, it is evident that Scandinavia offers an incomparably larger array of suitable habitats than Central Europe (Cukor et al., 2022). From a phytocoenological point of view, in Europe, these are mainly fens and transition bogs, highlands, alpine and subalpine scrub vegetation, peat cranberry forests, dry heaths of lowlands and uplands, dry heather forests of continental bogs and peat, and waterlogged spruces (Chytrý et al., 2010). Therefore, the basic prerequisite for the conservation of the black grouse as an endangered species is the effectual care of its listed habitats per the European Union Directive No. 92/43/EEC on the conservation of natural habitats, wild fauna and flora, and Directive No. 2009/147/EC on the conservation of wild birds.

5.3 Climate change

In recent decades, we have observed phenomena associated with climate change that have had adverse effects on black grouse populations. The evidence of climate change is clear and unmistakable worldwide. In the Czechia, for example, the mean annual air temperature has increased by 2°C between 1961 and 2021 as a result of climate change Český hydrometeorologický ústav (2022) and the temperatures in Southern and Central Europe are predicted to increase by a further 2°C by 2047 (Geßler et al., 2007). The changing quality, duration, and height of snow cover, temperature fluctuations, and uneven distribution of precipitation are particularly important factors for the black grouse (Prellwitz, 2002; Ludwig et al., 2006; Canonne et al., 2021). All the factors mentioned show fluctuations in environmental conditions, which have detrimental effects on the laying date, breeding success, chick survival, and the size of black grouse populations (Ludwig et al., 2006; Bocca et al., 2014; Barredo et al., 2020; Canonne et al., 2021).

Black grouses are well adapted to long and harsh winters by their feeding habits and their ability to dig snow burrows (Marjakangas, 1992). The primary causes of black grouse decline in the Alps are thought to be a long-term reduction in snow cover, changes in snow quality and increasing average winter temperatures (Canonne et al., 2021). Frequent temperature changes and recurring rainfall in winter combined with the snow melting and freezing again, create layers of frozen snow, or sometimes, ice, which the grouse cannot burrow through (Bocca et al., 2014). In this case, the grouse is forced to overwinter outside the snow burrows, where it is more likely to be seen by predators (Flousek, 2019). The length of the winter also affects the number of natural predators of grouse in the mountains, particularly martens and foxes (Bartoń and Zalewski, 2007). It is highly advisable to monitor the long-term trends in snow conditions at sites where black grouse are present and to carefully monitor the effects of these changes on their populations.

An earlier onset of spring can lead to earlier mating, earlier laying of eggs, and a temporary mismatch with the optimum time for the offspring to hatch (Ludwig et al., 2006; Wegge and Rolstad, 2017). The first clutches are often destroyed by adverse weather, such as the return of winter and frequent weather changes (Ludwig et al., 2006, 2010). For example, in a Scottish study (Moss et al., 2001), the decline in capercaillie breeding success between 1975 and 1999 was associated with the mid-April cooling period. Conversely, some studies do not support the general idea that a warmer climate will negatively affect the reproduction of birds and animals in northern latitudes (Virkkala et al., 2008; Wegge and Rolstad, 2017). Instead, Wegge and Rolstad (2017) found that the reproductive output of capercaillie and black grouse increased with warmer and earlier springs. However, the authors admit that a warmer climate may have negative effects, for example, on the survival of adult birds, which can moderate the positive effects on the reproductive process.

In recent years, climate change could have caused a mismatch between the timing of breeding and the amount of food available to chicks after they hatch (Visser et al., 2004). A warmer spring can lead to earlier nesting, but this timing may no longer coincide with the optimal amount of insects available, which could lead to poorer chick survival (Ludwig et al., 2006; Wegge et al., 2010). Another scenario can also take place. High spring temperatures can accelerate the development of invertebrate larvae, which presents a threat to chicks by transforming their primary food source into an imago (adult) before the chicks have had time to hatch. This leaves them with insufficient basic food.

Another challenge for black grouse can be recurring high summer temperatures. Prellwitz (2002) found that greater sage-grouse (*Centrocercus urophasianus*) are less vigilant at high temperatures (above 30°C) because they spend more time and energy cooling down, which reduces their vigilance against predators. There is also a risk of dehydration at high temperatures, especially in chicks (Prellwitz, 2002). Similar problems may be expected with black grouse. Black grouse populations can respond to changes in climate both locally and regionally, with these changes being more pronounced in coastal areas than inland areas (Kvasnes et al., 2010; Viterbi et al., 2015).

5.4 Adult mortality

In general, adult mortality has been adequately studied in the past decades (e.g., Warren and Baines, 2002; Svobodová et al., 2011a; Pekkola et al., 2014), and it is evident that adult mortality plays a critical role in the black grouse population dynamics and the current population decline. The black grouse survival probability was predominately studied by radiotelemetry of tagged individuals (Spidsø et al., 1997; Warren and Baines, 2002; Bowker et al., 2007; Svobodová et al., 2011a; Pekkola et al., 2014), which also offers acceptable solutions for evaluation of mortality causes.

Previously published studies have shown that the annual survival rate varies from year to year, ranging from 0.53 to 0.72 (Warren and Baines, 2002; Pekkola et al., 2014), but some studies have reported higher mortality rates, e.g., in Norway, 72% of radio-tagged birds died during a 12-month monitoring period (Spidsø et al., 1997). Differences in mortality rates are caused by several factors, including the age of birds, climatic conditions, the density of the black grouse population, and the abundance of predators with fluctuations between years. For example, Warren and Baines (2002) estimated an annual survival rate for adult individuals of 0.72 (for both sexes), but the survival rate of yearlings was significantly lower (0.46) in the same conditions. The lower survival of young birds was also confirmed by Pekkola et al. (2014) for the black grouse females in Finland. Moreover, the survival probability between adults and yearlings differs throughout the year. In winter (September–February), the survival rate can be 0.54 for yearlings and 0.73 for older individuals. In contrast, during the summer period (March–August), it can be 0.95 for yearlings and 0.84 for older birds (Warren and Baines, 2002). From the wider perspective, the mortality of adult females is most challenging for the black grouse population because this represents a high risk for the reproduction process. Black grouse females mature at one year of age and can have a potential lifespan of five to six years in the wild. Unfortunately, female predation most often occurs during the spring mating and subsequent egg laying and incubation (Willebrand, 1988; Pekkola et al., 2014), and again, there is a clear difference between the survival of young and older females (Pekkola et al., 2014).

Regarding the causes of black grouse mortality, predation is a principal proximate mortality reason for adult black grouse individuals (Tornberg et al., 2006; Pekkola et al., 2014; Sein and Väli, 2024). According to previously published research, it is evident that the proportion of avian and mammalian predators varies along the black grouse distribution range according to predator species composition and natural conditions. In a large study from Finland, where 253 females were radio-tagged, predation was confirmed as the primary cause of all-natural mortality. From the total proportion, the avian predators were responsible for 51.8% of caused mortality, and 26.7% was classified to mammals (Pekkola et al., 2014). This confirms the general assumption that raptors are the main predators of adult grouse (Spidsø et al., 1997; Warren and Baines, 2002; Tornberg et al., 2012; Pekkola et al., 2014). However, the exact determination of predator species involved can be problematic in relation to the decomposition of the found carcass of the monitored individual (Caro and Girling, 2006).

Nevertheless, more specific species composition of black grouse predators has been published in several studies. In the study from North Wales, raptors again played a crucial role in black grouse predation when the goshawk (*Accipiter gentilis*) and peregrine falcon (*Falco peregrinus*) were responsible for 64% of the predation caused, followed by the red fox (*Vulpes vulpes*), which was found to be a predator in the remaining 36% (Bowker et al., 2007). The goshawk was also identified as a primary predator in Norway, where almost half (46%) of the radio-tagged birds were killed by this predator, followed by pine marten (*Martes martes*; 23%), and the rest (31%) were killed by unknown predators (Spidsø et al., 1997). Those findings are supported by the fact that forest grouse generally represents the favorite prey species of the northern goshawk (Valkama et al., 2005; Tornberg et al., 2006, 2012). For example, in certain winters, female grouse are the optimal prey for male goshawks (Tornberg, 2000; Tornberg and Colpaert, 2001). The description of the main predators of black grouse is well-known in the Scandinavian countries where it is possible to tag a sufficient number of black grouse individuals, as was done in the studies mentioned above (Spidsø et al., 1997; Tornberg, 2000; Bowker et al., 2007; Pekkola et al., 2014).

On the other hand, the data from radiotelemetry monitoring of black grouse in Central Europe indicate that mammalian predators are the primary cause of adult mortality (Svobodová et al., 2011a). Data on causes of mortality are available, e.g., from the Czechia (Svobodová et al., 2011a). The results confirmed an extremely low survival rate of tagged male grouse. Only 21% of the male grouse survived one year. Eight of the 12 tagged males were killed by predators within one year (67%). Seven of these were killed by a mammalian predator (88%) that could not be accurately identified. These results suggest that the goshawk is not a significant threat to adult grouse in the Ore Mountains (Krušné hory) study area in the Czechia. On the contrary, the main predators were martens and foxes, which can be controlled by hunting (Svobodová et al., 2011a). Survival rates of 93 radio-tagged black grouse in two populations in the southern French Alps were higher for females than males and tended to be higher for adults than juveniles. Most adult deaths occurred in spring (females and males) or early summer (males). The causes of mortality were as follows: raptors 51%, mammals 27%, unidentified predators 11%, and hunting 11% (Caizergues and Ellison, 1997).

Black grouse populations have declined throughout most of Europe (Caizergues and Ellison, 1997; TenDen and Niewold, 2001; Jahren et al., 2016), making it difficult to capture and tag birds on their breeding grounds. For example, in the Czechia, between 2000–2003 when grouse telemetry was executed, the population in the study area was relatively stable, with an abundance of 1.2–3 grouse/100 ha (Svobodová et al., 2011a). However, due to a decline in the local populations, it will no longer be possible to conduct further adult telemetry studies in Central Europe. The populations are already so weak that any threats, including adult trapping, can significantly impact the local subpopulation, and therefore, cannot be risked.

5.5 Breeding success and chick mortality

Large-scale population declines have been the result of low levels of reproductive success (Ludwig et al., 2006; Jahren et al., 2016; Zbinden et al., 2022). A comprehensive study by Jahren et al. (2016) showed a dramatic decline in grouse breeding success between 1934 and 2014 in Fennoscandia and Central Europe. Jahren et al. (2016) found that breeding success in Fennoscandia declined from 0.9 to 0.55 for black grouse and from 0.89 to 0.35 for capercaillie between 1934 and the present. In Central Europe, the number of broods per female decreased for both species. Conversely, in the British Isles, there were no significant changes in black grouse brood frequencies between 1934 and 2002. These results suggest that black grouse populations in Britain have been more productive than elsewhere for some time (Jahren et al., 2016). The breeding success of black grouse populations studied in Switzerland was monitored from 1981 to 2020 (Zbinden et al., 2022). The results showed that the long-term average reproductive rate was 2.0 chicks/hen in northern Ticino and did not show any decline. However, reproductive rates in central/southern Ticino declined in the early years of the study period and then stabilized at the level of northern Ticino. Reproductive rates were highly variable from year to year and were influenced by a combination of weather and habitat parameters (Zbinden et al., 2022).

Successful reproduction is significantly affected by predation of nests, which occurs in the first days after their establishment (Merta et al., 2009). Martens, foxes and corvids, but also wild boars (*Sus scrofa*), are the most common predators of nests (Svobodová et al., 2004; Cukor et al., 2021). Studies focused on grouse predation show its high variability related to factors such as the number of predators, the nature of habitats, the population density or hunting management (Svobodová et al., 2004, 2011a; Merta et al., 2009; Cukor et al., 2021). However, grouse eggs are not a principal food source for predators but are only an alternative seasonal prey item. The main prey of mammalian grouse predators in the boreal zone are rodents, whose abundance fluctuates strongly between years (Hansson and Henttonen, 1989; Wegge and Storaas, 1990). Thus, breeding success may vary depending on the abundance of small mammals in a given area. If there are insufficient small mammals, grouse nests and chicks become alternative prey for mammalian predators (Šálek et al., 2004). The reproductive success of grouse is positively correlated with the abundance of the main prey (rodents) and is well documented by data from Scandinavia (Hansson and Henttonen, 1989; Kurki et al., 1997; Tornberg et al., 2012), whereas clear evidence from Central Europe is lacking (Ježková et al., 2014; Matysek et al., 2020).

Many studies agree that post-hatch mortality of grouse is high, especially during the first year of life, and that predation is the primary cause of this mortality (Hannon and Martin, 2006; Park et al., 2008). Predation explained 68% of total chick mortality during the first month after hatching, with up to 90% of predation by avian predators in Wales (Johnstone and Lindley, 2003). Also, in Finland, avian predators pose a threat to grouse chicks, especially in years when rodents are scarce (Reif et al., 2001, 2004). During the breeding season, hawks predated about 6% of grouse chicks there, while buzzards predated about 4% (Tornberg et al., 2012). Approximately 36% of females lost their chicks within the first ten days after hatching, based on telemetric monitoring of chicks from 81 successfully hatched nests in Finland (Ludwig et al., 2010). However, the probability of chick survival, in this case, did not depend on the local abundance of martens and foxes during the previous winter, so the authors conclude that the chief cause of chick mortality here was not predation risk. In this study, the authors identify that the most salient predictor of chick survival is the bilberry cover, which provides food for the chicks as well as safe shelter from predators (Ludwig et al., 2010), and that food availability for chicks is particularly important during the post-hatching period (Wegge et al., 2022). Other limiting factors for black grouse chicks are unfavorable weather conditions, especially sudden temperature changes, low temperatures or snowfall during the critical post-hatching period, which have a major impact on their survival rate and therefore impact to whole reproduction process (Rotelli et al., 2021).

5.6 Parasites and diseases

Parasites are another reason for the decline in the number of black grouse. Although they do not cause pronounced and sudden population declines, they have shown to affect population dynamics and the survivability of grouse (Isomursu et al., 2017). A higher parasitic incidence is observed in artificially reared individuals (Sokól and Pluta, 2022) compared to individuals in the wild (Strauß et al., 2022), while the decreasing population density and distribution of the grouse is characterized by a decrease in parasitic diseases (Coates et al., 2017). For an individual, parasites can increase the stress hormone level, as it affects the organism's resistance (Berto and Lopes, 2020). The most common group of grouse parasites are coccidia, specifically protozoa from the genus Eimera (Jankovská et al., 2012; Sokól and Galecki, 2018; Sokól and Koziatek-Sadlowska, 2020; Tizzani et al., 2021; Sokól and Pluta, 2022; Strauß et al., 2022) and the coccidia *Cryptosporidium baileyi*, first recorded in England in 2010 (Coldwell et al., 2012). There are also nematodes in grouse, e.g., the species *Capillaria caudinflata* (Formenti et al., 2013; Fanelli et al., 2020; Tizzani et al., 2021; Sokól and Pluta, 2022), *Trichostrongylus tenuis*, *Heterakis* spp., and *Syngamus trachea* (Jankovská et al., 2012; Strauß et al., 2022) and, last but not least, flatworms and borers (Jankovská et al., 2012; Tizzani et al., 2021).

5.7 Recreation pressure and human disturbances

Disturbance caused by human outdoor recreation and tourism activities is increasingly viewed as threatening to wildlife (Storch, 2013). An inescapable factor negatively affecting the distribution and abundance of black grouse individuals is human activity, associated, for example, with the construction of wind farms in areas that may largely overlap with locations suitable for black grouse (Zeiler and Grünschachner-Berger, 2009; Coppes et al., 2020). These construction projects mainly cause a change in the distribution and use of grouse leks in the given location. For example, the construction of a wind power plant itself did not affect the behavior of male black grouse in the lek sites in the Austrian Alps, however, the number of lekking males in the monitored lek site decreased from 12 recorded individuals before the construction to zero two years after construction (Zeiler and Grünschachner-Berger, 2009). A similar reduction of lekking males was recorded in Scotland, when before and during the construction of the wind farm, they recorded nine and eight males, respectively, yet throughout the two years after the construction, during the monitoring of the same lek site, only four females were found, but no lekking males (Percival et al., 2018). On the other hand, Zwart et al. (2015) did not record a significant decline in males after the construction of a wind farm at seven lek sites in Scotland. The lek sites were originally located within 500 m (n = 4, median distance = 250 m) of the wind farm but moved up to 803 m (median distance) further from the wind turbines. In addition, this structure located near the lek and breeding area can also directly cause the mortality of black grouse individuals (Wöss and Zeiler, 2003; Zeiler and Grünschachner-Berger, 2009; Coppes et al., 2020). For example, in Austria, within two years, mortality was recorded in five individuals, which was most likely caused by a collision with the tower of the wind power plant itself, not with the wind turbines, as this species usually flies only up to approx. 27 m above the ground (Zeiler and Grünschachner-Berger, 2009). However, it is still not clear whether there is a higher number of collisions and thus increased mortality, which could negatively affect the abundance of the local population of this species (Coppes et al., 2020).

Human activities are also causing other significant land-use changes. On the one hand, traditional grazing on forest pastures is being abandoned, leading to the overgrowth of these habitats with scrub and forest. On the other hand, outdoor winter recreation (as well as summer recreation) is critically expanding. Ski infrastructure is damaging fragile mountain habitats and snow sports causing disturbance and stress to wildlife (Patthey et al., 2012; Storch, 2013) which is, in case of black grouse, essential to minimize energy expenditures of overwintering birds. Negative impacts of human disturbance have been documented on the reproduction success (Ingold, 2005; Storch, 2013; Rutkowski et al., 2018) but also on the distribution and survival of adult individuals of the black grouse. These effects are resulting to the stress and energy expenditure associated with tourism in the form of outdoor activities, skiing, mountain biking, walking in nature, photography or gathering forest fruits (Storch, 2000; Baltić et al., 2004; Arlettaz et al., 2007, 2013; Immitzer et al., 2014; Formenti et al., 2015; Jäger et al., 2020; Tost et al., 2020). In addition, every disturbance means the necessity of unexpected movement of threaten individuals and therefore also increased risk of crash to the iron fence used in forestry or other obstacles in the terrain (Baines and Andrew, 2003). Long-term tourism in a given location can also cause a change in the behavior of males, who may, for this reason, switch to a solitary lekking pattern (Zeitler, 2000). For example, Arlettaz et al. (2007) found sustained increases in the stress hormone corticosterone over three days of up to 60% in three captive individuals exposed to a single daily disturbance during the experiment. Similar results were obtained by Formenti et al. (2015), who found a higher level of stress hormones in winter in locations that were more frequently used by people for winter sports. Due to this, the black grouse can exert more energy for thermoregulation after leaving their snow burrows (igloos), but also for escape in wintering individual or when searching for and creating new snow burrows. This activity, in turn, increases the probability of detection by a predator (Arlettaz et al., 2007; Formenti et al., 2015). Additionally, Baltić et al. (2004) found that disturbed birds increased their foraging duration by up to 23% during the morning, while predation risk for these disturbed individuals increased by up to 12%. Immitzer et al. (2014), in turn, found that the presence of used hiking trails during the summer reduced the probability of black grouse occurrence in potentially suitable habitats within 50 m by up to 93%. Similar results were also found in the study by Tost et al. (2020), who also noted the effect of tourist routes on the distribution of black grouse. Marked individuals avoided heavily used trails, and the use of these habitats varied throughout the day, with the presence of marked individuals near the trail mostly recorded at night and dawn, but grouse avoided these habitats during the peak human activity phase around midday and afternoon (Tost et al., 2020). As can be seen from these studies, human activity can impose a significant effect on the physiology, behavior, and demography of the black grouse, causing, together with other factors, the reduction of the population of this species throughout Europe.

6 Key actions to support black grouse populations

6.1 Forest management

In times of ongoing climate change, carbon sequestration by forests is a crucial factor for mitigation (Bellassen and Luyssaert, 2014; Cukor et al., 2017; Vacek et al., 2023a). On the other hand, extensive afforestation (especially moorlands) harms black grouse populations (Baines, 1996; Pearce-Higgins et al., 2007; White et al., 2015). As grouse have adapted to dynamic environments with changing mosaics of different successional stages, they are sensitive to anthropogenically homogenized and human-disturbed habitats (Angelstam, 2004; Ludwig et al., 2008; Immitzer et al., 2014; Tost et al., 2020).

In terms of forest management and silvicultural practices, small-scale management practices using shelterwood methods and selection principles, preferably with natural regeneration, create a mosaic structure of stands which is favored by grouse (Poleno et al., 2009; Vacek et al., 2023b). The recommended measures include a reduction in planting density (Baines et al., 2000; Scridel et al., 2017), tree planting in smaller patches over a longer time period, creation of small-scale heterogenous forest mosaics with the loose stand canopy and locally open landscapes (Grant et al., 2009; Tost et al., 2022; Mazziotta et al., 2024). It is also important to restore and promote wet habitats, peat bogs, and waterlogged forest stands with the specific tree species composition, including alders (*Alnus glutinosa*, *A. viridis*) and willows (*Salix caprea*, *S. cinerea*, *S. aurita*) (Ramanzin et al., 2000; White et al., 2015). Furthermore, the reduction of tree natural regeneration and of young trees, (pioneer vegetation), preservation of solitary trees, such as birches (*Betula pendula*, *B. pubescens*), rowan (*Sorbus aucuparia*), pines (*Pinus sylvestris*, *P. cembra*, *P. uncinata*), larch (*Larix decidua*), and juniper (*Juniperus communis*) as food sources and shelter (Sim et al., 2008; Patthey et al., 2012; Bocca et al., 2014), thinning of forest stand edges and creation of transition gradients over several hundred meters (Sim et al., 2008), mixing pastures with habitat elements, such as loose shrub formations for cover (Zeitler, 2003; Signorell et al., 2010; Tost et al., 2022). Finally, reducing fencing in the forest to protect regeneration from game damage to prevent collisions leading to grouse mortality (Catt et al., 1994; Baines and Andrew, 2003; Stevens et al., 2012) and improving habitat connectivity (Andrén, 1994).

The ensuing steps in local grouse research are focusing on vegetation microhabitats by examining in detail the species composition and evaluating management practices, e.g., heathland burning and sheep grazing, which significantly affect forest regeneration and its tree and shrub species composition (Wegge and Kastdalen, 2008; Patthey et al., 2012). In addition, the overlap between the grouse habitats and the habitats of the most common predators is currently being investigated, thereby identifying conflict zones (Signorell et al., 2010). Some isolated and very small-scale forest planting on open ground may have a significant effect for predator attractiveness. Paradoxically, the decline of spruce stands over the last 20 years, particularly as a result of storm damage and bark beetle outbreaks, may have helped black grouse by accelerating the creation of clearings and the transformation of conifer monocultures into mosaic stands that suit them (Thorn et al., 2016). The current development of unmanned aerial vehicles (UAVs), or simply ‘drones’, offers an innovative way of efficiently mapping changes in black grouse habitat, as drones can be used to monitor larger areas, including those that are difficult to access by humans, which can help us better plan management measures (Han et al., 2017).

6.2 Game management

Game management includes several activities that can significantly help the black grouse population conservation. Primarily, the hunting of their main mammalian predators such as red fox, beech marten (*Martes foina*) and pine marten, European badger (*Meles meles*), but also occasional nest predators, such as wild boar should be intensified in designated black grouse areas. Invasive predator species, such as the raccoon dog (*Nyctereutes procyonoides*) and raccoon (*Procyon lotor*), are also a significant threat, and their numbers in grouse habitats are increasing every year (Cove and O'Connell, 2022; Holopainen et al., 2024). Reducing the abundance of these predators has a positive direct effect on black grouse breeding success and adult survival (Grant et al., 2009). However, it is imperative to focus on all mammalian predators on the site, not only foxes, for example because compensatory recruitment of unhunted predators would occur almost immediately, as shown in the study by Smedshaug et al. (1999). Hunting large ungulates also means leaving unnecessary entrails in forest ecosystems, inadvertently encouraging scavengers and predators to consume the remains and return to the area. In addition, high concentrations of wild boar and deer (family Cervidae) disturb black grouse and by grazing on bilberry vegetation, they also negatively affect the availability of food resources and safe cover for chicks. Thus, reducing high numbers of wildlife not only contributes to improved black grouse survival but also leads to a fundamental change in habitat suitability (Cole et al., 2012).

Another very effective measure, often not applied in practice, is a strict ban on feeding game animals in black grouse areas. Overfeeding has a direct impact on the abundance of target species, which are attracted to certain areas due to that. In upland areas, wild boars are often overfed, which leads to a higher predation rate of grouse nests in the feeding sites. This fact has been demonstrated by experiments with artificial nests (Selva et al., 2014; Oja et al., 2015; Cukor et al., 2021).

However, the primary risk of overfeeding is the potential indirect impact on the populations of the grouse's main predator species. The food offered (even of plant origin) is also consumed by rodents, which increases the likelihood of the main predators being present in the area. This relationship was demonstrated in a study carried out in Poland (Selva et al., 2014). The probability of predation on artificial nests placed near feeding sites was 30% higher than on randomly placed artificial nests in the forest. In addition, artificial nests near feeding sites were found quickly by predators. When comparing photo-trap records, it was also found that feeding sites attracted more potential predators of grouse nests (82% of records) than the target species (8%, the rest of the records being other species). In this study, the authors confirmed evidence of increased predation pressure on artificially laid nests within 1 km of feeding sites (Selva et al., 2014). The study by Oja et al. (2015) also confirmed that the predation risk decreases with increasing distance from the feeding site. In addition, the predation risk level is affected after the end of the feeding period. In the case of the cessation of feeding at the feeding site, the risk of predation was higher for another four years. Therefore, it can be concluded that recently abandoned feeding sites still pose an increased risk of predation on black grouse nests and possibly chicks (Oja et al., 2015). The feeding of game animals to reduce their numbers must, therefore, be carried out in pre-selected places and to a limited extent. Otherwise, wild boar, as well as deer and other animals, may be concentrated in locations where they would not naturally appear (Ježek et al., 2013). Therefore, the feeding of game animals should not be allowed in core black grouse areas, especially during the breeding and winter seasons.

6.3 Monitoring populations

Monitoring the distribution, abundance, density, and presence or absence of the watched species are critical indicators describing how populations respond to environmental changes (Williams et al., 2002; Egwumah et al., 2017). Systematic and long-term monitoring of changes and trends in populations can effectively help protect declining or endangered species, document the effectiveness of conservation measures, and also reveal negative impacts on populations of monitored species associated with anthropogenic activity (Goldsmith, 2012). That is why monitoring the abundance and distribution of the black grouse has been—and still is—a vital tool that contributes to the conservation of this species throughout Europe.

However, monitoring methods are diverse (Haider et al., 2024). The most commonly used method is based on the visual and acoustic recording of male grouse by a given observer in the field (Hancock et al., 1999; Dumont et al., 2019; Policht et al., 2019). Monitoring of lekking males is carried out two hours before and no later than two hours after sunrise (Cayford and Walker, 1991; Canonne et al., 2021) and in suitable weather conditions, to avoid distortion or underestimation of the abundance of the monitored population (Hancock et al., 1999; Canonne et al., 2021). Another method, used mainly in northern regions, is counting grouse on pre-marked linear transects with the help of trained dogs that systematically search the surroundings on both sides of the transect and with the help of a mobile application that automatically recalculates the detected abundance for the entire area of interest (e.g., Wegge and Rolstad, 2011; Cukor et al., 2020). Among the non-invasive methods of monitoring black grouse is the observing of local lek sites using camera traps. Compared to traditional monitoring methods, large amounts of data can easily be collected over a relatively long period. For example, Gregersen and Gregersen (2014) found that black grouse males visit lek sites most of the year, primarily searching for food, lekking, or simply socializing. With the help of camera traps, it is relatively easy to monitor populations of this species without increased disturbance by nearby observers of lek habitats (Gregersen and Gregersen, 2014).

Another non-invasive monitoring tool can be passive acoustic monitoring using a recording device. This method can significantly reduce the risk of overestimating the population and lead to a more accurate determination of the abundance of the monitored populations of black grouse (Hambálková et al., 2021). A more suitable signal for this method is a hissing call, which, unlike rookooing, does not overlap each other and is easier to filter out in acoustic software, as it is located at higher sound frequencies (Hambálková et al., 2021). Acoustic performance also has the potential for distinguishing individual subpopulations of the black grouse across its range (Hambálková et al., 2023). One of the reasons why the differentiation of acoustic performance can occur is the isolation of subpopulations. Monitoring and evaluating acoustic variability have the potential to non-invasively assess changes in population across its distributional range.

7 Conclusions

According to our review analysis, it is clear that the status of black grouse in Europe can be characterized by population declines across almost the entire range. However, the main causes vary according to the specific conditions in each country. Central Europe is typically affected most by habitat loss, where black grouse still occur mainly in mountainous habitats and moorlands. In addition, published studies have highlighted increasing predation rates and the impact of human activities, including tourism. Hunting management is another aspect that needs revision in Central European countries where supplementary feeding of wild boar and other ungulates is a common and typical practice, e.g., in the Czechia, attracting not only the target species but also predators such as red fox or marten. In the case of the Scandinavian countries, where black grouse is a commonly hunted species, the gradual population decline can be attributed to decreasing breeding success and increasing chick mortality, with less impact from habitat changes and tourism.

Generally speaking, it is clear that the causes of black grouse decline vary across Europe, with different environmental conditions and human impacts on nature. The positive finding is that many of the identified factors responsible for population decline could be influenced by conservation measures. However, it is important to stress that environmental protection should work hand in hand with wildlife managers to improve these conditions. It is essential that conservation efforts and research continue, particularly in areas where black grouse are rapidly declining and at risk of extinction.

Author contributions

LH: Data curation, Writing – original draft, Writing – review & editing. JC: Conceptualization, Methodology, Supervision, Writing – original draft, Writing – review & editing. KB: Data curation, Writing – original draft, Writing – review & editing. RŠ: Data curation, Writing – original draft, Writing – review & editing. ZV: Visualization, Writing – original draft, Writing – review & editing. SV: Writing – original draft, Writing – review & editing. VS: Writing – original draft, Writing – review & editing. RL: Data curation, Visualization, Writing – review & editing. OA: Writing – review & editing, Supervision.

Funding

The author(s) declare financial support was received for the research, authorship, and/or publication of this article. The research was financially supported by the Ministry of Agriculture of the Czech Republic, institutional support MZE-RO0123 and also by project RAGO (n. 3201200001) supported by Norwegian funds.

Acknowledgments

The authors thank Jitka Šišáková, an expert in the field, and Richard Lee Manore, a native speaker, for checking English and to the two reviewers for their constructive comments.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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5.2 Akustická individualita v pšoukaní samečků tetřívka obecného (*Lyrurus tetrix*)

Výsledky druhé kapitoly přináší zásadní objev hlasové individuality v akustickém projevu kohoutků tetřívka obecného. Analyzovány byly nahrávky jedinců z Finska a Skotska a bylo zjištěno, že tzv. pšoukání nese informaci o specifitě jedinců. Tento výsledek je navíc významný vzhledem k tomu, že testovány byly signály, které nejsou řazeny mezi vokální. Pšoukání je produkováno vzduchem procházejícím konstrikcemi dýchacích cest, nikoli syringem. Nevokálními projevy živočichů se zabývá pouze omezené množství výzkumů, a ještě méně v souvislosti s individualitou jedinců. Výstupy této části splňují II. a III. cíl disertační práce.

Tetřívka obecného je možné monitorovat např. pomocí vzorkování trusu či peří, nebo, jak je u tohoto druhu obvyklé, sčítáním jedinců na tokaništích během období páření. Tato metoda však nemusí být vždy přesná. Ačkoli jsou kohoutci považovaní za věrné svému tokaništi, jejich přesun na jiný lek v rámci jedné sezóny či výměna stanoviště během let není zcela vyloučená. Kromě toho, během namlouvacího rituálu dochází na tokaništi k pohybu kohoutků a při větším počtu jedinců může být situace nepřehledná. Tyto případy mohou vést k nepřesným výsledkům. Monitoring založený na identifikaci jedinců pomocí jejich akustické individuality může zvýšit efektivitu sčítání. Zejména v kombinaci se vzorkováním pobytových znaků by pak bylo možné získat jedinečné údaje o konkrétních tetřívcích. Právě analyzované pšoukání je vhodné pro akustické nahrávky kohoutků tetřívka obecného a jejich následný rozbor. Oproti bublání zaujímá pšoukání vyšší frekvenční rozsahy, díky čemuž netrpí překryvem s hlukem v pozadí a je možné provést měření parametrů.

Publikováno jako:

Hambálková, L., Policht, R., Horák, J., and Hart, V. (2021). Acoustic individuality in the hissing calls of the male black grouse (*Lyrurus tetrix*). PeerJ 9. doi: 10.7717/peerj.11837

Příspěvek autorů:

Richard Policht vytvořil koncept studie a plán metodiky.
Lucie Hambálková, Richard Policht, Vlastimil Hart a Jiří Horák provedli nahrávání akustických projevů kohoutků tetřívka obecného v terénu. Dále se podíleli na zpracování získaných dat pomocí akustických programů a následné testování statistickými analýzami.
Lucie Hambálková a Jiří Horák připravili vizualizaci a tabulky.

Lucie Hambálková vypracovala základní strukturu, obsah a formátování textu.

Richard Policht a Vlastimil Hart recenzovali návrh textu a schválili jeho konečnou podobu.

Acoustic individuality in the hissing calls of the male black grouse (*Lyrurus tetrix*)

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ABSTRACT

Acoustic individuality may well play a big role during the mating season of many birds. Black grouse (*Lyrurus tetrix*) produces two different long-distance calls during mating on leks: rookooing and hissing calls. The first one represents low frequency series of bubbling sounds and the second one represents hissing sound. This hissing represents a signal not produced by the syrinx. We analyzed 426 hissing calls from 24 individuals in Finland and Scotland. We conducted cross-validated discrimination analyses (DFA). The discrimination model classified each call with almost 78% accuracy (conventional result) and the validated DFA revealed 71% output, that is much higher than classification by chance (4%). The most important variables were Frequency 95%, 1st Quartile Frequency, Aggregate Entropy and Duration 90%. We also tested whether between individual variation is higher than within individual variation using PIC (Potential for individual coding) and we found that all acoustic parameters had PIC > 1. We confirmed that hissing call of black grouse is individually distinct. In comparison to the signals produced by the syrinx, non-vocal sounds have been studied rarely and according to our knowledge, this is the second evidence of vocal individuality in avian hissing sounds which are not produced by syrinx. Individuality in the vocalization of the male black grouse may aid females in mating partner selection, and for males it may enable competitor recognition and assessment. Individually distinct hissing calls could be of possible use to monitor individuals on leks. Such a method could overcome problems during traditional monitoring methods of this species, when one individual can be counted multiple times, because catching and traditional marking is problematic in this species.

Subjects Animal Behavior, Zoology
Keywords Acoustic individuality, Hissing call, *Lyrurus tetrix*, Monitoring, Phasianidae

INTRODUCTION

At the time of a decline in the black grouse (*Lyrurus tetrix*) population across its distribution range (*Ciach, 2015*; *Jankovska et al., 2012*; *Kasprzykowski, 2002*), determining actual number of individuals is becoming increasingly important. The causes for this decline vary: change of the environment and climate (*Kurhinen et al., 2009*; *Kvasnes et al., 2010*; *Viterbi et al., 2015*; *White, Warren & Baines, 2013*), parasite infestation (*Jankovska et al., 2012*), predation (*Charnov, Orians & Hyatt, 1976*; *Korpimaki, Koivunen & Hakkarainen, 1996*; *Pekkola et al., 2014*; *Policht et al., 2019*; *Summers et al., 2004*; *Tornberg et al., 2013*; *Widen et al., 1987*), reducing genetic diversity (*Segelbacher, Hoglund &*

Submitted 8 October 2020
Accepted 1 July 2021
Published 9 September 2021

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Academic editor
Maria Servedio

Additional Information and Declarations can be found on page 11

DOI **10.7717/peerj.11837**

How to cite this article Hambálková L, Policht R, Horák J, Hart V. 2021. Acoustic individuality in the hissing calls of the male black grouse (*Lyrurus tetrix*). **PeerJ 9:e11837 DOI 10.7717/peerj.11837**

Storch, 2003; Segelbacher et al., 2014) and human activities (Formenti et al., 2012; Hess & Beck, 2012; Ingold, 2005; Nichter, Lipp & Gregory, 2017; Storch, 2013). Methods and options for protection and conservation of grouse are manifold and are realized at the local, regional, and national levels (Storch, 2013).

An integral part of any conservation measures in general, and thus also in the case of black grouse populations in particular, is monitoring. Methods of monitoring are diverse. Franceschi et al. (2014) simulated two monitoring approaches: plot sampling and distance sampling. According to their study, distance sampling is a better way to monitor grouse in terms of accuracy. On the other hand, this approach is also costly, as it requires 4–5 sampling points per km^2 for reliable outcomes (Franceschi et al., 2014). The most common counting method for black grouse is to register males displaying in the spring (Hancock et al., 1999). Depending on the size of the area to be monitored, it is possible to perform a full-area survey or to select sample areas at random (Hancock et al., 1999). Monitoring based on acoustic features of bird vocalization could be a more efficient method. Laiolo et al. (2007) recommended combining counting based on vocalization with physical marking.

Black grouse males produce the following kinds of sounds: resonant rookooing call and hissing calls. The latter is further subdivided into tones of aggression and alarm calls (Cramp, 1983). This study is focused on a particular type of hissing call—crowing-hiss, described by Cramp (1983) as harsh and angry sound, which is produced during the display of male black grouse. This hissing sound is not produced by syrinx. Such non-vocal sounds are produced by some constriction located on the way from the lungs to the bill (Fitch & Hauser, 2003). Potential information encoded in non-vocal sounds of birds remains almost unstudied (Budka et al., 2018). Recent research of hissing sounds produced by geese confirmed encoding of individual identity during antipredator behavior (Policht et al., 2020). In comparison to non-vocal acoustic signals of birds, majority of bioacoustic studies focused on research of sounds produced by syrinx. A hissing sound also appears in black grouse chicks above the age of 3 weeks, but we do not suppose it is the same sound category that is the focus of our study (Meinert & Bergmann, 1983). This type of vocalization, along with the rookooing call, is the most prominent sound made by black grouse, which can be heard over long distances and even in closed habitats such as forests with dense undergrowth. Such calls are frequently used for population monitoring to find actually used leks and counting present males. Therefore, this type of call may play an important role in noninvasive monitoring of black grouse. The rookooing call can be characterized as a low-frequency, repetitive sound within a range of about 200 to 1,000 Hz. This is why this type of call often overlaps with background noise frequencies. Compared with this, the hissing call is found in the frequency range of 350 to 4,500 Hz and is therefore easier to filter out from background noise and to mark this type of call for measurement using acoustic software. Thanks to these characteristics, the hissing call may be more suitable for acoustic monitoring of black grouse.

In an effort to ensure quiet conditions for game wildlife, non-invasive monitoring, such as that based on vocalization, is the method of choice. This method relies on distinguishing individuals without physical marking. In our study, we analyzed the vocalization of male black grouse to examine variation between individuals, and to find out whether vocalization characteristics could serve as a unique identifying trait.

METHODS

Study areas and recording

We recorded the hissing calls of male black grouse during their mating season. Recording took place in Finland in 2012 and 2013, and in Cairngorms National Park, Scotland in 2019. Field experiments were approved by the Department of Natural Resources, Ministry of Agriculture and Forestry, Finland and by the Game & Wildlife Conservation Trust, Scotland. According to Finnish legislation in general and to the hunting legislation, this type of scientific project does not require any special permits or licenses. All appropriate permissions were in place for the fieldwork in Scotland. The research was conducted in accordance with the guidelines of the Animal Behavior Society for the ethical use of animals in research. The study was carried out in accordance with the recommendations in the Guide for Care and Use of Animals of the Czech University of Life Sciences, Prague. The Animal Care and Use Committee of the Czech Ministry of the Environment approved the protocol (Permit number: 15106/ENV/14-825/630/14).

Vocalization of male black grouse was recorded with the audio recorder Olympus LP-100 in combination with a Sennheiser ME 66 directional microphone (frequency response 20 Hz–20 kHz ± 2.5 dB) complemented by a K6 powering module. Recordings were saved in .wav format (48 kHz sampling rate, 16-bit sample size). We recorded all individuals in the wild during courtship at leks. Lek is an area where two or more males perform courtship displays to gain an advantage for mating with females. All leks were approached before the arrival of males, about 2 h before sunrise. Each recording session took on average 1 h and was performed from a portable hide so that the males could be observed without being disturbed. The distance of the hide from display sites was 10 m on average. During the pilot study, we only tested the variability between multiple individuals on one lek, and it turned out that the individual variability is much larger. To avoid the risk of multiple counting of the same individual, we chose the option of selecting only one, maximum of two individuals on each lek. The distance between visited display sites was at least one km and, according to *Borecha, Willebrand & Nielsen (2017)*, black grouse males show strong fidelity to their lek; therefore, the risk of recording the same individual at the two display sites was low.

Acoustic analyses

Recordings were analyzed using Raven Pro 1.5 software with a 512 sample size and a Hann window. We selected good quality calls with high signal to noise ratio, non-overlapping with other hissing calls or background noise and wind. Each selected hissing call was manually bounded by the selection frame that is defined by the beginning and end of the signal and the lowest and highest frequency of the signal. Temporal and frequency variables were then measured automatically. These measurements were entered into the statistical analysis.

Statistical analyses

We analyzed 426 good-quality calls from 31 individuals (at least ten separate hissing calls per individual). We measured 29 variables (Table 1). We excluded variables with low or no variation. The remaining variables were standardized using *Z*-score transformation (subtracting the mean and dividing by standard deviation). In order to test individual variation, we used stepwise Discrimination Function Analysis (DFA) using IBM SPSS Statistics 24.0 software (IBM Corp., Armonk, NY, USA). We applied a leave-one-out cross-validation procedure (IBM SPSS Statistics 20) to validate the results of DFA.

To test the potential for individual variation (Potential of Individual Coding—PIC) for each parameter, we compared the coefficient of variation (CV) within and between individuals. The PIC ratio was computed for each acoustic parameter by dividing the $CV_{between}$ by the mean of the CV_{intra} values related to each individual (*Robisson, 1992*). For these tested parameters, a PIC value greater than one means that an inter-individual variability is higher than intraindividual variability. We tested a significance using Kruskal–Wallis test.

RESULTS

Hissing call description

The hissing calls of black grouse represent wideband acoustic signals, in which energy is spread across a wide frequency range. The duration of such calls ranged from 0.1 to 1.21 s (0.76 ± 0.16, mean ± SD). This type of call can consist of one or two notes; however, the occurrence of a two-syllable form was rare ($\sim n < 1\%$)—so we did not analyze these calls.

The Low frequency ranged from 352.9 to 1,310.3 Hz (830.2 ± 195.6 Hz, mean ± SD) and the High frequency from 1,702.4 to 4,482.8 Hz (2,687.5 ± 536.4 Hz, mean ± SD) for all individuals. Frequency range reached 729.6 to 3,241.4 Hz (1,857.3 ± 478.6 Hz, mean ± SD). The spectrograms of black grouse recorded in Finland and Scotland are shown in the figures below (Figs. 1 and 2). The spectrograms were generated in Avisoft-SASLab Pro with FFT length, 1,024 sample size, a Hamming window and 87.5% overlap. For a representative recording of a hissing call of one individual form Scotland and one individual from Finland see Audio S1 and Audio S2.

Individual variation

From selected parameters the resulting model (see Table S1) included 13 significant acoustic variables ($p < 0.001$; $r \leq 0.87$): 1st Quartile Frequency, Relative 1st Quartile Frequency, Aggregate Entropy, Average Entropy, Relative Center Time, Call Duration, Duration 90%, Frequency 5%, Relative 3rd Quartile Frequency, Frequency 95%, Inter-Quartile Range Bandwidth, Inter-Quartile Range Duration and Time 5% (Table 1). The first four discriminant functions had Eigenvalues > 1 and explained 79.7% of the variation. With the first discrimination function mostly correlated F95% (Frequency 95%) (r = 0.767) and Q1F (Quartile 1 Frequency) (r = 0.707) and the second discriminant function correlated best with AggEnt (Aggregate Entropy) ($r = 0.390$) and Dur 90% (Duration 90%) (r = 0.387) (Fig. 3). The Discriminant Function Analysis excluded seven

Table 1 **Descriptions of acoustic parameters measured in Raven Pro 1.5 that entered statistical analysis.**

Acoustic parameter name	Abbreviations (Units)	Description
*1st Quartile frequency	Q1 Freq (Hz)	The frequency that divides the signal into two frequency intervals containing 25% and 75% of the energy in the signal.
*Relative 1st quartile frequency	Q1 Freq rel,	The frequency that divides the signal into two frequency intervals containing 25% and 75% of the energy in the signal relative to the frequency range of the signal.
*3rd Quartile frequency	Q3 Freq (Hz)	The frequency that divides the signal into two frequency intervals containing 75% and 25% of the energy in the signal.
Relative 3rd quartile frequency	Q3 Freq rel,	The frequency that divides the signal into two frequency intervals containing 75% and 25% of the energy in the signal relative to the frequency range of the signal.
1st Quartile time	Q1 Time (s)	The time that divides the signal into two time intervals containing 25% and 75% of the energy in the signal.
Relative 1st quartile time	Q1 Time rel,	The time that divides the signal into two time intervals containing 25% and 75% of the energy in the signal relative to signal duration.
Relative 3rd quartile time	Q3 Time rel,	The time that divides the signal into two time intervals containing 75% and 25% of the energy in the signal relative to signal duration.
*Aggregate entropy	Agg entropy (bits)	The aggregate entropy measures the disorder in a sound by analysing the energy distribution. Higher entropy values correspond to greater disorder in the sound whereas a pure tone with energy only one frequency bin would have zero entropy. It corresponds to the overall disorder in the sound.
*Average entropy	Avg Entropy (bits)	This entropy is calculated by finding the entropy for each frame in the signal and then taking the average of these values.
Bandwidth 90%	BW 90% (Hz)	The difference between the 5% and 95% frequencies.
Center frequency	Center freq (Hz)	The frequency that divides the signal into two frequency intervals of equal energy.
Center time	Center time (s)	The point in time at which the signal is divided into two time intervals of equal energy.
*Relative center time	Center time rel,	The point in time at which the signal is divided into two time intervals of equal energy relative to the signal duration.
*Call duration	Duration (s)	The difference between begin time and end time for the signal.
*Duration 90%	Dur 90% (s)	The difference between the 5% and 95% times.
*Frequency 5%	Freq 5% (Hz)	The frequency that divides the signal into two frequency intervals containing 5% and 95%.
Relative frequency 5%	Freq 5% rel,	The frequency that divides the signal into two frequency intervals containing 5% and 95% relative to frequency range.
*Frequency 95%	Freq 95% (Hz)	The frequency that divides the signal into two frequency intervals containing 95% and 5%.
Relative Frequency 95%	Freq 95% rel,	The frequency that divides the signal into two frequency intervals containing 95% and 5% relative to frequency range.
*Inter-quartile range bandwidth	IQR BW (Hz)	The difference between the 1st and 3rd quartile frequencies.
*IQR (Inter-quartile range) duration	IQR Dur (s)	The difference between the 1st and 3rd quartile times.
Max entropy	Max entropy (bits)	Maximum entropy calculated from each frame.
Max frequency	Max freq (Hz)	The frequency at which max power occurs within the signal.
Max time	Max time (s)	The first time in the signal at which a spectrogram point with power equal to max power/peak power occurs.
Min entropy	Min entropy (bits)	The minimum entropy calculated for a spectrogram slice within the signal bounds.
Peak time	Peak time (s)	The first time in the signal at which a sample with amplitude equal to peak amplitude occurs.

(Continued)

Table 1 (continued)

Acoustic parameter name	Abbreviations (Units)	Description
*Time 5%	Time 5% (s)	The time that divides the signal into two time intervals containing 5% and 95%.
Relative time 5%	Time 5% Rel,	The time that divides the signal into two time intervals containing 5% and 95% relative to signal duration.
Relative time 95%	Time 95% Rel,	The time that divides the signal into two time intervals containing 95% and 5% relative to signal duration.

Note:
13 parameters (*) were included in resulting DFA model.

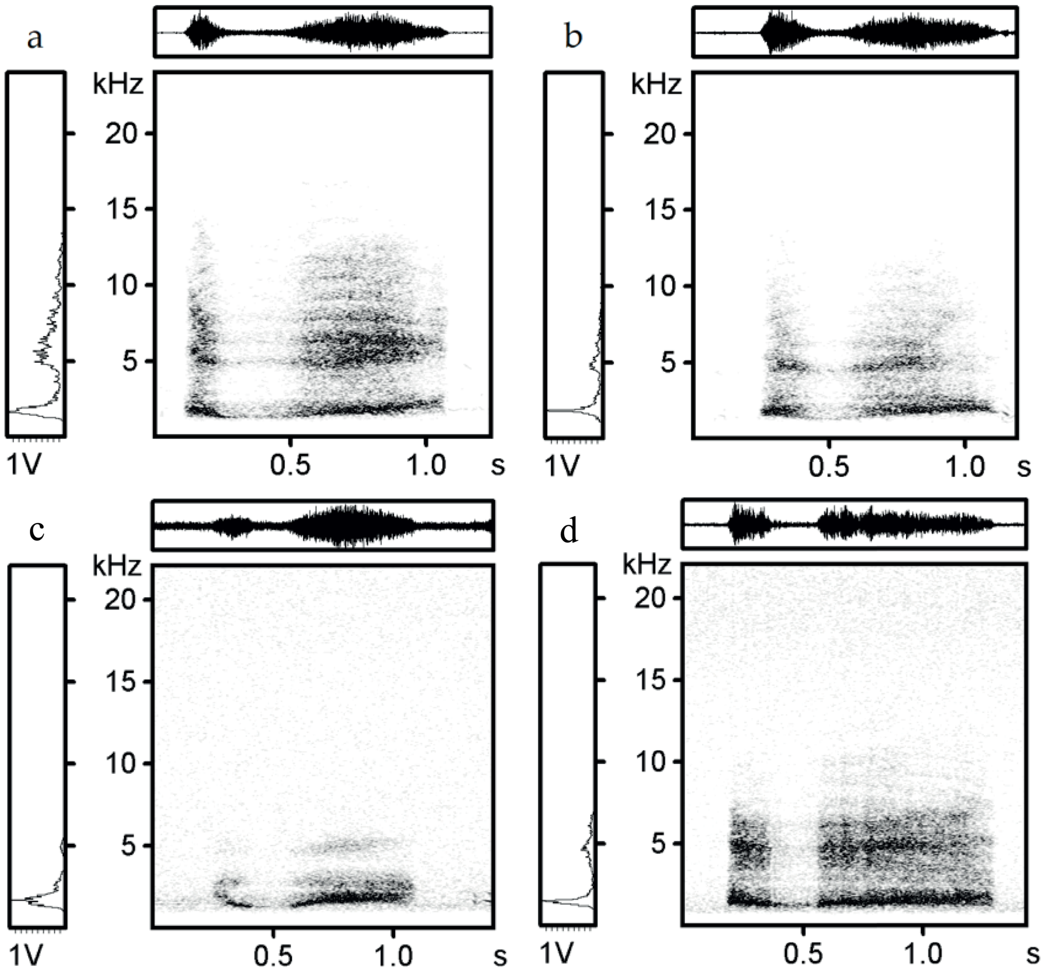

Figure 1 Spectrograms and oscilograms: Representative hissing calls of two of the black grouse from Scotland (A, B) and Finland (C, D). Each lettered panel refers to one individual bird. Spectrograms indicate observable differences between four individuals. Full-size DOI: 10.7717/peerj.11837/fig-1

out of 31 individuals due to their missing or extreme values of the measured parameters. The cause could be a poorer degree of sound quality that did not pass the analysis. This selection has been made by model procedure automatically. The resulting DFA model correctly classified 77.9% (71.1%, cross-validated result) hissing calls. Six individuals showed the highest classification accuracy (80–100%), and most individuals ($N = 15$) were

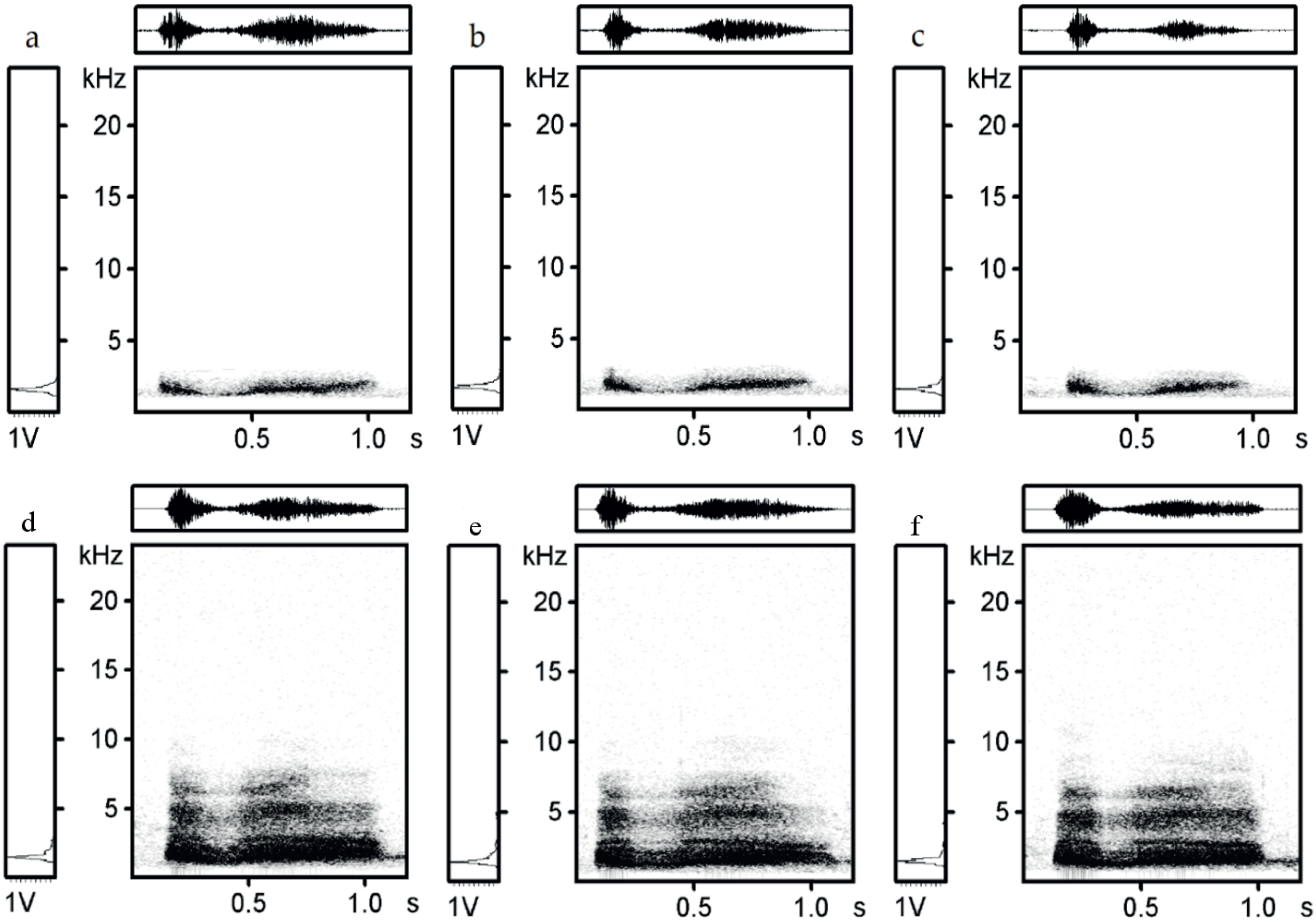

Figure 2 Spectrograms and oscilograms of three hissing calls of black grouse from one individual from Scotland (A–C) and one individual from Finland (D–F). Each lettered panel refers to one hissing call. Spectrograms in rows indicate consistent stability of individual pattern within the same individual.

Full-size DOI: 10.7717/peerj.11837/fig-2

classified with 60–79% success. Only three males were classified with a lower than 59% success. These results were much higher than classification by chance (4%). The output of classification results is shown in Table S2. We tested whether observed classifications differed from the expected classifications (by chance) and we found a significant difference: Chi-Square = 307.1, df = 23, $p < 0.001$. We also tested whether between individual variation is higher than within individual variation using PIC and we found that all acoustic parameters had PIC > 1 (Table 2).

DISCUSSION

Our results reveal that the wideband hissing call of male black grouse is individual specific. The discrimination model classified each call with almost 78% accuracy, and the first four discriminant functions explained nearly 80% of variation. The PIC ratio was higher than one for all parameters tested, demonstrating that the variability between individuals was higher than the variability within individuals. Therefore, the hissing call is

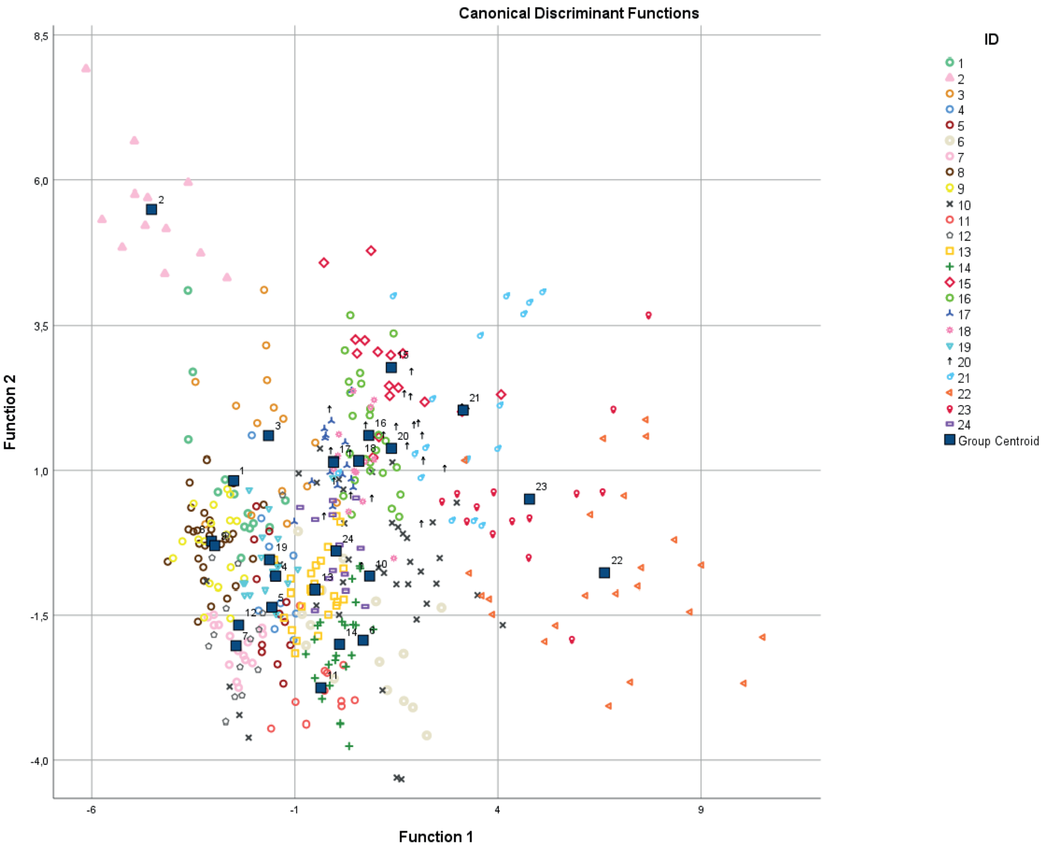

Figure 3 Scatter plot of hissing calls. Numbers refer to individuals, squares represent group centroids. Discrimination function 1 represents Frequency 95% and function 2 represents 1st Quartile Frequency.

Full-size DOI: 10.7717/peerj.11837/fig-3

a type of vocalization that carries information about individuality. Considering this type of call is a wideband, non-vocal sound, such a result is quite unique. There are not many studies focused on non-vocal animal sounds and even fewer of them have provided results confirming individuality in this type of vocalization; however, there are several. Individual variation was found in the male Houbara Bustard (*Chlamydotis undulata undulata*), which produces sounds called booms during courtship (*Cornec, Hingrat & Rybak, 2014*). Acoustic variation between individuals was also investigated in the Greater Prairie-chicken (*Tympanuchus cupido*) and the boom vocalization of this species was found to have individual characteristics (*Hale, Nelson & Augustine, 2014*). Thanks to temporal patterns, along with the number of drumming strokes, it is possible to discriminate individuals of the Great Spotted Woodpecker (*Dendrocopos major*) (*Budka et al., 2018*). According to acoustic analysis in the male Greater Sage-grouse (*Centrocercus urophasianus*), the "rustling" of wings differs between individuals (*Koch, Krakauer & Patricelli, 2015*). Therefore, mechanical sounds can also carry acoustic information about individuality.

Vocal individuality in some non-passerine groups has been intensively studied, such as colonial birds or nocturnal birds. On the other hand, gallinaceous species has not been

Table 2 **Descriptive statistics and Potential for individual coding.**

Variable	DFA	Mean	Min	Max	SE	Kruskal–Wallis	Mean CVw	CVa	PIC
1st Quartile frequency	X	1,444.3	0.9	3,000.0	271.8	*	38,503.6	73,887	1.919
Relative 1st quartile frequency	X	3.3	0.0	1500.0	62.4	*	219.9	3,896	17.714
3rd Quartile frequency	X	197.8	0.1	3,027.8	436.6	*	70,423.4	190,607	2.707
Relative 3rd quartile frequency		0.3	0.0	1.0	0.2	*	0.0	0	1.960
1st Quartile time		1,747.2	0.5	3,562.5	367.6	*	60,556.2	135,130	2.231
Relative 1st quartile time		2.4	0.1	1,687.5	56.2	*	229.5	3,159	13.761
Relative 3rd quartile time		246.2	0.2	4,3525.0	1508.0	*	216,894.9	2,274,186	10.485
Aggregate entropy	X	3.2	0.7	4.8	0.5	*	0.2	0	1.846
Average entropy	X	2.8	1.7	4.0	0.4	*	0.1	0	1.869
Bandwidth 90%		839.2	187.5	2,437.5	355.2	*	69,079.2	126,142	1.826
Center frequency		1,589.0	468.8	3,375.0	303.2	*	45,489.3	91,910	2.020
Center time		198.1	0.1	3028.1	436.6	*	70,428.0	190,611	2.706
Relative center time	X	0.5	0.1	1.0	0.2	*	0.0	0	2.470
Call duration	X	1.0	0.2	1.9	0.2	*	0.0	0	1.460
Duration 90%	X	0.7	0.1	1.6	0.2	*	0.0	0	1.657
Frequency 5%	X	1,209.8	375.0	2,250.0	249.9	*	42,818.7	62,427	1.458
Relative Frequency 5%		0.2	0.0	0.5	0.1	*	0.0	0	1.303
Frequency 95%		2,049.0	1,125.0	4,125.0	432.2	*	84,005.1	186,777	2.223
Relative frequency 95%		0.7	0.3	1.0	0.1	*	0.0	0	1.823
Inter-quartile range	X	301.8	86.1	1,218.8	188.9	*	17,712.6	35,694	2.015
IQR (Inter-quartile range) duration	X	0.4	0.0	1.2	0.1	*	0.0	0	2.301
Max entropy		3.9	2.9	4.9	0.3	*	0.0	0	2.044
Max frequency		1,572.4	468.8	3,468.8	336.3	*	58,737.8	113,076	1.925
Max time		197.9	0.1	3,027.5	436.6	*	70,409.4	190,584	2.707
Min entropy		1.6	0.1	2.9	0.4	*	0.1	0	1.685
Peak time		197.9	0.1	3,027.5	436.6	*	70,409.3	190,583	2.707
Time 5%	X	197.9	0.0	3,027.5	436.5	*	70,738.2	190,565	2.694
Relative time 5%		0.1	0.0	0.4	0.0	*	0.0	0	2.247
Relative time 95%		0.8	0.6	1.0	0.1	*	0.0	0	2.143

Note:

(DFA) 13 variables included in final DFA model (X). (SE) standard error of the mean. (Kruskal–Wallis) Kruskal–Wallis test after Bonferroni correction, (*) $p < 0.001$. (Mean CVw) within individual comparison. (CVa) between individual comparison. (PIC) Potential for Individual Coding.

studied frequently. Acoustic displays of the Japanese quail (*Coturnix coturnix japonica*) are characterized by a potential for vocal individuality in terms of temporal parameters. Spectral characteristics of the voice are then associated with the possibility of greater stability during the development of the individual, which is important in the question of long-term recognition of individuals (*Sezer & Tekelioglu, 2010*). Call analyses of European and Japanese quail (*Coturnix c. japonica, C. c. coturnix*) confirm a difference between these two subspecies based on the time structure of vocalization (*Collins & Goldsmith, 1998*). The hazel grouse (*Bonasa bonasia*), studied in Switzerland, exhibits 6 to

11 elements of singing during flight. These elements (individual tones or syllables) are characterized by their individual specificity (*Mulhauser & Zimmermann, 2003*). Specific parameters responsible for acoustic individuality were also found in males and females of the common quail (*Coturnix coturnix*); the results of this study also indicated that the male's inter-individuality is dependent on sexual maturation and age (*Guyomarc'h, Aupiais & Guyomarc'h, 1998*). Our study demonstrates a vocal individuality in gallinaceous species with lek mating system.

What role acoustic individuality plays in the black grouse's voice is still a question for future research. Calls of individual birds may carry information about male quality (*e.g.*, physiological state, age) for females (*Guyomarc'h, Aupiais & Guyomarc'h, 1998*), and, at the same time, it might be a signal for other males providing information about the strength of a rival. Finally, individuality can serve to easily identify individuals among each other within a group. Its potential for scientists lies in the possibility of use for noninvasive monitoring. Taking an observation, census may be inaccurate; due to overflights of individuals within the lekking site, repeated census of the same individuals may occur and therefore the results of counting may be overestimated. Monitoring based on acoustic recognition could provide the required accuracy and assistance in areas where observation is limited by environmental conditions (*e.g.*, the situation when males of black grouse lek individually hidden in the undergrowth).

CONCLUSION

The black grouse population is affected by many factors that contribute to its decline, and as part of its conservation, efforts are being made to develop better methods of protection, including monitoring. Vocalization recording and analysis could be a non-invasive monitoring tool, especially if there is individuality in the voice of individuals. This method could significantly reduce the risk of multiple counting of the same individual. Surprisingly, we found this individuality in the black grouse in the non-vocal type of display. The discrimination model classified each call with high accuracy and important variables turned out to be Frequency 95% and Quartile 1 Frequency. In comparison to the signals produced by the syrinx, non-vocal sounds have been studied rarely and according to our knowledge, this is the second evidence of vocal individuality in avian hissing sounds which are not produced by syrinx. Finding specific identifiers in vocalization could lead to a more accurate determination of the number of individuals.

ACKNOWLEDGEMENTS

We very much appreciate the help and support of Mr. Christian Krogell, Department of Natural Resources, Ministry of Agriculture and Forestry, Finland. We are also thankful to Mr. Ilkka Ala-Ajos for logistical support for our research in Finland. Furthermore, we would like to thank Dr. David Parish, Marlies Nicolai and Dr. Kathy Fletcher from the Game & Wildlife Conservation Trust and the gamekeepers in Cairngorm National Park, Scotland. We would like to express our gratitude to Robert B. Davis for correction of the English language. Thanks for help in translating articles also goes to Mr. Roland Kralik.

ADDITIONAL INFORMATION AND DECLARATIONS

Funding

This research was funded by the IGA of the Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, Prague. Project number: B_04_18. There was no additional external funding recieved for this study. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Grant Disclosures

The following grant information was disclosed by the authors:
IGA of the Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, Prague: B_04_18.

Competing Interests

The authors declare that they have no competing interests.

Author Contributions

- Lucie Hambálková performed the experiments, analyzed the data, prepared figures and/or tables, and approved the final draft.
- Richard Policht conceived and designed the experiments, performed the experiments, analyzed the data, authored or reviewed drafts of the paper, and approved the final draft.
- Jiří Horák performed the experiments and approved the final draft.
- Vlastimil Hart conceived and designed the experiments, performed the experiments, authored or reviewed drafts of the paper, and approved the final draft.

Animal Ethics

The following information was supplied relating to ethical approvals (*i.e.*, approving body and any reference numbers):

The Animal Care and Use Committee of the Czech Ministry of the Environment approved the protocol (Permit number: 15106/ENV/14-825/630/14).

Field Study Permissions

The following information was supplied relating to field study approvals (*i.e.*, approving body and any reference numbers):

Field experiments were approved by the Department of Natural Resources, Ministry of Agriculture and Forestry, Finland and by the Game & Wildlife Conservation Trust, Scotland.

Data Availability

The following information was supplied regarding data availability:

The raw data are available as Supplemental Files.

The resulting model of statistical analysis shows all individuals and significant variables tested. The output of classification results shows classification accuracy percentages for each individual.

Supplemental Information

Supplemental information for this article can be found online at http://dx.doi.org/10.7717/peerj.11837#supplemental-information.

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5.3 Pšoukání tetřívka obecného vykazuje geografickou variabilitu napříč distribuční oblastí

V rámci třetí části této práce byly opět analyzovány akustické syčivé signály, tedy pšoukání. Potenciál individuality v hlase kohoutků na geografické úrovni bylo provedeno na nahrávkách z Finska, Skotska, České republiky a Ruska. Analýzy ukázaly, že mezi jednotlivými populacemi existuje variabilita, ne však natolik výrazná, aby bylo možné ji označit za dialekty. Bylo zjištěno, že populace ze Skotska a Ruska vykazovaly větší vnitřní variabilitu ve srovnání s těmi z České republiky a Finska. Výsledky studie jsou vhodným podkladem pro další analýzy zaměřené na variabilitu, respektive individualitu v akustických projevech tetřívka obecného.

Tetřívek má poměrně rozsáhlý areál výskytu, lze tedy předpokládat, že mezi jednotlivými populacemi mohou existovat geografické rozdíly v akustickém projevu. Podobně jako u zpěvných ptáků by se i u tetřívka mohly projevit různé dialekty vázané na danou oblast. V současné době, kdy dochází z důvodu poklesu početnosti vlivem negativních faktorů k fragmentaci populací a vznikají tak izolované skupinky, by znalost původu jedinců mohla pomoci při jejich stabilizaci a ochraně. Výstupy této části naplnily IV. cíl disertační práce.

Publikováno jako:

Hambálková, L., Policht, R., Cukor, J., Hart, V., and Ševčík, R. (2023). Black Grouse Hissing Calls Show Geographic Variability across the Distribution Area. Animals 13. doi: 10.3390/ani13111844

Příspěvek autorů:

Koncept studie a plán metodiky vytvořil Richard Policht.
Na nahrávání akustického projevu kohoutků tetřívka obecného během období páření se podíleli **Lucie Hambálková**, Richard Policht a Vlastimil Hart.
Správu dat a formální analýzu provedla **Lucie Hambálková**, stejně tak zpracování dat v akustických programech.
Dohled a konzultace při provedení akustických a statistických analýz a tvorbě manuskriptu měli na starosti Richard Policht, Jan Cukor, Vlastimil Hart a Richard Ševčík.
Vizualizace získaných nahrávek a výsledků analýz vytvořila **Lucie Hambálková**.

Základní strukturu, obsah a formátování textu připravila **Lucie Hambálková**, následnou revizi a úpravy provedli Richard Policht a Jan Cukor.

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Article

Black Grouse Hissing Calls Show Geographic Variability across the Distribution Area

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Simple Summary: Geographical variability of acoustic signals is studied more often in songbird species, which does not include the black grouse. The black grouse males use different calls during the mating performance, including vocal rookooing. No studies have yet dealt with a more detailed analysis of these signals, except one. Although the studied hissing calls of this species are classified as non-vocal acoustic signals, individuality was observed in these calls. To discern whether there is also geographical variability across the range or distribution area of the black grouse, we analyzed and compared hissing calls from four countries. Individuals in the Czech Republic, Finland, Scotland, and Russia were recorded during mating seasons. The results of the analysis revealed differences between the four subpopulations, although not at the level of dialect distinction. The study of acoustic variability, supported by genetic research, will help to better understand the links or, conversely, the differentiation processes between subpopulations.

Abstract: The black grouse is a species whose population development requires constant monitoring due to a rapidly declining trend, especially in Central Europe. Variability in the voices of geographically separated populations can aid in counting within individual populations. This has been investigated with the black grouse. However, the variability of the acoustic behavior of black grouse between populations was investigated for the first time. In total, 82 male black grouse were recorded during the lekking season in four countries: the Czech Republic, Scotland, Finland, and Russia. We analyzed recordings of hissing calls, i.e., the non-vocal signal. DFA analysis correctly classified almost 70% of the recordings. The results indicate a certain degree of difference between the grouse populations from the four countries examined. The mean frequency of hissing calls for populations was 1410.71 ± 170.25 Hz, 1473.89 ± 167.59 Hz, 1544.38 ± 167.60 Hz, and 1826.34 ± 319.23 Hz in the Czech Republic, Finland, Russia, and Scotland, respectively. Populations from Scotland and Russia have greater intra-variability compared to grouse from the Czech Republic and Finland, indicating that population density is not the principal factor in the geographical variability of black grouse hissing calls. Range-level differences enhance knowledge and facilitate the assessment of species evolution.

Keywords: *Lyrurus tetrix*; bioacoustics; conservation; acoustic variability

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Citation: Hambálková, L.; Policht, R.; Cukor, J.; Hart, V.; Ševčík, R. Black Grouse Hissing Calls Show Geographic Variability across the Distribution Area. *Animals* **2023**, *13*, 1844. https://doi.org/10.3390/ani13111844

Received: 8 May 2023
Revised: 27 May 2023
Accepted: 29 May 2023
Published: 1 June 2023

1. Introduction

The black grouse (*Lyrurus tetrix*) distribution area extends from Great Britain through Russia to North Korea and from Fennoscandia to the Alps with scattered populations in Central Europe and Albania [1,2]. The populations of this species are experiencing a non-negligible decline, especially in Central and Eastern Europe [3–5] and in Fennoscandia [6]. The black grouse as a species is classified as of Least Concern [2]; however, there are countries where it struggles to survive [7–11]. The main reasons for the decline are nest predation and increasing chick and subadult bird mortality [6,12–14]. Other factors are changes in the environment [15–18], parasite infestation [19], predation of adults [20–26], reduced genetic diversity [10,27], human activities [28–33], and global climate changes [6,33–36]. Based on the above-mentioned reasons, there is a great deal of effort in the above countries to address declining populations [37–41] with the help of reintroductions and effective monitoring methods. Currently, there are several methods for the census of Phasianidae, including black grouse. Baillie [42] presents these census methods for terrestrial breeding bird species: territory mapping, line transects, and point counts. The ideal method for monitoring birds involves a statistically rigorous study design with unbiased estimates against the likely number of observers. Recording males displaying in the spring during the lekking season is the most common method of counting black grouse [43]. Methods currently used in Norway—determination by vocal expressions during display and using dogs on transects—or in combination with physical marking [44,45], are not suitable for low-density populations, such as in Central Europe [19,46–49].

A census based on the recording of the acoustic displays of the male grouse during the courtship on the lek can bring many advantages. It is a non-invasive method that doesn't disturb birds on the leks and can be more accurate thanks to the individual recognition of males. In black grouse, acoustic signals are divided into two main categories of sounds, which are resonant rookooing and hissing calls [50]. Hissing calls represent a non-vocal signal produced by partial constriction of the windpipe between the lungs and bill [51]. These signals are an important part of courtship on leks because both males and females decide which lek to visit based on acoustic performance [52]. Recently, it was found that the grouse's non-vocal hissing calls carry an individual specificity that makes it possible to distinguish individuals from each other [53].

Therefore, this article is focused on the acoustic expression of the black grouse from a broader perspective. Due to the relatively large area of occurrence of this species [6], there is likely geographical variability in its acoustic display. It could help to differentiate the origin of individuals by their acoustic signals because one of the problems of the black grouse population is its fragmentation and isolation [9,18,27,39,54]. On the other hand, it could theoretically hinder efforts to reintroduce black grouse from remote areas, as during the courtship, the individual's acoustic display is one of the characteristics to which both females and competing males respond.

So far, only a few studies have paid attention to this part of the grouse's behavior. This study aimed to find (i) whether there is an acoustic variability in black grouse male's display at geographical range and (ii) if it would allow for the determination of the original population of individual black grouse based on their vocal or non-vocal performance.

2. Materials and Methods

2.1. Study Areas and Recording

The recording of male black grouse took place in four regions: Finland, Russian Federation, and Czech Republic in 2012–2014, and in Scotland in 2019. In total, six locations were visited for recording purposes (Figure 1, Table 1). To prevent the black grouse from being disturbed at its sites, the exact coordinates of the locations where the recording took place are not given. The hissing calls of black grouse were recorded during the spring mating season, which takes place in April and May. All individuals were recorded in the wild. The leks were approached approximately two hours before the arrival of males to ensure an uninterrupted course of data collection. Recording sessions were performed in a portable blind or by hiding in natural vegetation. Each session took about one hour. The distance of the microphone from lekking grouse was 10 m on average. Acoustic signals of male black grouse were recorded with the dictaphone Olympus LP-100—in combination with a Sennheiser ME 66 directional microphone (frequency response 20 Hz–20 kHz ± 2.5 dB) complemented by a K6 powering module. Recordings were saved in .wav format (48 kHz sampling rate, 16-bit sample size). Multiple sites were visited at each of the six locations and, at each site, only individuals that could be distinguished from each other were recorded, usually one or two males per site. Each lek was visited only once to avoid the repeated recording of the same individual. The risk of recording the same individual at two sites was low; according to Borecha, Willebrand, and Nielsen [55], black grouse males show strong fidelity to their leks, and in our study, the leks were at least one kilometer apart.

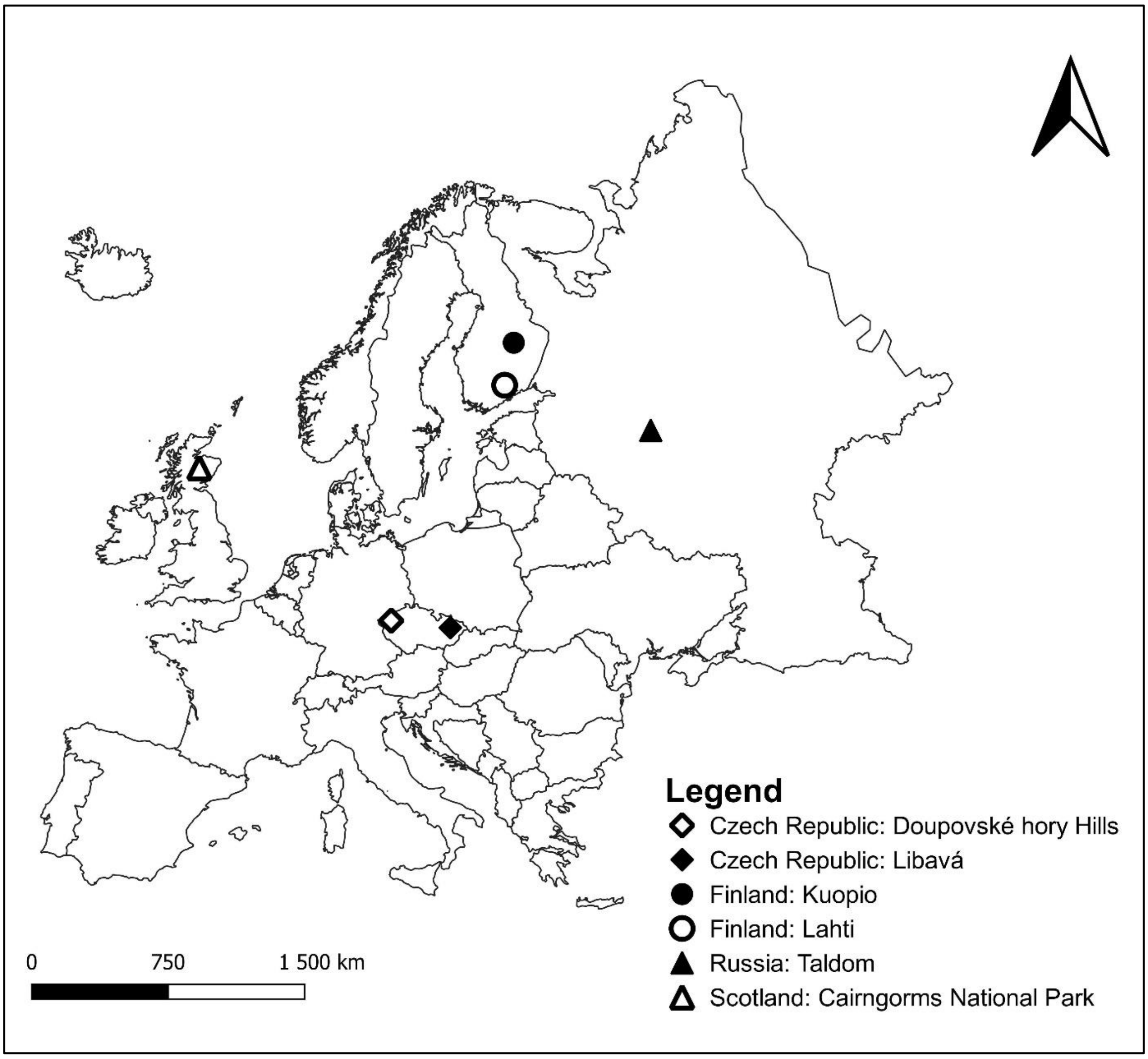

Figure 1. Six locations of black grouse recording: Doupovské hory Hills and Libavá in the Czech Republic, Kuopio and Lahti in Finland, Taldom in Russia, and Cairngorms National Park in Scotland.

Table 1. Basic information about the black grouse population in four monitored countries.

Country	Estimated Population (Lekking Males)	Location of Study	Males (n)	Calls (n)	ID of Males
Czech Republic	355	Libavá, Doupovské hory Hills	20	176	1–20
Scotland	3400	Cairngorms National Park	17	262	21–37
Russia	11.3 mil.	Taldom	18	169	38–55
Finland	425,000	Lahti, Kuopio	27	246	56–82
Total			82	853	

Note: Estimated populations refer to dates known to 2022 [56–59].

2.2. Acoustic Analyses

The recordings were analyzed using Raven Pro 1.5 software with a 512 sample size and a Hann window. Only good quality calls with a high signal-to-noise ratio that were non-overlapping with other hissing calls, background noise, and wind were selected for the analysis. The specific area of hissing calls was manually labeled in the analysis to include the beginning to end of the call and the lowest and highest frequencies. Temporal and frequency variables were measured automatically by the software within the indicated areas of the signals. These measurements were entered into the following statistical analysis. The spectrograms were generated in Avisoft-SASLab Pro with FFT length, 1024 sample size, a Hamming window, and 87.5% overlap.

2.3. Statistical Analyses

In total, 853 hissing calls from 82 male black grouse from four countries were analyzed. For every individual, a minimum of five calls were included in the analysis (11 ± 5; mean ± SD), and the maximum number of calls was 26. Thirty variables were measured since variables with no or low variance were excluded (Table 2).

Table 2. Descriptions of acoustic parameters measured in Raven Pro 1.5 that entered statistical analysis.

Acoustic Parameter Name	Abbreviations/Units	Description
Low Frequency	Low Freq (Hz)	The lower frequency bound of the selection.
* High Frequency	High Freq (Hz)	The upper frequency bound of the selection.
* Aggregate Entropy	Agg Entropy (bits)	The aggregate entropy measures the disorder in a sound by analyzing the energy distribution. A pure tone concentrated in only one frequency level corresponds to zero value. Disordered sound that spans more than one frequency level corresponds to higher entropy values. It corresponds to the overall disorder in the sound.
Average Entropy	Avg Entropy (bits)	This entropy is calculated by finding the entropy for each frame in the signal and then taking the average of these values.
Bandwidth 50%	BW 50% (Hz)	The difference between the 25% and 75% frequencies.
Bandwidth 90%	BW 90% (Hz)	The difference between the 5% and 95% frequencies.
Center Frequency	Center Freq (Hz)	The frequency that divides the selection into two frequency intervals of equal energy.
Center Time	Center Time (s)	The point in time at which the selection is divided into two time intervals of equal energy.
Relative Center Time	Center Time Rel,	The point in time at which the selection is divided into two time intervals of equal energy relative to the signal duration.
Delta Frequency	Delta Freq (Hz)	The difference between the upper and lower frequency limits of the selection.
* Delta Time	Delta Time (s)	The difference between Begin Time and End Time for the selection.
* Duration 50%	Dur 50% (s)	The difference between the 25% and 75% times.
Duration 90%	Dur 90% (s)	The difference between the 5% and 95% times.
* Frequency 25%	Freq 25% (Hz)	The frequency that divides the selection into two frequency intervals containing 25% and 75% of the energy in the signal.
* Frequency 5%	Freq 5% (Hz)	The frequency that divides the selection into two frequency intervals containing 5% and 95% of the energy in the signal.
* Frequency 95%	Freq 95% (Hz)	The frequency that divides the selection into two frequency intervals containing 95% and 5% of the energy in the signal.
Length	Length (frames)	The number of frames contained in a selection. For waveform views, the number of frames equals the number of samples in a single channel. For spectrogram and spectrogram slice views, the number of frames equals the number of individual spectra in the selection in one channel. For selection spectrum views, the number of frames always equals 1.
Maximum Entropy	Max Entropy (bits)	Maximum entropy calculated from each frame.
Maximum Frequency	Max Freq (Hz)	The frequency at which Max Power occurs within the selection.
Maximum Time	Max Time (s)	The first time in the selection at which a spectrogram point with power equal to Max Power/Peak Power occurs.
* Minimum Entropy	Min Entropy (bits)	The minimum entropy calculated for a spectrogram slice within the selection bounds.

Table 2. *Cont.*

Acoustic Parameter Name	Abbreviations/Units	Description
Relative Peak Time	Peak Time Rel (s)	The first time in the selection at which a sample with amplitude equal to Peak Amplitude occurs.
Time 25%	Time 25% (s)	The time that divides the signal into two time intervals containing 25% and 75% of the energy in the signal.
* Relative Time 25%	Time 25% Rel (s)	The time that divides the signal into two time intervals containing 25% and 75% of the energy in the signal relative to signal duration.
Time 5%	Time 5% (s)	The time that divides the signal into two time intervals containing 5% and 95% of the energy in the signal.
* Relative Time 5%	Time 5% Rel,	The time that divides the signal into two time intervals containing 5% and 95% of the energy in the signal relative to signal duration.
Time 75%	Time 75% (s)	The time that divides the signal into two time intervals containing 75% and 25% of the energy in the signal.
Relative Time 75%	Time 75% Rel,	The time that divides the signal into two time intervals containing 75% and 25% of the energy in the signal relative to signal duration.
* Time 95%	Time 95% (s)	The time that divides the signal into two time intervals containing 95% and 5% of the energy in the signal.
* Relative Time 95%	Time 95% Rel,	The time that divides the signal into two time intervals containing 95% and 5% of the energy in the signal relative to signal duration.

Note: Description of variables measured for hissing calls. Marked variables (*) were included in the final DFA model.

To test the potential for individual variation (Potential of Individual Coding—PIC) for each parameter, we compared the inter- and intra-individuality. The PIC ratio was computed for each acoustic parameter by dividing the coefficient of variance between individuals by the mean of the CV intra-values related to each individual [60]. For these tested parameters, a PIC value greater than one means that inter-individual variability is higher than intra-individual variability, and therefore, the monitored variable has the potential to enter further analyses. Significance was tested using the Kruskal–Wallis test.

The variables were standardized using Z-score transformation (subtracting the mean and dividing by standard deviation). To test individual variations, the stepwise Discrimination Function Analysis (DFA) using IBM SPSS Statistics 24.0 software (IBM Corp., Armonk, USA) was employed. A leave-one-out cross-validation procedure was applied (IBM SPSS Statistics 20) to validate the results of DFA. To evaluate the combined explanatory potential of the DFA variables and for a more appropriate interpretation of the results, the Principal Component Analysis (PCA) was used.

3. Results

3.1. Hissing Call Description

The hissing calls of black grouse represent wideband acoustic signals. The energy is spread across a wide frequency range. This type of call can consist of one or two notes; however, the occurrence of a two-syllable form is rare ($\sim n < 1\%$). We excluded two-syllable calls from the analysis. The duration of analyzed calls ranged from 0.1 to 1.21 s (1.00 ± 0.16, mean ± SD).

The Low Frequency ranged from 136.0 to 1411.8 Hz (835.0 ± 171.7 Hz, mean ± SD), and the High Frequency from 1523.8 to 4637.7 Hz (2464.1 ± 435.2 Hz, mean ± SD) for all individuals. The frequency ranged from 775.2 to 3375.0 Hz (1580.3 ± 280.7 Hz, mean ± SD).

The spectrograms of black grouse recorded in the Czech Republic, Scotland, Russia, and Finland are shown in the figures below (Figure 2). For a representative recording of a hissing call of one individual from each study country, see Audios S1–S4.

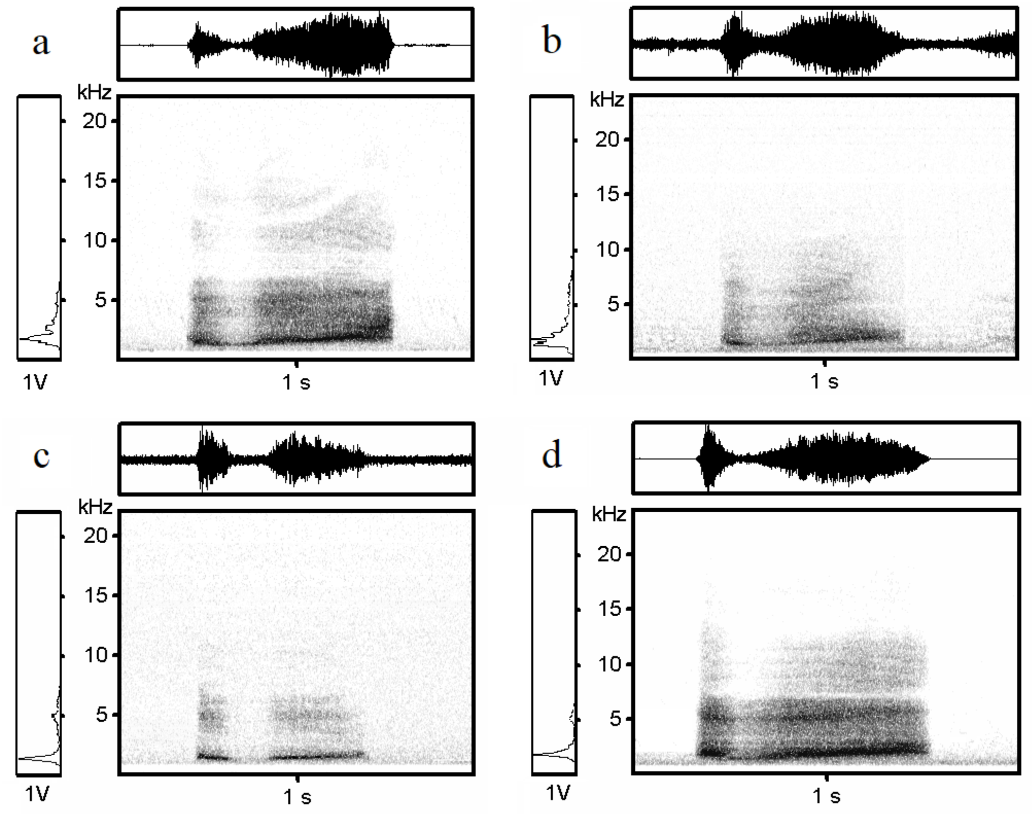

Figure 2. Spectrograms and oscillograms: representative hissing calls of male black grouse from (**a**) Czech Republic, (**b**) Russia, (**c**) Finland, and (**d**) Scotland.

3.2. Geographical Variation

According to PIC analysis, the variability between countries (inter-variability) was higher than the variability in individuals (intra-variability). All 30 variables could enter the following analyses to differentiate the populations of individual countries based on their vocal activity (Table 3). All Kruskal–Wallis tests were significant ($p < 0.001$).

Table 3. Descriptive statistics and Potential for individual coding.

Variable	DFA	Mean	Min	Max	SE	Mean CVw	CVa	PIC
Low Frequency		834.97	0.00	1411.77	171.74	10.34	20.57	1.99
High Frequency	X	2464.05	1523.80	4637.68	435.49	5.81	17.67	3.04
Agg Entropy	X	3.16	1.89	4.81	0.55	7.31	17.48	2.39
Avg Entropy		2.70	1.86	4.00	0.35	5.15	12.94	2.51
BW 50%		287.38	86.13	1125.00	173.59	31.14	60.41	1.94
BW 90%		794.41	258.40	2156.25	340.44	18.47	42.85	2.32
Center Frequency		1580.29	775.20	3375.00	280.88	4.72	17.77	3.76
Center Time		400.08	0.41	3476.43	571.01	49.42	142.72	2.89
Center Time Relative		0.48	0.06	0.84	0.17	25.75	35.47	1.38
Delta Frequency		1629.08	761.89	3478.26	400.54	9.96	24.59	2.47
Delta Time	X	1.00	0.47	1.52	0.16	9.66	15.57	1.61
Duration 50%	X	0.42	0.04	0.77	0.14	25.83	32.88	1.27
Duration 90%		0.75	0.29	1.18	0.13	11.50	17.62	1.53

Table 3. *Cont.*

Variable	DFA	Mean	Min	Max	SE	Mean CVw	CVa	PIC
Frequency 25%	X	1442.80	187.50	3000.00	239.46	5.73	16.60	2.90
Frequency 5%	X	1222.17	0.00	2250.00	218.52	8.36	17.88	2.14
Frequency 95%	X	2016.58	1291.99	4218.75	426.80	5.80	21.16	3.65
Length		188.50	89.00	467.00	41.32	9.67	21.92	2.27
Maximum Entropy		3.71	2.95	4.83	0.29	3.73	7.92	2.12
Maximum Frequency		1557.99	562.50	3468.75	296.88	7.42	19.06	2.57
Maximum Time		399.91	0.21	3476.39	570.99	49.48	142.78	2.89
Minimum Entropy	X	1.54	0.18	2.83	0.31	10.26	20.07	1.96
Peak Time Relative		0.30	0.01	0.93	0.28	67.33	90.52	1.34
Time 25%		399.85	0.29	3476.30	571.01	49.52	142.81	2.88
Time 25% Relative	X	0.24	0.05	0.66	0.16	43.52	66.79	1.53
Time 5%		399.68	0.17	3475.92	570.99	49.61	142.86	2.88
Time 5% Relative	X	0.08	0.01	0.50	0.05	25.30	61.34	2.42
Time 75%		400.27	0.79	3476.53	571.01	49.33	142.66	2.89
Time 75% Relative		0.67	0.11	0.89	0.10	10.14	15.29	1.51
Time 95%	X	400.43	0.96	3476.66	571.01	49.25	142.60	2.90
Time 95% Relative	X	0.83	0.51	0.97	0.06	4.81	6.96	1.45

Note: Descriptive statistics and Potential for individual coding. (DFA) variables included in the DFA model. (SE) standard error of the mean. (Mean CVw) within individual comparisons. (CVa) between individual comparisons. (PIC) Potential for Individual Coding.

From selected parameters, the resulting model included 12 significant acoustic variables ($p < 0.05$; $r \leq 0.89$): High Frequency, Aggregate Entropy, Delta Time, Duration 50%, Frequency 5%, Frequency 25%, Frequency 95%, Minimum Entropy, Relative Time 25%, Relative Time 5%, Relative Time 95%, and Time 95% (Table 3). Table S1 shows the values of the measured variables included in the resulting DFA model.

The first discriminant function had Eigenvalues > 1, which explained 70.7% of the variation. The cumulative percentage of explained variance of the first two discriminant functions was 94.2%. The first discrimination function mostly correlated F25% (Frequency 25%) (r = 0.708) and Freq 95% (Frequency 95%) (r = 0.651), and the second discriminant function correlated best with T95% (Time 95%) (r = 0.569) and T5% Rel (Relative Time 5%) (r = 0.419). The Discriminant Function Analysis did not exclude any individual or country. The resulting DFA model correctly classified 68.0% (66.2%, cross-validated result) hissing calls from four countries. The same result from the classification was given by the DFA model with standardized variables (68.0%; 66.2% cross-validated result). Hissing calls from the Czech Republic were correctly classified with 54.5% accuracy (51.7%, cross-validated result), calls from Scotland with 78.2% accuracy (77.1%, cross-validated result), calls from Russia with 57.4% accuracy (56.2%, cross-validated result), and from Finland with 74.0% accuracy (72.0%, cross-validated result). The first two principal components in PCAs captured 54.0% of the variation (Figure 3).

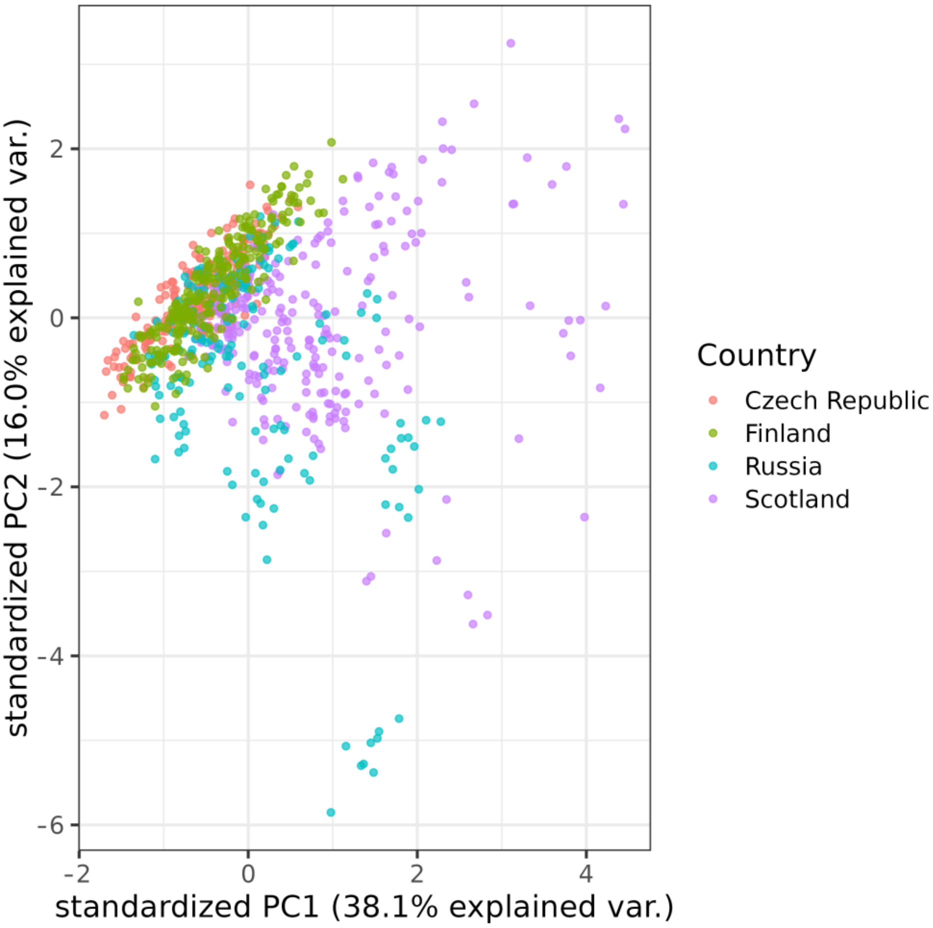

Figure 3. The results of PCA.

4. Discussion

Our results suggest that even a non-vocal signal can carry acoustic variability, and in this case, variability between populations of black grouse from the four countries was studied. The principal component analysis indicates that populations in Scotland and Russia have greater intra-group variability than grouse from the Czech Republic and Finland. Despite this variation, we cannot claim that the four studied black grouse populations have different dialects.

Studies on the topic of geographical variability in bird acoustic performance have been performed for both song-learning species [61–66], and species with innate vocalizations, including orders Gruiformes, Psittaciformes, and Sphenisciformes [67–70]. Although there have been cases with landfowl that suggest that the evolution of vocal expression in these species may also be affected by encounters [71], it is thought that the black grouse does not belong to the group of song-learning birds. Moreover, the hissing calls that are the subject of this study cannot even be considered song, since they are not produced by a syrinx. All the more interesting is the finding that even non-vocal signals can be characterized by variability at the subpopulation level. Variability in acoustic performance on a population scale may occur for different reasons. One of them is diverse habitats, shaping the vocal signals of birds from different regions [62,69]. These reasons also include long-distance segregation, morphological features, and environmental influences; gender or social selection are also likely to contribute to variability, as found in the four species of Australian fairy-wrens (*Malurus*) [63,64]. In the black grouse distribution areas, there are many fragmented or even isolated populations [18,27,39,54], and as a result of this, acoustic variability can develop between them.

On the other hand, the opposite can also occur, where different acoustic signal features are displaced by hybridization or competition, or features converge directly to promote the coexistence of individuals [64] while some bird species may not even have a geographical vocal variation [72–75].

So far, the only way to more accurately determine the origin of individuals and distinguish populations is genetic analysis. Although many studies focus on the genetics of the black grouse, information on the genetic structure of populations from different areas is not unified. According to taxonomy, black grouse from all over the European area genetically belong to one species. However, differences may appear at the population level [76]. Populations in Great Britain have some degree of genetic variation, and microsatellites in black grouse show that the population can be divided into at least several management units [77]. An indication of two different genetic groups of the black grouse was discovered in Poland [9]. Eastern Alpine black grouse show similar amounts of genetic variation in populations like Scandinavia [78]. On a general level, studies agree that genetic diversity in the black grouse population is declining [7,10]. The loss of genetic diversity is the result of the decline of the black grouse population and the isolation of subpopulations in individual countries. As our study suggests, the difference between the investigated subpopulations in acoustic performance may play a larger role in the future.

5. Conclusions

Our study revealed potential acoustic variability between black grouse populations from four countries across the distribution area. The accuracy of discriminant model classification of hissing calls was 75%, with the highest values for Scotland (79.8%, cross-validated). The black grouse is not classified as a song-learning bird, and that is precisely why it is interesting that acoustic variability at the subpopulation level was detected in this species. One of the reasons for the evolution of variation in bird acoustic performance is the isolation of populations. Monitoring and assessing acoustic variability have the potential to assess population evolution across a distribution range in a non-invasive manner.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/ani13111844/s1, Audios S1–S4: a hissing call of male Black grouse from Czech Republic (Audio S1), Russia (Audio S2), Finland (Audio S3) and Scotland (Audio S4) and Table S1 showing values of the variables included in the resulting DFA model.

Author Contributions: Conceptualization, R.P.; Data curation, L.H.; Formal analysis, L.H.; Investigation, L.H., R.P. and V.H.; Methodology, R.P.; Software, L.H.; Supervision, R.P., J.C., V.H. and R.Š.; Visualization, L.H. and R.Š.; Writing—original draft, L.H.; Writing—review and editing, R.P. and J.C. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the IGA of the Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, Prague. Project number: B_04_18. There was no additional external funding received for this study. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Institutional Review Board Statement: Field experiments were approved by the Department of Natural Resources, Ministry of Agriculture and Forestry, Finland and by the Game & Wildlife Conservation Trust, Scotland. According to Finnish legislation in general and to the hunting legislation, this type of scientific project does not require any special permits or licenses. All appropriate permissions were in place for the fieldwork in Scotland. The research was conducted in accordance with the guidelines of the Animal Behavior Society for the ethical use of animals in research. The study was carried out in accordance with the recommendations in the Guide for Care and Use of Animals of the Czech University of Life Sciences, Prague. The Animal Care and Use Committee of the Czech Ministry of the Environment approved the protocol (Permit number: 15106/ENV/14-825/630/14).

Informed Consent Statement: Not applicable.

Data Availability Statement: The data that support the findings of this study will be openly available in any publicly accessible repository, such as Dryad, as soon as this manuscript is accepted.

Acknowledgments: We are thankful for the help and support of Christian Krogell, Department of Natural Resources, Ministry of Agriculture and Forestry, Finland. We also appreciate help from Ilkka Ala-Ajos for support of our research in Finland and from Viktor Salovarov in Russia. Furthermore, we would like to thank David Parish, Marlies Nicolai and Kathy Fletcher from the Game & Wildlife Conservation Trust and the gamekeepers in Cairngorm National Park, Scotland. Thanks for software support also goes to Rostislav Linda. Last but not least, we would like to acknowledge Jitka Šišáková (the expert in the field) and Richard Lee Manore (the native speaker) for checking English. Moreover, we acknowledge three anonymous reviewers for their beneficial comments.

Conflicts of Interest: The authors declare no conflict of interest.

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6. Diskuze

6.1 Sumarizace údajů o tetřívku obecném

6.1.1 Zpracování získaných zdrojů a výstupy studie

Vyhledané zdroje pro studii sumarizující údaje o tetřívku obecném byly rozděleny do tří kategorií. Kritérium pro toto rozdělení bylo řízeno podle toho, zda lze v pramenech zmiňovaný negativní dopad na populaci tetřívka obecného snížit, popřípadě eliminovat zásahem lidského managementu a v jakém časovém horizontu je to uskutečnitelné. Možné zlepšení v krátké době po implementaci opatření bylo přiřazeno problematice vyrušování lidmi, cestovního ruchu a změny stanovišť. Témata související s vývojem populace, reprodukčním procesem, predací, parazitací a změnou klimatu spadají do kategorie jevů, jejichž krátkodobé zlepšení není možné. Vyhledané publikace, které se nevěnují přímo negativním dopadům na tetřívka, vytvořily kategorii třetí. Zařazena sem byla např. témata týkající se chování tetřívků a metodologie, studie věnující se genetice či akustickým projevům. Celkem bylo zpracováno 228 pramenů, jejichž rozdělení podle typu a roku vydání je možné shlédnout v grafice studie (I.)

Ze získaných údajů je patrné, že tetřívek obecný čelí mnoha vlivům ohrožujícím jeho populace, jejichž stav se liší dle oblastí areálu výskytu. Zatímco v zemích Fenoskandie nebo v Rakousku patří tetřívek stále mezi lovenou zvěř (Statistisk Sentralbyra, 2022; Statistics Austria. Federal Institution under Public Law, 2023; Statistics Finland, 2023; Svenska Jägareförbundet, 2023), ve střední a východní Evropě byl již zařazen mezi ohrožené druhy (Danko et al., 2002; Sim et al., 2008; Elts et al., 2013; Ķerus et al., 2021; European Environment Agency, 2023; The Forest Management Institute Brandýs nad Labem, 2024). Oblasti, do nichž spadají např. Skotsko nebo Česká republika, se potýkají s problematikou úbytku pro tetřívka vhodného životního prostředí (Doenecke and Niethammer, 1970; Loneux and Ruwet, 1997; Ludwig et al., 2009b; Gimmi et al., 2011; Strauß et al., 2018), mortalitu způsobenou predací lze vysledovat napříč distribučním areálem (Spidsø et al., 1997; Tornberg et al., 2006, 2012; Warren et al., 2012; Pekkola et al., 2014), podobně jako vliv měnícího se klimatu (Prellwitz, 2002; Ludwig et al., 2006; Bocca et al., 2014; European Commission et al., 2020; Canonne et al., 2021). V zemích, kde se rozvíjí cestovní ruch a zvyšuje se návštěvnost volné přírody, čelí tetřívci neúspěchům reprodukčního procesu a nízkému přežívání zimního období (Zeitler, 2000; Wöss and Zeiler, 2003; Baltić et al., 2004; Ingold, 2005; Arlettaz et al., 2007, 2013; Zeiler and Grünschachner-Berger, 2009; Patthey et al., 2012; Storch, 2013; Immitzer et al., 2014; Zwart et al., 2015; Formenti et al., 2015; Rutkowski et al., 2018; Percival et al., 2018; Tost et al., 2020; Coppes et al., 2020; Adamowicz et al., 2023).

Vlivy jednotlivých faktorů na sebe navazují a dopady na populaci tetřívka obecného se tím stupňují. Rušení během lekování na tokaništích vede k nezdarům v páření, kohoutci mohou opouštět svá stanoviště a tokat solitérně, což vede ke snižování genetické rozmanitosti populace, dochází k její fragmentaci a celkovému poklesu (Höglund and Stohr, 1997; Zeitler, 2000; Caizergues et al., 2003; Angelstam, 2004; Höglund et al., 2007; Svobodová et al., 2011b; Chamberlain et al., 2012; Rutkowski et al., 2018). Nedostatek odpočinku během zimního období snižuje kondici jedinců, kteří jsou následně zranitelnější vůči predátorům nebo nemocem, čímž se zvyšuje jejich mortalita přispívající opět k poklesu početnosti (Storch, 2000; Baltić et al., 2004; Arlettaz et al., 2007, 2013; Ludwig et al., 2008; Zeiler and Grünschachner-Berger, 2009; Immitzer et al., 2014; Formenti et al., 2015; Coppes et al., 2020; Tost et al., 2020; Adamowicz et al., 2023). Dopady části těchto činitelů však lze i v současné době zmírnit či eliminovat.

6.1.2 Klíčové aktivity pro podporu a ochranu populací tetřívka obecného

Tetřívek obecný je citlivý na přeměnu otevřených lokalit v zapojené porosty a změny ve vegetační struktuře jeho habitatů (Rolstad et al., 2009). Zavádění pěstebních metod vedoucích k vytváření mozaikovité struktury porostů je jednou z částí podpory populace tetřívků v rámci lesnického managementu (Poleno et al., 2009; Vacek et al., 2023). Konkrétní postupy zahrnují mimo jiné snížení hustoty výsadby, vytváření dlouhodobých maloplošných porostů s různorodým složením a volným zápojem (Grant et al., 2009; Tost et al., 2022), obnova mokřadů a rašelinišť s jejich charakteristickým druhovým složením (Ramanzin et al., 2000; White et al., 2015), dále zabránění sukcesi porostů a zachování solitérních stromů, vytváření přechodových vegetačních pásů s bohatým podrostem a omezení použití oplocenek v oblastech s výskytem tetřívků (Catt et al., 1994; Baines and Andrew, 2003; Sim et al., 2008; Patthey et al., 2012; Stevens et al., 2012; Bocca et al., 2014). V rámci zlepšování životních podmínek je vhodné zajišťovat propojení jednotlivých tetřívčích center (Andrén, 1994), bránit zarůstání lokalit pomocí vypalování vřesovišť nebo pastvy dobytka (Wegge and Kastdalen, 2008; Patthey et al., 2012) a věnovat pozornost souvislostem mezi složením vegetace a přítomností predátorů (Signorell et al., 2010).

Konkrétním příkladem je oblast Krušných hor v České republice, která v současné době čelí rekonstrukci porostů smrku pichlavého, jenž byly vysazeny namísto lesů zničených imisemi v 70.

letech minulého století. Obnovení zde probíhá odstraněním dřevní hmoty nebo výsadbou smrku ztepilého v počtech daných legislativou. Vznikají tak nepropustné mlaziny, u nichž lze v následujících letech předpokládat přechod do tyčkovin, tyčovin a kmenovin. Takový homogenizovaný porost však neposkytuje tetřívkům téměř žádné potravní příležitosti, jelikož postrádá bylinný a keřový podrost, na nějž se vážou různé druhy hmyzu. Pro tetřívky vhodným postupem by bylo odstranění stávajícího porostu a ponechání volných ploch, které poskytnou příležitost k růstu bohatému spektru bylin, a které mohou tetřívci využít jako tokaniště. Solitérní výsadba druhů stromů, jako je jeřáb ptačí nebo bříza pýřitá, dále rozšíří potravní nabídku. Výsadby těchto dřevin je nutné opatřit ochranou proti zvěři, vzhledem k riziku nárazů tetřívků do drátěných ploch se však doporučuje využívat dřevěné oplocenky, případně zviditelnit oplocení fáborky nebo rákosovými rohožemi (Cukor et al., 2022).

Na postupy lesnického hospodaření následně navazuje myslivecký management, který je pro ochranu tetřívka potřeba zaměřit na snížení početnosti predátorů. Zejména v oblastech s výskytem tetřívků je doporučeno navýšit odlov druhů jako je liška, kuny, jezevec, ale také prase divoké, které sice není aktivním predátorem tetřívků, nicméně může mít na svědomí devastaci jejich hnízd (Svobodová et al., 2004; Cukor et al., 2021, 2022). Opomenout nelze ani invazní druhy, jako je mýval severní a psík mývalovitý, kteří se stávají novou hrozbou nejen pro populaci tetřívka obecného, ale také mnoho dalších druhů živočichů (Cove and O’Connell, 2022). Ke snížení početnosti predátorů je však potřeba přistupovat komplexně a nezaměřovat se pouze na jeden druh. V daných oblastech je dále potřeba udržovat nízké stavy spárkaté zvěře, která jednak tvoří potravní nabídku pro predátory, jednak svou aktivitou narušuje tetřívčí lokality (Cole et al., 2012). Důležitým krokem je přísný zákaz přikrmování, které přitahuje zejména černou zvěř a zvyšuje tím její koncentraci, což vede ke zvýšené predaci tetřívčích hnízd (Selva et al., 2014; Oja et al., 2015; Cukor et al., 2021). Vnadění černé zvěře představuje také nepřímé riziko, jelikož předkládané krmivo láká ke konzumaci velké množství hlodavců, jenž jsou kořistí hlavních druhů predátorů tetřívka obecného (Selva et al., 2014).

O mysliveckém managementu samotného tetřívka obecného lze diskutovat pouze v zemích, kde je jeho lov stále povolen. Těmito zeměmi jsou např. Finsko, Švédsko, Norsko, Bělorusko, Litva nebo Rakousko (Ķerus et al., 2021; Pavljushchik and Shakun, 2021; Statistisk Sentralbyra, 2022; Statistics Austria. Federal Institution under Public Law, 2023; Statistics Finland, 2023; Svenska Jägareförbundet, 2023). Lovecké aktivity mohou vést častější létání, vyšší potřebu bdělosti či dočasné změny využití prostředí, které jsou příčinou zhoršeného příjmu potravy (Casas et al., 2009; Bonnot et al., 2013; Lone et al., 2015). Lov může mít také dopady na populační genetiku, kdy cílený výběr jedinců ovlivňuje fenotyp i genetické varianty (Harris et al., 2002; Coltman et al., 2003; Grift et al., 2003; Proaktor et al., 2007; Allendorf et al., 2008; Fenberg and Roy, 2008; Allendorf and Hard, 2009; Jeke et al., 2019). U finských tetřívků však bylo zjištěno, že jejich genetická diverzita není lovem ohrožena. Na lokalitách, kde dochází k lovu, následně dochází k imigraci nových jedinců, čímž je podpořen přísun nových genů (Chen et al., 2022). Autoři proto doporučují chránit oblasti, ve kterých tetřívek není loven, a zároveň vytvářet mozaiku těchto oblastí s lokalitami, kde je lov aktivní. Pomocí propojení těchto míst pak vzniká prostředí, ve kterém dochází k přesunu jedinců a je zachována genetická diverzita populace, a je zajištěna udržitelnost lovu tetřívka obecného (Chen et al., 2022).

V neposlední řadě je pro ochranu tetřívků důležité znát průběh vývoje jejich početnosti a distribuce a projevující se změny prostředí. Systematický a dlouhodobý monitoring populačních trendů může na straně jedné odhalit, které faktory jsou zvláště rizikové pro dané oblasti, na straně druhé dokumentovat implementovaná ochranná opatření a jejich efektivitu (Goldsmith, 2012). Metody monitoringu se však liší. V severních zemích se nejčastěji využívá sčítání na transektech za pomoci vycvičených psů a záznamu do aplikace, která přepočítává údaje na celou zájmovou oblast (Wegge and Rolstad, 2011; Cukor et al., 2020). Další metodou je pozorování a nahrávání jedinců v terénu prováděné v době dvou hodin před a po západu slunce (Cayford and Walker, 1991; Hancock et al., 1999; Dumont et al., 2019; Canonne et al., 2021). K neinvazivním postupům sčítání patří monitorování tokanišť pomocí fotopastí, díky nimž lze získat velké množství dat za krátkou dobu a to nejen z období páření, jelikož kohoutci tokaniště navštěvují i v průběhu roku (Gregersen and Gregersen, 2014). Získávání znalostí o průběhu života tetřívků a dokumentace dopadů negativních faktorů i provedených opatření je zásadním nástrojem tohoto vzácného druhu.

6.2 Akustická individualita v pšoukání kohoutků

K efektivnímu monitoringu tetřívků obecných by mohla přispět akustická individualita v jejich projevu. Analýza pšoukání kohoutků odhalila akustickou specifitu v těchto signálech produkovaných během lekování. Diskriminační model s téměř 78% úspěšností identifikoval jednotlivá zvolání jedinců a bezmála 80 % variace byly vysvětleny prvními čtyřmi diskriminačními funkcemi. Poměr potenciál individuální variability pro všechny testované parametry prokázal vyšší variabilitu mezi jedinci než v rámci jedinců. Pšoukání tedy nese informaci o individualitě kohoutků, přestože se jedná o nevokální typ signálu. Výstup této studie je poměrně unikátní, jelikož nevokálním projevům živočichů se výzkum příliš nevěnuje. Individualita byla odhalena v tzv. dunění, které během toku vydávají samci dropa obojkového afrického (*Chlamydotis undulata undulata*) (Cornec et al., 2014), akustické variace byly sledovány také u samců tetřívka prériového (*Tympanuchus cupido*) v jejich rezonantních signálech (Hale et al., 2014). Informaci o individualitě mohou nést také mechanické zvuky, jako je klepání strakapouda velkého, jehož jedince lze rozeznat na základě počtu a časových vzorců úderů (Budka et al., 2018), nebo šustění křídel kohoutků tetřívka pelyňkového (*Centrocercus urophasianus*) (Koch et al., 2015).

Navazující výzkum je možné zaměřit na konkrétní roli akustické individuality v hlase kohoutků tetřívka obecného, a to jak v nevokálním pšoukání, tak rezonujícím bublání. Signály mohou nést informaci o kvalitě a kondici samce (Guyomarc'h et al., 1998) a sloužit k identifikaci interagujících jedinců. V této souvislosti lze v akustické individualitě spatřovat potenciál pro využití během monitoringu. Samotné pozorování může způsobit chyby ve sčítání v důsledku pohybu kohoutků na tokaništi. Monitoring podložený identifikací jedinců na základě jejich hlasu by mohl poskytnout kýženou přesnost. Navíc by tato neinvazivní metoda mohla pomoci se sčítáním na těžko přístupných a nepřehledných lokalitách.

6.3 Geografická variabilita v pšoukání kohoutků

Výstupy druhé analýzy pšoukání tetřívků obecných naznačují, že kromě akustické individuality mohou tyto nevokální signály nést také informaci o variabilitě na úrovni populací z jednotlivých oblastí výskytu tohoto druhu. Testovány byly nahrávky kohoutků ze čtyř zemí, a to Finska, Ruska, České republiky a Skotska. Analýza principiálních komponent (PCA) ukázala, že jedinci Skotské a Ruské populace mají větší variabilitu v rámci skupin než tetřívci z České republiky a Finska. Navzdory těmto výsledkům, odhalujícím prvky variace, nelze tvrdit, že tyto čtyři sledované populace mají různé dialekty.

Jedinou možností, jak s přesností určit původ jedinců a odlišit jednotlivé populace, zůstává genetická analýza. Ačkoli se na genetiku tetřívka obecného zaměřuje část výzkumu věnovaná tomuto druhu, údaje o genetické struktuře populací z různých oblastí nejsou sjednocené. Dle taxonomie patří tetřívek obývající Evropu k jednomu druhu, na úrovni populace se však mohou objevit genetické rozdíly (Duque, 2011). Určitý stupeň genetické variace se projevuje u populace Velké Británie, na základě mikrosatelitů zde lze tetřívka obecného rozdělit do několika managementových jednotek (Hoglund et al., 2011). Indikace dvou různých genetických skupin tetřívka byla objevena v Polsku (Rutkowski et al., 2018), jedinci z východních Alp vykazují podobné množství genetických variací jako populace ve Skandinávii (Sittenthaler et al., 2018).

Studie v tomto oboru se shodují na tom, že celková genetická diverzita v populaci tetřívka obecného klesá (Höglund et al., 2007; Segelbacher et al., 2014) v důsledku poklesu jeho početnosti a vzniku izolovaných skupinek v jednotlivých oblastech výskytu. V budoucnu by údaje o variabilitě zkoumaných subpopulací mohly být podpořeny informacemi získanými analýzou akustického projevu tetřívků.

7. Závěr

Disertační práce se věnuje třem tematickým oblastem. První z nich je souhrn dat o populační dynamice tetřívka obecného, faktorech, které ji negativně ovlivňují a managementovým opatřením pro podporu tohoto druhu. Z výstupů získaných dat vyplývá, že populace tetřívka obecného zažívá pokles napříč areálem rozšíření. Příčiny snižování početnosti se však liší v různých oblastech. Ve střední Evropě tetřívci trpí nejvíce ztrátou vhodného prostředí v důsledku zarůstání stanovišť, stále častěji jsou vyrušováni lidskými aktivitami a na jejich mortalitě se velkou mírou podílejí predátoři. V zemích severní Evropy pak za poklesem populace stojí zejména zvyšující se neúspěšnost reprodukčního procesu a mortalita kuřat, i zde však narůstá tlak turismu a dochází ke ztrátám tetřívčích lokalit. Díky identifikaci těchto konkrétních faktorů je možné uzpůsobit péči o tetřívka obecného dané oblasti.

V první části disertační práce se podařilo vyčerpávajícím způsobem sumarizovat dostupné informace o tetřívku obecném a vytvořit tak příspěvek, který se stává důležitým podkladem pro ekologii a ochranu tohoto druhu. Získané údaje jsou přehledně rozděleny dle jednotlivých témat, od současných stavů početnosti tetřívka obecného napříč jeho areálem, přes jednotlivé přírodní i antropologické vlivy, jenž se liší dle oblastí výskytu, až po probíhající či doporučená opatření vedoucí ke stabilizaci jednotlivých populací.

Jedním z těchto managementových opatření, je efektivní monitoring, v návaznosti na nějž pokračuje druhá část disertační práce, zaměřená na akustickou individualitu a identifikaci individuálně specifických parametrů v hlase kohoutků tetřívka obecného. Pomocí analýzy nahrávek tokajících tetřívků ze Skotska a Finska se podařilo zjistit, že pšoukání, syčivý signál vyluzovaný během namlouvacího rituálu, je nositelem individuality jedince. Diskriminační model s vysokou přesností klasifikoval jednotlivé signály a jako důležité parametry byly vyhodnoceny Frekvence 95% a Frekvence 1. kvartilu. Tento objev je unikátní, individualitě ve vokalizaci živočichů se věnuje pouze malá část výzkumu, a ještě méně studií se zaměřuje na tzv. nevokální signály. Pšoukání je výsledkem vzduchu proudícího konstrikcemi dýchacích cest, proto jsou výstupy této části disertační práce jedinečné. Právě individualita v hlase jedinců může pomoci s monitorováním jednotlivých populací tetřívka obecného. Sčítání založené na zvukových záznamech přináší přesnější metodu a umožňuje sledovat jedince i skupiny tetřívků dlouhodobě v navazujících sezónách. Jedná se o neinvazivní způsob monitoringu i na nepřístupných a nepřehledných lokalitách.

Třetí část disertační práce pokračuje v analýze akustických signálů kohoutků tetřívka obecného z širšího hlediska. Zaměřuje se na geografickou variabilitu v pšoukání, která u tetřívka může vznikat mimo jiné v důsledku fragmentace populací a vzniku izolovaných skupinek. Analýza nahrávek ze čtyř zemí (Česká republika, Skotsko, Finsko a Rusko) naznačuje, že i v nevokálních signálech se může projevit variabilita na úrovni oblastí, ačkoli nelze hovořit o dialektech. Diskriminační model opět s vysokou přesností klasifikoval jednotlivá pšoukání s nejlepšími hodnotami pro Skotsko (79.8 %). Výsledky této části disertační práce jsou podkladem pro navazující výzkum akustických projevů tetřívka obecného. Akustická variabilita může být podkladem pro neinvazivní sledování vývoje populací napříč areálem výskytu tetřívka obecného. Spolu s ostatními výstupy tato část rozšiřuje znalosti o tetřívku obecném, které mohou pomoci v ochraně tohoto vzácného druhu.

Poznatky této práce lze dobře uplatnit při tvorbě ochranného plánu pro tetřívka obecného v České republice. Přináší možnost srovnání početnosti tetřívků v jiných zemích, ať už na základě sčítání nebo loveckých statistik, dále informace o negativních faktorech působících na populační dynamiku, jejich přehled, rozsah dopadů a vzájemnou provázanost. Ochranná opatření, která jsou soustředěna do oboru lesnictví a myslivosti, se velmi úzce dotýkají situace v České republice, jelikož spadá do oblasti, kde tetřívek trpí zejména ztrátou prostředí v důsledku zarůstání volných ploch a změn vegetační struktury po vysoušení mokřadů. Problematika nadbytečného přikrmování zvěře, které je příčinou zvýšené koncentrace predátorů, ale také jelenovitých, není v České republice v současnosti dostatečně řešena, a sčítání zbytkových populací u nás komplikuje jednak přechod k solitérnímu toku, jednak častá nepřehlednost lokalit. Doporučená opatření lze uplatnit jak v lesnickém hospodaření, tak v mysliveckém managementu, a výsledky akustických analýz lze aplikovat při tvorbě efektivní metody monitoringu.

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