PĀRSKATS

PAR LAUKSAIMNIECĪBĀ IZMANTOJAMO ZINĀTNES PĒTĪJUMU

PĒTĪJUMA NOSAUKUMS: Meža cūku skaita un populācijas blīvuma kontroles metodikas izstrāde un sistēmas ieviešana Latvijā, lai novērstu Āfrikas cūku mēra (ĀCM) izplatību (2. posms)

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PĒTĪJUMA VADĪTĀJS: ____________________

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Par sadarbību izpētes materiāla nodrošināšanā pateicamies:

LVMI "Silava" pētniecei **Laurai Ķēniņai**, Valsts meža dienesta Medību daļas vecākajam referentam **Ilgvaram Zihmanim**, Pārtikas un veterinārā dienesta (PVD) Dzīvnieku infekcijas slimību uzraudzības daļas vadītāja vietniekam **Mārtiņam Seržantam** un PVD Ziemeļkurzemes pārvaldes vadītājam **Ivaram Kolodam.**

Saturs

Ievads

Baltijas valstīs gūtā pieredze liecina, ka Āfrikas cūku mēra (ĀCM) vīruss var saglabāties meža cūku populācijā vai vidē, tostarp meža cūku līķos, pat, ja to populācijas blīvums ir 0,5 dzīvnieki uz 1 km^2, savukārt līdzšinējos datos balstīta informācija ļauj izvirzīt pieņēmumu, ka ĀCM izplatība izbeigtos, ja meža cūku populācijas blīvums būtu 0,15 dzīvnieki/km^2 vai mazāks. Medību statistikā izmantotajā blīvumu raksturojošā izteiksmē tas nozīmē < 1,5 dzīvnieki/1000 ha. Saskaņā ar Valsts meža dienesta (VMD) 2024. un 2025. gadā veikto populācijas novērtējumu un noteikto nomedīšanas apjomu, meža cūku populācijas blīvums tikai nelielā Latvijas daļā ir nokrities zem šīs robežvērtības, un teritorijas ar augstāku blīvumu joprojām ir savstarpēji savienotas. Tas dod visas iespējas vīrusa izplatības viļņiem pārvietoties pa teritoriju dabiskā ceļā, jo Latvijā nav ģeogrāfisku barjeru, kuras meža cūkas nespētu šķērsot. Šis pētījums veikts, lai atrastu piemērotāko veidu, kā, izmantojot zinātnē balstītas metodes, pārliecināties, ka populācija tiešām ir samazināta gan valstī kopumā, gan lokāli, kas nozīmētu populācijas teritoriālu sadrumstalošanu uz laiku, kamēr vīrusa klātbūtne nomedīto un bojāgājušo cūku ķermeņos vismaz 3 gadus netiek konstatēta.

Pētījumam izvirzīti 2 mērķi:

1) izstrādāt un validēt mežacūku populācijas uzskaites metodiku izmantošanai Valsts meža dienesta noteiktajās medījamo dzīvnieku uzskaites vienībās;

2) izstrādāt kontroles sistēmu, kas ļautu pārliecināties par mežacūku faktiskā skaita un populācijas blīvuma atbilstību ĀCM uzraudzības un apkarošanas stratēģijā noteiktajam mērķim.

Pētījuma pirmajā etapā tika izstrādāts teorētiskais pamatojums un īstenoti praktiskie priekšdarbi. Šajā pārskatā sniegta informācija un izdarīti secinājumi par praksei vispiemērotāko sistēmu, kas ļautu VMD sadarbībā ar medību tiesību lietotājiem iegūt pārliecinošus pierādījumus, ka meža cūku populācijas blīvums nepārsniedz ĀCM uzraudzības un apkarošanas stratēģijā noteikto robežu, kā arī sagatavoti priekšlikumi nepieciešamām rīcībām, ar kurām iepazīstināt atbildīgās institūcijas un iesaistītās sabiedrības grupas.

1. Meža cūku populācijas struktūras un blīvuma savstarpējā atkarība

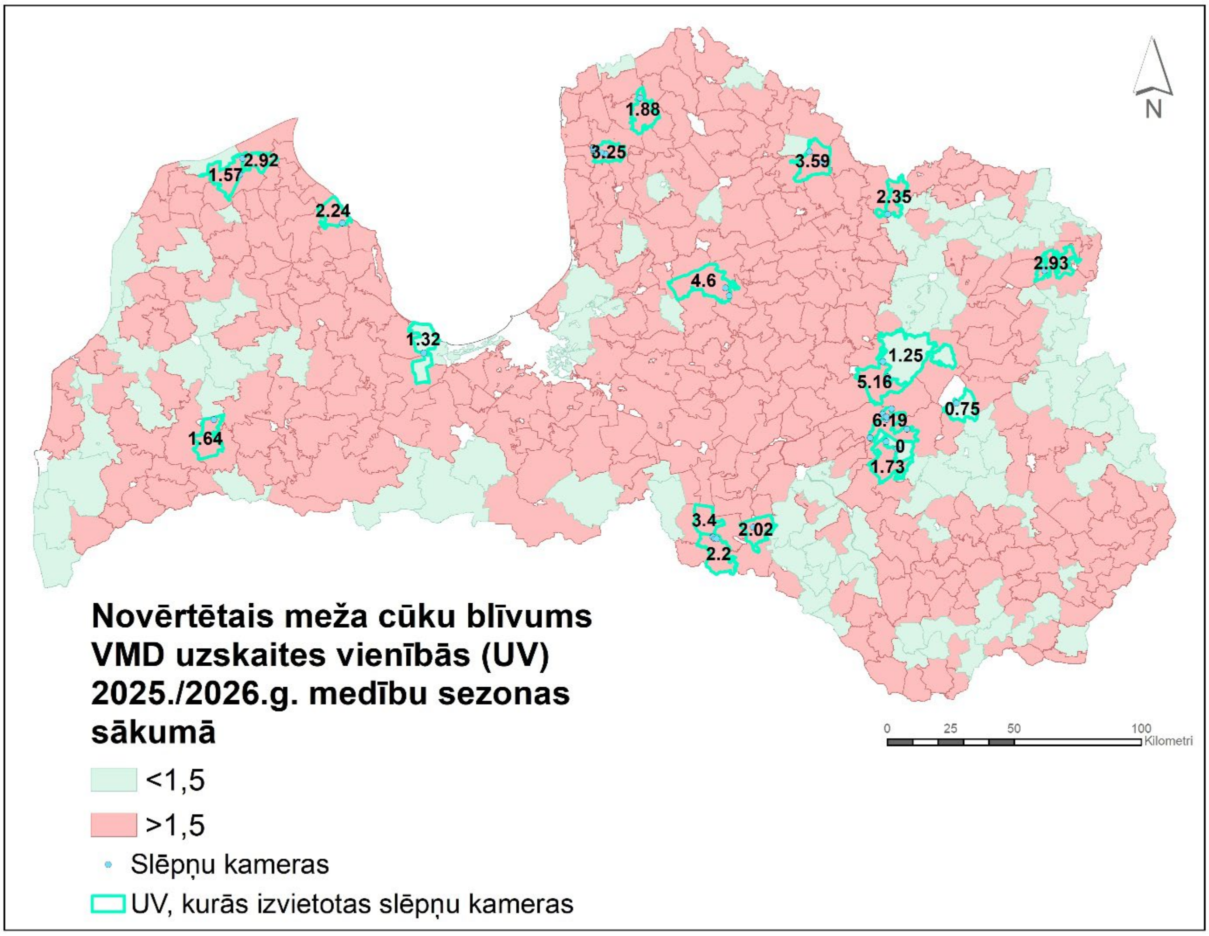
1.1. Metodika

Lai novērtētu meža cūku populācijas demogrāfisko struktūru, izmantojot lietotnes MEDNIS datus, veikta nomedīto indivīdu dzimuma un vecuma datu analīze par laika posmu 2024. gada 1. decembris–2025. gada 31. oktobris. Minēto informācijas avotu dati ir izmantoti nomedīto sivēnu īpatsvara aprēķinam. Mātīšu indekss aprēķināts, dalot nomedīto mātīšu skaitu ar nomedīto tēviņu skaitu.

Lietotnē MEDNIS reģistrētās meža cūkas analizētas ar mērķi nodalīt datu kopu par dzīvniekiem, kas nomedīti gaides medībās, tātad iespēju robežās selektīvi izvēloties nomedījamā dzīvnieka dzimumu un vecumu (lielumu). Šajā nolūkā, izmantojot ģeotelpiskās informācijas ĢIS lauku bloku slāni, meža cūku nomedīšanas vietas sadalītas mežā un ārpus meža platībām izvietotajās. Tā kā arī mežu platībās var notikt gaides medības piebarošanas vietās, tad no šīm vietām atlasītas diennakts tumšajā laikā un termiņā, kad nav atļautas medības ar dzinējiem, nomedītās meža cūkas. Šīs meža cūkas kopā ar visu gadu lauksaimniecības zemēs nomedītajām šajā pētījumā uzskatītas par dzīvniekiem, kas nomedīti barošanās vai piebarošanas vietās.

Pārbaudīta arī iespēja iegūt datus par meža cūku populācijas struktūru neinvazīvā ceļā, proti – pēc slēpņa kamerās fiksētiem foto un video uzņēmumiem. Izmantotas LVMI "Silava" īpašumā esošās slēpņa kameras (1. att.). Izveidot brīvprātīgu medību tiesību lietotājiem piederošo slēpņa kameru tīklu medījamo dzīvnieku uzskaitei un novērošanai ir ilgtermiņa uzdevums un risinājums efektīvākai medību resursu uzraudzībai un pārvaldībai, taču pašlaik tas neizdodas vairāku iemeslu dēļ:

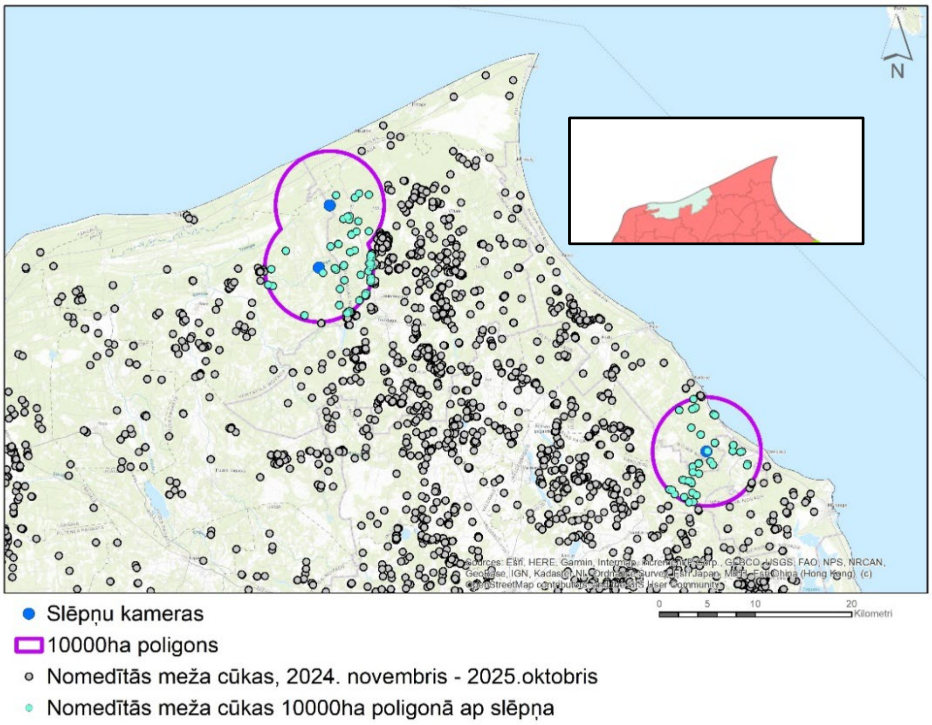
1) kameru darbības režīms, laika uzstādījumi un uztveramības zonas nav vienoti;
2) nav izveidota vienota sistēma datu apkopošanai un sasaistei ar konkrētām kameru atrašanās vietām;
3) mednieku sabiedrībā valda aizspriedumi par informācijas nodošanu vai bažas par kameru drošību;
4) nav vienota juridiski saistoša protokola par sadarbību starp kameru īpašniekiem un informācijas lietotājiem, piemēram, VMD;
5) vēlme dalīties ar informāciju sociālajos tīklos vai publicēt sabiedriskajos mēdijos ir lielāka par gatavību iesaistīties vienotā datu apmaiņā ar uzraugošām iestādēm vai zinātniekiem.



1. attēls. LVMI "Silava" veiktajos pētījumos izmantoto slēpņa kameru izvietojums. Norādītajās vietās var būt uzstādītas vairākas kameras saskaņā ar metodiku vairāku pētniecības uzdevumu veikšanai.

Šajā pētījumā esam izmantojuši datus ar meža cūku novērojumiem no 304 slēpņa kameru novietošanas punktiem, kas laikā no 2024. gada 1. decembra līdz 2025. gada 25. novembrim bijušas uzstādītas LVMI "Silava" vairākos veiktajos pētījumos: "Audzes strukturālās dinamikas un bioloģiskās daudzveidības novērtējums vecās skuju koku mežaudzēs hemiboreālajos mežos dabai tuvākas mežsaimniecības attīstībai" (https://www.silava.lv/petnieciba/petijumi/postdoc-biologiskas-daudzveidibas-novertejums-vecas-mezaudzes), "Lāču monitorings 2023.–2025. gadā" (https://www.silava.lv/petnieciba/petijumi/lacu-monitorings-2023-2025), "Izpratne par dzīvu novājinātu vakcīnu darbības rādītājiem Āfrikas cūku mēra profilaksei un kontrolei mežacūkām un mājas cūkām" (https://bior.lv/lv/projekts/apstiprinats-apvarsnis-eiropas-projekts-izpratne-par-dzivu-novajinatu-vakcinu-darbibas-raditajiem-afrikas-cuku-mera-profilaksei-un-kontrolei-mezacukam-un-majas-cukam/), kā arī šeit aprakstītajā projektā. Kopējais iegūtais kameru diennakšu skaits ir 86 910. Šajā laikā meža cūkas kamerās fiksētas 1234 foto un/vai video uzņēmumos, t.sk. sivēni 268, pieaugušas meža cūku mātītes 146, tēviņi 139 un nenosakāma dzimuma pieauguši indivīdi 681 uzņēmumā. Datus analizējot, iespēju robežās precizēts visu minēto dzimuma un vecuma grupu indivīdu skaits, izvēloties lielāko vienlaikus redzamo indivīdu daudzumu un atmetot vienā uzņēmumu sērijā ietverto indivīdu uzņēmumus, kas radušies meža cūkām ilgstoši uzkavējoties kameras uztveramības zonā.

Lai saistītu neinvazīvi iegūtos datus par meža cūku populācijas blīvumu un medību rezultātiem, salīdzināts ne tikai VMD sniegtais skaita blīvuma vērtējums medījamo dzīvnieku uzskaites vienībās, bet arī slēpņa kamerās iegūtie meža cūku novērojumi ar nomedīto meža cūku skaitu un dzimuma/vecuma struktūru 5,62 km rādiusā (t.i. 10 000 ha platībā) ap katru kameru uzstādīšanas vietu. Tas ir izdarāms ar ģeotelpisko datu (ĢIS) apstrādes programmu, pateicoties lietotnē MEDNIS atzīmētajām meža cūku nomedīšanas vietu koordinātām (2. att.).



2. attēls. Piemērs meža cūku medību rezultātu atlasei 10 000 ha platībā ap trijām slēpņa kameru uzstādīšanas vietām Ziemeļkurzemē, kuru tuvumā pēc VMD vērtējuma 2025. gada 1. aprīlī populācijas blīvums gan pārsniedzis 1,5 indivīdus uz 1000 ha (sarkanais tonējums), gan samazinājies zem noteiktās robežas (pelēkais tonējums).

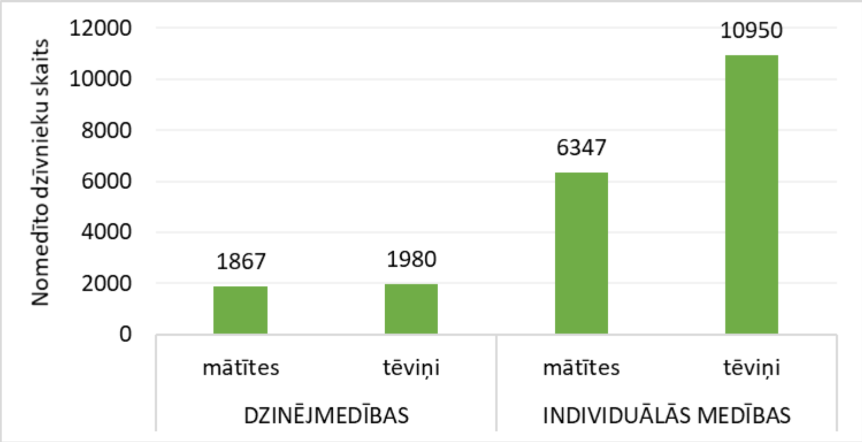
Analizēti kamerās fiksēto meža cūku dati, salīdzinot ar novērtēto meža cūku blīvumu attiecīgajā VMD uzskaites vienībās. Lai noteiktu sakarības starp kameru datiem un uzskaites vienībās novērtēto blīvumu, kā arī ar nomedīto meža cūku skaitu, izmantota Spīrmena rangu korelācija.

1.2. Rezultāti

Kopumā ar lietotnes MEDNIS palīdzību iegūta informācija par 21 230 nomedītām meža cūkām, no kurām 8217 bija mātītes, 12 942 tēviņi un 71 nenoteikta vai lietotnē nereģistrēta dzimuma meža cūka. Datubāzē atrodama informācija arī par 15 ar automašīnu notriektām meža cūkām – 12 tēviņiem un 3 mātītēm. Šie 15, kā arī dzīvnieki ar datu bāzē neievadītu dzimumu no tālākas apstrādes izslēgti.

Individuālo un dzinējmedību salīdzinājums

Lielākā daļa (17 297 jeb 81,8%) meža cūku nomedītas individuālo jeb gaides medību laikā (3. att.), atšķirības ir statistiski būtiskas (χ^2 tests, $\chi^2 = 183,16$, $P < 0,01$). Dzinējmedību laikā starp nomedīto mātīšu un tēviņu skaitu nav statistiski būtiskas atšķirības, savukārt individuālo medību laikā nomedīto tēviņu skaits gandrīz divas (1,7) reizes pārsniedz mātīšu skaitu, atšķirības ir statistiski būtiskas (χ^2 tests, $\chi^2 = 1964,16$, $P < 0,001$).

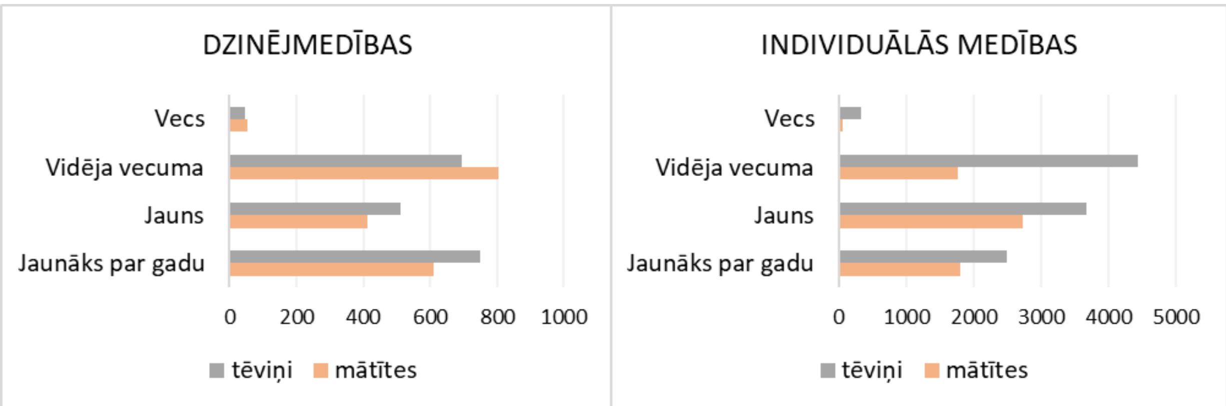


3. attēls. Nomedīto meža cūku dzimuma sadalījums individuālajās un dzinējmedībās laika posmā no 2024. gada decembra līdz 2025. gada oktobrim ieskaitot.

Analizējot nomedīto meža cūku dzimuma/vecuma struktūru, redzams, ka dzinējmedību laikā nomedīto tēviņu pārsvars statistiski būtiski lielāks ir jaunu un jaunāku par gadu dzīvnieku grupā, savukārt vidēja vecuma dzīvnieku grupā būtiski vairāk nomedītas mātītes (4. att. un 1 .tab.). Lai gan dzinējmedību laikā nomedīto dzīvnieku dzimuma atšķirības ir statistiski būtiskas, tomēr nav ar lielu efektu (vidēji 0,094), kas no zīmē, ka šīs atšķirības ir vairāk salīdzinoši lielās paraugkopas katrā dzimuma grupā dēļ, nevis tādēļ, ka šīs atšķirības patiešām būtu nozīmīgas populācijas apsaimniekošanā. Tomēr konstatētais fakts apliecina, ka populācijā ir pietiekoši daudz pieaugušu mātīšu, kas arī izskaidro straujo skaita atjaunošanos pēc lieliem zaudējumiem medību un ĀCM vīrusa izraisītās mirstības rezultātā.

Individuālo medību laikā nomedīto tēviņu pārsvars pār mātītēm ir ļoti izteikts visās vecuma grupās un īpaši liels – vidēja vecuma dzīvnieku grupā (χ^2 tests, $\chi^2 = 1156{,}86$; $P < 0{,}001$; V=0,702).

Šie rezultāti vedina secināt, ka joprojām apstākļos, kad teorētiski iespējamas izlases medības, neskatoties uz epidemioloģisko situāciju valstī, daudzi mednieki mērķtiecīgi saudzē cūku mātītes.



4. attēls. Nomedīto meža cūku dzimuma/vecuma struktūra dzinējmedību un individuālo medību laikā.

1. tabula

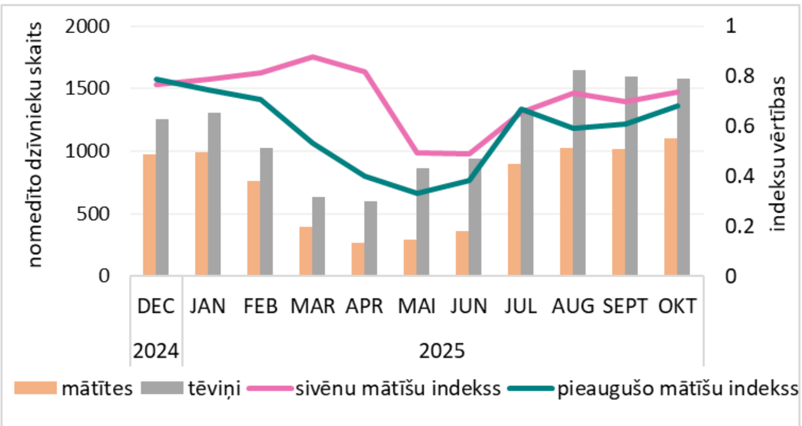
Dzinējmedību un individuālo medību laikā nomedīto meža cūku dzimuma/vecuma struktūras salīdzinājums, χ^2 testa rezultāti (χ^2 – testa vērtība, p – būtiskuma lielums, Cramer's V – efekta vērtība (ja V < 0,1 – nebūtisks efekts; 0,1–0,3 – mazs; 0,3–0,5 – vidējs un > 0,5 – liels efekts))

	Dzinējmedības			**Individuālās medības**		
	χ^2	P vērtība	Efekta lielums (Cramer's V)	χ^2	P vērtība	Efekta lielums (Cramer's V)
Jaunāks par gadu	14,24	< 0,001	0,102	115,23	< 0,001	0,164
Jauns	10,57	0,001	0,107	138,97	< 0,001	0,147
Vidēja vecuma	7,94	0,004	0,073	1156,86	< 0,001	0,432
Vecs	0,84	0,361		188,02	< 0,001	0,702

Meža cūku mātīšu indekss

Ja iepriekšējā sezonā visvairāk meža cūku nomedīts vasaras mēnešos, tad šajā gadā tas noticis laika periodā no augusta līdz oktobrim (5. att.). Divreiz vairāk tēviņu nekā mātīšu nomedīts laika posmā no aprīļa līdz jūnijam ieskaitot, arī pārējos vasaras mēnešos un visā gadā kopumā nomedīto tēviņu skaits būtiski (χ^2 tests, P < 0,001) pārsniedz nomedīto mātīšu skaitu. Līdzīgi kā iepriekš, arī šogad par gadu jaunāku nomedīto mežacūku grupā tēviņu pārsvars pār mātītēm ir mazāks nekā pieaugušo nomedīto grupā – mātīšu indekss attiecīgi 0,74 un 0,60. Abās salīdzinātajās grupās atšķirība starp dzimumiem ir statistiski būtiska (χ^2 tests, P < 0,001).

Gada griezumā ik mēnesi nomedīto pieaugušo meža cūku grupā (vecuma kategorija "jauns", "vidēji vecs" un "vecs") mātīšu skaits ir būtiski mazāks par tēviņu skaitu (χ^2 tests, P < 0,001); tas pats novērojams arī sivēnu grupā, izņemot martu un aprīli, kad šīs atšķirības nav statistiski būtiskas (2. tab.). Apskatot nomedīto dzīvnieku dzimumstruktūru gada griezumā pa mēnešiem un pieliekot klāt informāciju par nomedīto mātīšu indeksu pieaugušo dzīvnieku un jaunāku par gadu dzīvnieku grupā, redzams, ka vairošanās laikā (mazuļu dzimšanas un zīdīšanas periodā) pieaugušo dzīvnieku grupās mātītes tikušas iespējami saudzētas. Tas izskaidrojams gan ar medību vietas un paņēmiena izvēli, gan mednieku ētisku un racionālu apsvērumu rezultātā veiktu selekciju.



5. attēls. Nomedīto meža cūku mātīšu un tēviņu skaita izmaiņas pa mēnešiem un nomedīto mātīšu indeksu vērtību izmaiņas pieaugušo un jaunāku par gadu (sivēnu) grupā (ar * atzīmēti mēneši, kuros nomedīto mātīšu indeksu vērtības pieaugušo un jaunāku par gadu dzīvnieku grupā statistiski būtiski atšķiras).

2. tabula

*Nomedīto mātīšu indeksu (mātītes/tēviņi) vērtību salīdzinājums pieaugušo un jaunāku par gadu dzīvnieku grupā (χ^2 tests, $p < 0,001$) (ar * atzīmētas būtiskās atšķirības)*

Mēnesis	**Jaunāki par gadu**	**Pieaugušie**	**P vērtība**
DEC	0,764	0,787	0,732
JAN	0,788	0,747	0,517
FEB	0,813	0,707	0,160
MAR	0,877	0,530	0,000*
APR	0,818	0,401	0,000*
MAI	0,492	0,331	0,080
JUN	0,490	0,381	0,316
JUL	0,654	0,666	0,891
AUG	0,732	0,591	0,022*
SEPT	0,697	0,609	0,114
OKT	0,734	0,682	0,357

Salīdzinot nomedīto meža cūku mātīšu indeksu vērtības ar iepriekšējā gadā nomedīto mātīšu indeksu vērtībām, statistiski būtiskas atšķirības ir vienīgi pieaugušo dzīvnieku grupā maijā, jūnijā un septembrī (3. tab.) (χ^2; $P < 0,001$), visos gadījumos efekta lielums ir ļoti mazs ($V < 0,1$). Tātad, lai arī 2025. gadā nomedīts būtiski mazāk meža cūku nekā iepriekšējā 2024. gadā, kopumā ņemot, mātīšu indeksu vērtības gan pieaugušo, gan jaunāku par gadu dzīvnieku grupā būtiski neatšķiras.

3. tabula

*Nomedīto mātīšu indeksu (mātītes/tēviņi) vērtību salīdzinājums pa mēnešiem pieaugušo un jaunāku par gadu dzīvnieku grupā starp 2025. un 2024. gadu (χ^2 tests, $p < 0,001$) (ar * atzīmētas būtiskās atšķirības)*

	Jaunāki par gadu					**Pieaugušie**				
	2025	**2024**	**χ^2**	**P vērtība**	**Efekta lielums V**	**2025**	**2024**	**χ^2**	**P vērtība**	**Efekta lielums V**
JAN	0,788	0,728	0,865	0,352	0,018	0,747	0,729	0,088	0,767	0,005
FEB	0,813	0,796	0,036	0,85	0,005	0,707	0,597	3,070	0,080	0,040
MAR	0,877	0,902	0,036	0,85	0,007	0,530	0,596	1,224	0,269	0,028
APR	0,818	0,711	0,382	0,536	0,033	0,401	0,464	1,906	0,167	0,034
MAI	0,492	0,633	0,864	0,353	0,058	0,331	0,407	5,100	0,024*	0,045
JUN	0,490	0,832	3,41	0,065	0,117	0,381	0,543	20,580	0,000*	0,078
JUL	0,654	0,542	1,081	0,299	0,045	0,666	0,684	0,177	0,674	0,006
AUG	0,732	0,699	0,136	0,713	0,011	0,591	0,640	1,374	0,241	0,019
SEPT	0,697	0,606	1,125	0,289	0,031	0,609	0,510	4,160	0,041*	0,040
OKT	0,734	0,744	0,014	0,905	0,003	0,682	0,699	0,099	0,754	0,006

Savukārt mātīšu indeksa būtiskais samazinājums mēnešos, kad pieaugušās cūku mātītes tiek saudzētas – maijā un jūnijā – drīzāk norāda uz to, ka parastās rekreācijas medības, kopējam meža cūku blīvumam valstī samazinoties, jāuzskata par apšaubāmu līdzekli ĀCM apkarošanas stratēģijas īstenošanā.

Meža cūku populāciju struktūras salīdzinājums teritorijās ar atšķirīgu populācijas blīvumu starp kameru datiem un nomedīto dzīvnieku datiem

Analīzei izmantoti dati par 224 novērotām meža cūkām no kurām 27 bija pieauguši tēviņi, 35 mātītes, 98 sivēni un pārējie – līdz dzimumam neidentificēti pieaugušie dzīvnieki.

Aplūkojot kamerās vienlaikus fiksēto meža cūku mātīšu un tēviņu skaitu un 10 000 ha lielajā poligonā ap šīm kamerām nomedīto pieaugušo meža cūku skaitu un salīdzinot to dzimumstruktūru (mātītes/tēviņi), redzams, ka daļā teritoriju un arī, visus datus skatot kopā, ir vērojamas statistiski būtiskas atšķirības (4. tab.). Daļā gadījumu χ^2 testa rezultāti ir ar vidēju vai lielu efektu (V > 0,3), kas apliecina mednieku selektīvas medīšanas praksi.

4. tabula

Kamerās novēroto pieaugušo meža cūku dzimumstruktūras salīdzinājums ar 10 000 ha poligonā ap kamerām nomedīto meža cūku dzimumstruktūru. χ^2 tests, $p < 0{,}001$, efekta lielums (ja $V < 0{,}1$ – nebūtisks efekts; 0,1–0,3 – mazs; 0,3–0,5 – vidējs un > 0,5 – liels efekts)

Aptuvena atrašanās vieta	Lielākais kamerās vienlaikus fiksētais meža cūku skaits		Nomedīti		χ^2	p	Efekta lielums V
	tēviņi	mātītes	tēviņi	mātītes			
Aloja	1	-	13	2	3,37	0,04	0,459
Balvi	-	-	14	5	-	-	-
Ķemeri*	1	4	15	13	6,65	0,005	0,449
Kuja*	4	4	12	7	0,98	0,246	0,191
Lejasciems	-	2	2	-	-	-	-
Lubāna*	-	-	-	2	-	-	-
Skrunda	-	1	22	12	1,96	0,11	0,237
Skujene	-	2	21	16	5,29	0,12	0,368
Talsi	3	4	23	15	2,18	0,09	0,22
Teiči	3	2	17	6	0,589	0,386	0,145
Valka	1		13	10	1,43	0,16	0,244
Ventspils	-	-	46	23	-	-	-
Viesīte	-	1	5	2	2,033	0,101	0,504
Viļķene	1	6	10	2	9,95	0	0,724
Zalve	1	2	19	15	3,28	0,04	0,298
KOPĀ:	15	28	232	130	19,16	0	0,222

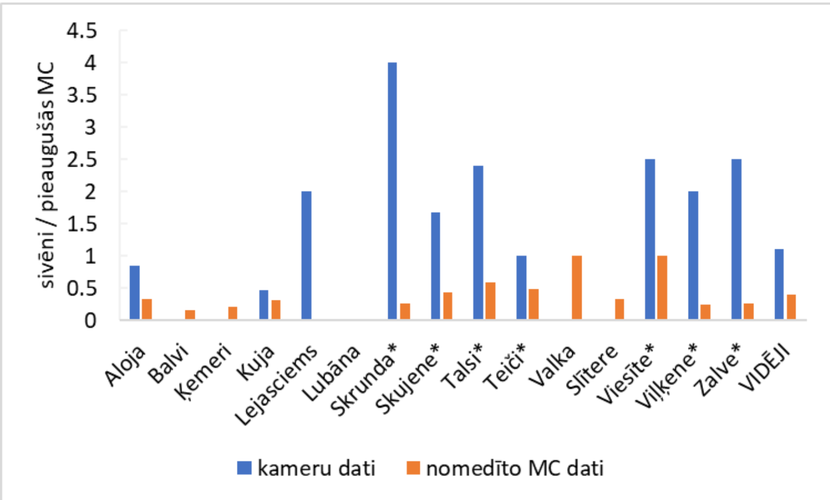
Ar * apzīmētajās vietās kamera atradusies medījamo dzīvnieku uzskaites vienībā, kur 01.04.2025. populācijas blīvums vērtēts ka < 1,5/1000 ha.

Salīdzinot kamerās lielāko vienlaicīgi fiksēto meža cūku skaitu dalījumā pa vecuma kategorijām (pieaudzis dzīvnieks un sivēns) ar nomedīto meža cūku vecuma sadalījumu 10 000 ha poligonā ap šīm kamerām, konstatētas statistiski būtiskas atšķirības: kamerās kopumā fiksēts proporcionāli vairāk sivēnu nekā tas ir starp nomedītajiem dzīvniekiem (5. tab., 6. att.).

5. tabula

Kamerās novēroto pieaugušo meža cūku vecumstruktūras salīdzinājums ar 10 000 ha poligonā ap kamerām nomedīto meža cūku vecumstruktūru. χ^2 tests, $p < 0,001$, efekta lielums (ja $V < 0,1$ – nebūtisks efekts; 0,1–0,3 – mazs; 0,3–0,5 – vidējs un > 0,5 – liels efekts)

	Lielākais kamerās vienlaikus fiksētais meža cūku skaits		**Nomedīti**		**χ^2**	**p**	**Efekta lielums V**
	pieaugušie	**sivēni**	**pieaugušie**	**sivēni**			
Aloja	13	11	15	5	2,22	0,088	0,225
Balvi	1	-	19	3	4,577	0,018	0,446
Ķemeri	4	-	28	6	6,11	0,007	0,401
Kuja	15	7	19	6	1,16	0,21	0,157
Lejasciems	2	4	2	-	3,88	0,03	0,696
Lubāna	1	-	2	-	1,54	0,14	0,716
Skrunda	1	4	34	9	7,98	0,003	0,408
Skujene	3	5	37	16	3,24	0,04	0,23
Talsi	5	12	38	22	10,33	0	0,366
Teiči	16	16	23	11	3,69	0,03	0,236
Valka	1	-	23	23	5,76	0,009	0,35
Ventspils	1	-	69	23	3,83	0,03	0,203
Viesīte	2	5	7	7	5,97	0,008	0,533
Viļķene	6	12	12	3	12,18	0	0,608
Zalve	2	5	34	9	7,64	0,003	0,391



6. attēls. Kamerās novēroto meža cūku vecumstruktūra (sivēni/pieaugušās meža cūkas (MC)) un 10 000 ha poligonā nomedīto meža cūku vecumstruktūra (ar * atzīmētas būtiskās atšķirības)

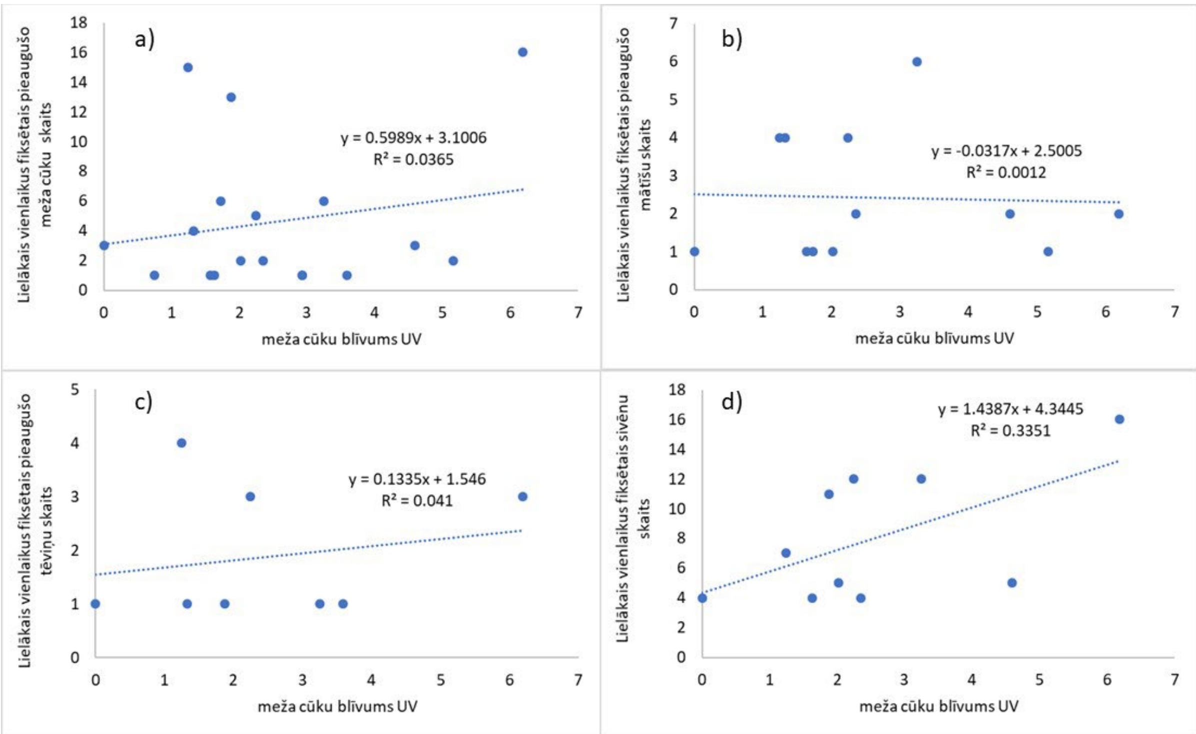
Ar Spīrmena rangu korelāciju pārbaudot sakarības starp lielāko kamerās fiksēto meža cūku skaitu un uzskaites vienībā novērtēto meža cūku blīvumu, nevienā gadījumā nav vērojamas statistiski būtiskas sakarības (6. tab.). Tendence lielākoties ir likumsakarīga – teritorijās ar lielāku novērtēto meža cūku blīvumu, tos arī biežāk iespējams novērot kamerās. Pieaugušajām meža cūku mātītēm vērojama pretēja tendence – teritorijās ar lielāku novērtēto meža cūku blīvumu, lielākais vienlaikus novērotais mātīšu skaits ir nedaudz mazāks (7. att.b) – vienādojuma x koeficients ar negatīvu zīmi, $R^2 = 0,0012$, p= 0,785).

Korelāciju analīzi nav iespējams veikt par kameru datiem, kas uzstādītas VMD uzskaites vienībās ar novērtēto meža cūku blīvumu zem 1,5. Tādas ir 4 kameras (Teiči, Lubāna, Kuja un Ķemeri – 4. tab.). Šajās uzskaites vienībās ir neliels fiksēto dzīvnieku skaits, un tas nav zināms arī visās vecuma un dzimuma grupās. Grafiski, aplūkojot sakarības starp lielāko kamerās fiksēto meža cūku skaitu un uzskaites vienībā novērtēto meža cūku blīvumu, vērojama līdzīga tendence kā visus datus aplūkojot kopā, proti, teritorijās ar lielāku novērtēto meža cūku blīvumu lielākais vienlaikus novērotais abu dzimumu un visu vecuma grupu dzīvnieku skaits arī ir lielāks (7. un 8. att.). Tā kā kamerās fiksēto dzīvnieku skaits ir neliels, šo tendenci tomēr jāvērtē ļoti kritiski.

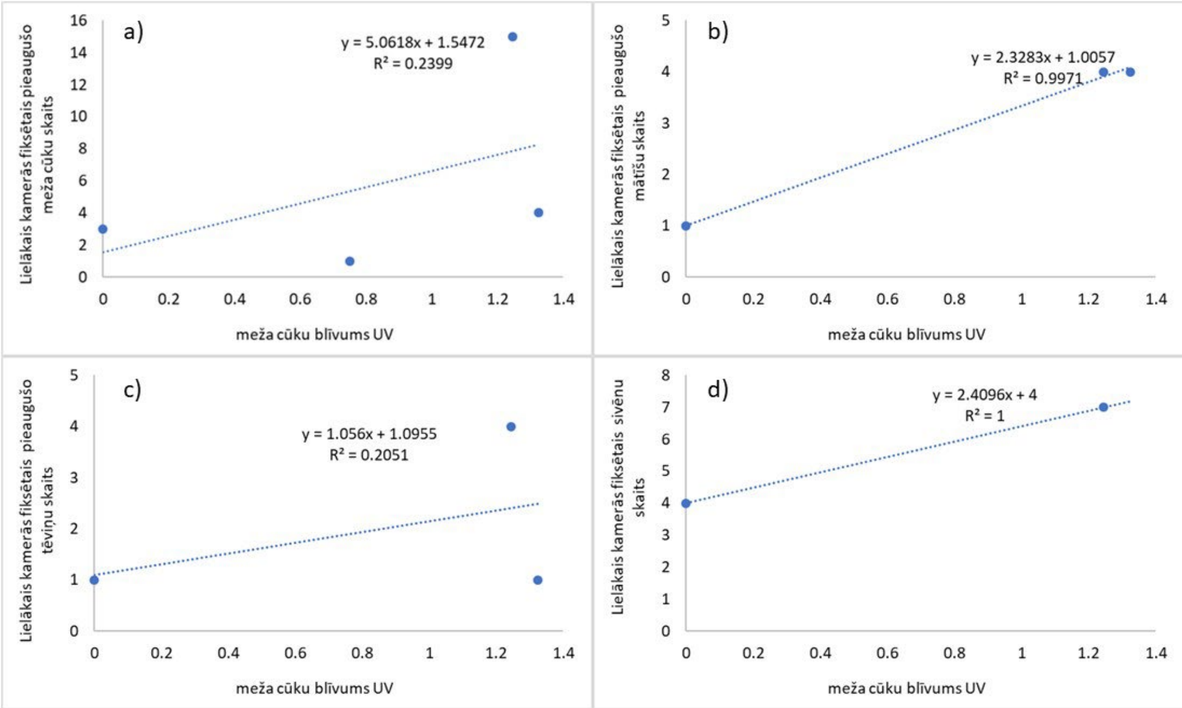
6. tabula

Spīrmena rangu korelācijas rezultāti

	Korelācijas starp blīvuma vērtējumu uzskaites vienībās		**Korelācijas starp nomedīto skaitu uzskaites vienībās**	
	S	**p**	**S**	**p**
mežacūku fiksējumu skaits	865,330	0,673	829,830	0,5697
lielākais vienlaikus fiksēto tēviņu skaits	80,536	0,923	83,419	0,987
lielākais vienlaikus fiksēto mātīšu skaitu	260,730	0,785	173,410	0,2055
lielākais vienlaikus fiksēto pieaugušo indivīdu skaitu	926,080	0,862	1207,800	0,3242
lielākais vienlaikus fiksēto tekošā gada sivēnu skaitu	80,448	0,130	181,910	0,7781



7. attēls. Sakarības starp lielāko kamerās vienlaikus fiksēto visu pieaugušo meža cūku (a), pieaugušo mātīšu (b), pieaugušo tēviņu (c) un sivēnu (d) skaitu un uzskaites vienībā novērtēto meža cūku blīvumu



8. attēls. Sakarības starp lielāko kamerās vienlaikus fiksēto visu pieaugušo meža cūku (a), pieaugušo mātīšu (b), pieaugušo tēviņu (c) un sivēnu (d) skaitu un novērtēto meža cūku blīvumu uzskaites vienībās, kur tas ir zem 1,5 meža cūkām uz 1000ha

Meža cūku populācijas blīvumam samazinoties, pieaugušo mātīšu īpatsvars lokālpopulācijās nesamazinās, kas izskaidrojams gan ar mātītes saudzējošu medību praksi, gan sugai piemītošo sociālo struktūru, kurā baru veido cūku mātes ar pēcnācējiem.

2. Kritēriji teritorijas klasificēšanai par platību, kurā populācijas blīvums nepārsniedz 1,5 meža cūkas uz 1000 ha

2.1. Metodika

Pētījumā divu gadu laikā veikta pieejamo datu un to ieguves metožu analīze, lai noteiktu uzticamus kritērijus, pēc kuriem pārliecināties par meža cūku populācijas blīvumu medību platībās. 2018. gadā Zemkopības ministrija grozīja noteikumus “Medījamo dzīvnieku populāciju stāvokļa novērtēšanas un pieļaujamā nomedīšanas apjoma noteikšanas metodika”, kuros aprakstītas dzīvnieku blīvuma noteikšanai paredzētās metodes: pēdu uzskaite sniegā, dzinējmedību laikā novēroto indivīdu skaitīšana, izkārnījumu skaits, novērojumi pie barošanas un piebarošanas vietām, kā arī mednieku novērojumi medību laikā. Medījamo dzīvnieku populāciju stāvokļa novērtēšanu VMD reģionālajās mežniecībās organizē virsmežziņi, kuri nosaka dzīvnieku uzskaites teritorijas – nepārtrauktus masīvus, kas noteikti pēc dabiskām robežām un ietver vienu vai vairākus nedalītus medību iecirkņus. Meža cūkām šīm teritorijām jābūt ne mazākām par 1500 hektāriem, ņemot vērā kopējo medību platību. Pamatojoties uz populācijas stāvokļa novērtēšanas datiem, katrai uzskaites teritorijai tiek pieņemts lēmums par pieļaujamo nomedīšanas apjomu, lai uzlabotu, saglabātu vai ierobežotu populāciju (Zemkopības ministrija, 2018). Tomēr praksē likumā aprakstītās metodes tiek izmantotas reti. Pārnadžu, tostarp meža cūku, populācijas blīvums un tendences galvenokārt tiek vērtēti, balstoties vienīgi uz nomedīto dzīvnieku datiem – dzimumu, vecumu, koordinātēm un laiku –, kā arī uz medību tiesību lietotāju aptauju, kas tiek veikta pēc medību sezonas beigām martā. Šajās aptaujās tiek vērtēts novērotais dzīvnieku blīvums un populācijas tendences (samazinās, stabila vai palielinās), kā arī jautāts, vai medību sezonas sākumā izsniegtais atļauju skaits bija atbilstošs un kā tas būtu jāmaina. Jāņem vērā, ka Āfrikas cūku mēra izraisītās epizootijas dēļ, lai samazinātu populācijas blīvumu, meža cūku medības kopš 2022. gada 20. aprīļa ir neierobežotas.

Kopš 2023. gada Latvijā tiek izmantota mobilā lietotne "Mednis", kurā medniekiem obligāti jāreģistrē nomedītās meža cūkas un citi medījumi, izmantojot digitālos marķējuma numurus. Šī sistēma novērš nepieciešamību pēc fiziskajiem meža cūku marķieriem un papildu informācijas iesniegšanas par izmantotajām atļaujām, vienlaikus nodrošinot precīzus laika un atrašanās vietas datus, kas automātiski tiek pievienoti medību protokolam (Valsts meža dienests, 2023). Pētījuma 1. posmā, kas norisinājās 2024. gadā, veicot literatūras analīzi, tika identificētas vairākas meža cūku populācijas monitoringa metodes, kuru precizitāte un praktiskums ievērojami atšķiras. Tās ietver medību datu analīzi, transektu novērojumus, telemetriju, pēdu un rakumu uzskaiti, izkārnījumu uzskaiti, neinvazīvo DNS paraugu ņemšanu, aerofotouzskaiti un mednieku aptaujas. Lai gan medību dati var būt noderīgi, to praktiskā izmantojamība lielā mērā ir atkarīga no medību slodzes ticamas uzskaites, kas Latvijā ir problemātiska ierobežotās mednieku iesaistes un ziņošanas dēļ. Izvērtējot pieejamo metožu piemērotību Latvijas apstākļiem, par vispraktiskāko un objektīvāko risinājumu tika atzīta fotokameru izmantošana. Tās nodrošina nepārtrauktu, maz invazīvu monitoringu un ir mazāk pakļautas cilvēka klātbūtnes ietekmei. Lai izmēģinātu šo metodi un novērtētu meža cūku blīvumu, LVMI "Silava" pievienojās Eiropas Savvaļas dzīvnieku observatorijas vadītajam projektam. Lai nodrošinātu, ka pētījuma teritorija ir piemērota dzīvnieku blīvuma novērtēšanai, tai jāatbilst konkrētiem kritērijiem: teritorijas platībai jābūt no 2000 līdz 6000 hektāriem, jābūt drošiem apstākļiem fotokameru uzstādīšanai un jābūt meža biotopam, kas mijas ar citu zemes izmantošanas veidu teritorijām. Nedrīkst praktizēt intensīvu pārnadžu piebarošanu, lai gan neliela piebarošana ārpus uzstādīšanas perioda vai pievilināšana ar ēsmu medību vajadzībām netiek uzskatīta par problēmu. Iespēju robežās būtu jāizvairās no fotokameru uzstādīšanas pārklāšanās ar medību aktivitātēm. Fotokameru uzskaitē balstītai blīvuma noteikšanai ir būtiski izmantot reprezentatīvu un nejaušu parauglaukuma dizainu. Kamerām jābūt izvietotām, izmantojot datorizēti ģenerētus nejaušus punktus, kuri nav atkarīgi no dzīvnieku pārvietošanās ceļiem vai pēdām. Kameras nedrīkst uzstādīt dzīvniekus piesaistošās vietās, piemēram, pie ūdens avotiem, sāls laizītavām vai barotavām, jo nerandomizēta izvietošana var radīt kļūdainu rezultātu, lietojot nejaušās sastapšanas modeli. Pētījumu teritorijām 2000–6000 ha platībā ieteicams izmantot vismaz 36 kameras. Attālums starp kameru punktiem var atšķirties, un lielākām teritorijām nepieciešams proporcionāli lielāks kameru skaits. Katrai kamerai jādarbojas vismaz četras nedēļas, ideālā gadījumā – sešas (ENETWILD Consortium, 2022).

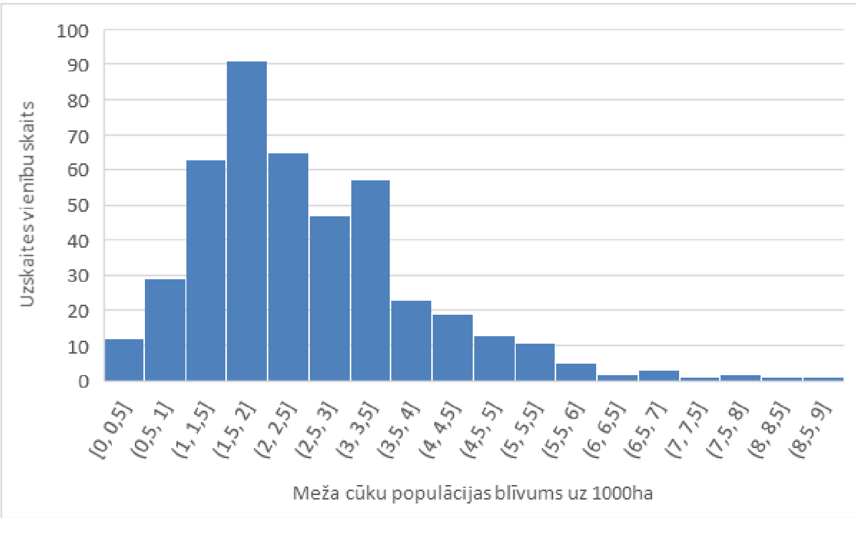
Viena no nejaušās sastapšanās principa priekšrocībām ir tā, ka pēc šī modeļa kameras vienlaikus var reģistrēt vairākas dzīvnieku sugas, ļaujot pētniekiem noteikt sugu klātbūtni vai to blīvumu bez tiešas mijiedarbības ar dzīvnieku. Šīs kameras sniedz arī informāciju par dzīvnieku pārvietošanos, ātrumu, blīvumu un uzskaites intensitāti katrā vietā. Turklāt tās spēj vākt datus par temperatūru, veģetāciju un fenoloģiskajiem procesiem, kas ļauj no viena fotogrāfiju kopuma veikt dažādus zinātniskos pētījumus.

Fotokameru datu apstrādei tika izmantota Agouti platforma – *Agouti platform and Random Encounter Model* (REM), kas ir tiešsaistes sistēma, ko izstrādājusi un uztur Vāgeningenas Universitāte (WUR) un Dabas un meža izpētes institūts (INBO, Brisele), lai pārvaldītu un apstrādātu fotokameru datus savvaļas dzīvnieku monitoringa vajadzībām. Eiropas Savvaļas observatorijas (EOW) un ENETWILD projekta ietvaros Agouti kalpo kā centrālā krātuve un analītiskais rīks visā Eiropā savāktajiem fotokameru attēliem (ENETWILD Consortium, 2024). Platforma ļauj veikt visas fotokameru datu apstrādes stadijas – no projekta izveides, attēlu augšupielādes un ar mākslīgā intelekta palīdzību veiktas sugu atpazīšanas līdz dzīvnieku pārvietošanās izsekošanai un parametru noteikšanai nejaušās sastapšanās modelim (REM). Platformā ir integrēta fotogrammetrija 3D kalibrēšanai, kas automatizē attāluma un ātruma noteikšanu un samazina cilvēka kļūdu iespējamību. Standartizējot darba plūsmas dažādās valstīs, Agouti nodrošina harmonizētus un reproducējamus savvaļas dzīvnieku blīvuma novērtējumus Eiropas mērogā (Casaer et al., 2019). Populācijas blīvuma novērtēšanai no apstrādātajiem datiem tie tika eksportēti uz R-Studio, un tika izmantots R pakotne *camtrapDensity* (Rowcliffe et al., 2016). Šī pakotne izmanto nejaušās sastapšanās modeli (REM), kombinējot informāciju par detekciju biežumu, kameras detekcijas zonu, detekcijas leņķi, dzīvnieku pārvietošanās ātrumu un aktivitātes līmeni, lai aprēķinātu dzīvnieku blīvumu. Šajā pētījumā izmantotās galvenās funkcijas bija: *remBoot* blīvuma aplēsēm ar *bootstrap* pieeju; *activityDensity* dzīvnieku diennakts aktivitātes aprēķināšanai un *cameraOperation* izvietojuma grafiku un izmantotās slodzes korekcijas pārvaldībai (ENETWILD Consortium, 2022).

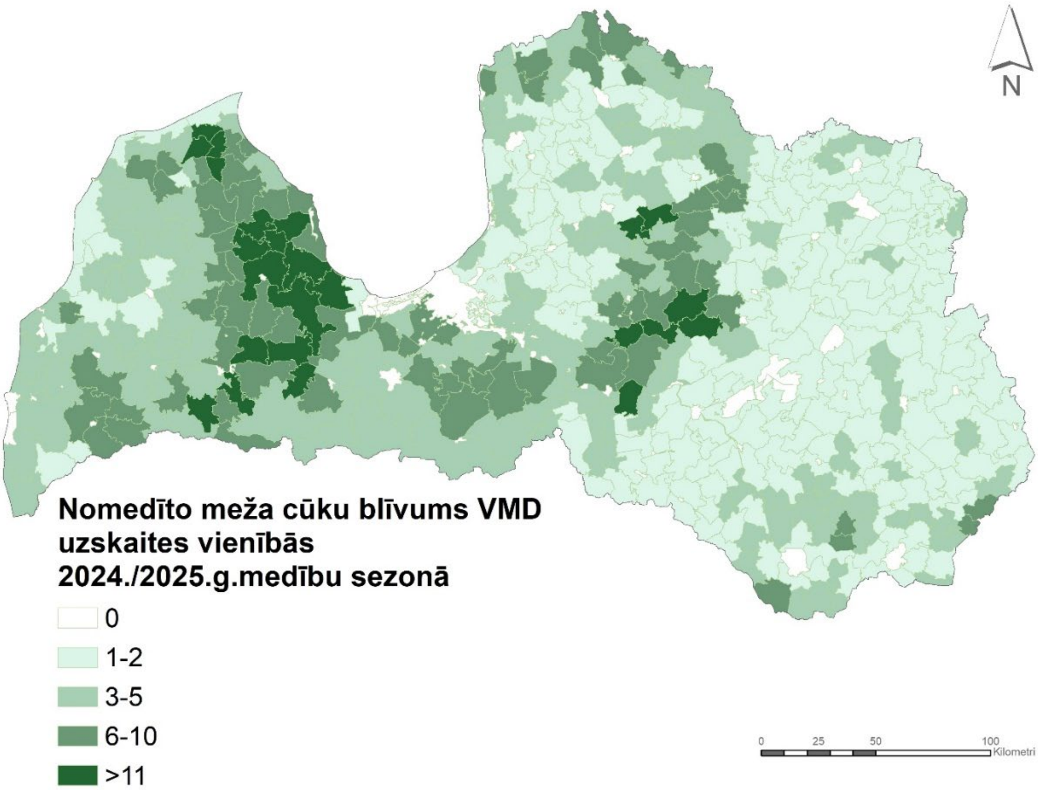
2.2. Rezultāti

Pēc VMD datiem 2025. gada 1. aprīlī 445 medījamo dzīvnieku uzskaites vienībās vidējais populācijas blīvuma vērtējums bijis 2,5 meža cūkas uz 1000 ha. Taču teritoriāli populācijas blīvums sadalīts izteikti nevienmērīgi (9. att.). Uzskaites vienību ar populācijas blīvuma vērtējumu zem 1,5 uz 1000 ha ir nepilna ceturtā daļa – 104 ar kopplatību 1 584 144 ha. Savukārt vairāk par 1,5 meža cūkām uz 1000 ha novērtēts 341 uzskaites vienībā ar kopplatību 4 747 215 ha. Arī lielākā daļa 2024./2025. gadā nomedīto meža cūku (10. att.) bijis platībās ar blīvumu > 1,5/1000 ha – attiecīgi 19 830 un 2386 meža cūkas.

2024. gada EOW projekta ietvaros Lubānas mežu iecirknī uzstādītās fotokameras pierādīja, ka slēpņa kameru metode ir efektīva bieži sastopamu savvaļas dzīvnieku blīvuma novērtēšanai. Tomēr neviena meža cūka netika reģistrēta nevienā no 72 izvietojumiem (36 kameras, kas pēc mēneša tika pārvietotas), līdz ar to nebija iespējams aprēķināt meža cūku blīvumu. Līdzīgi arī teritorijā fiksētie vilku un lūšu novērojumi bija pārāk reti, lai veiktu blīvuma aplēses, kas norāda, ka teritorijās ar zemu meža cūku blīvumu līdzīgas problēmas ir sagaidāmas.



9. attēls. Uzskaites vienību (N = 445) sadalījums pēc meža cūku populācijas blīvuma uz 1000 ha apmedījamo platību.



10. attēls. Sezonā nomedīto meža cūku skaits VMD medījamo dzīvnieku uzskaites vienībās uz 1000 ha.

2025. gada fotokameru izvietošanas darbu laikā tajā pašā teritorijā tika novērota vairāk nekā 15 meža cūku liela grupa – pārsvarā sivēni. Tomēr attēlu sērijās nekad netika fiksēti vairāk nekā četri sivēni kopā ar cūku māti, kas norāda, ka nejauši izvietotas fotokameras var neuztvert visu meža cūku baru. Līdzīgi Mērsraga mežu iecirknī kameru uzstādīšanas laikā tika konstatētas svaigas pēdas un citas meža cūku klātbūtnes pazīmes, taču divu mēnešu laikā neviena cūka netika reģistrēta, vēl vairāk uzsverot nejaušās sastapšanās fotokameru metodes ierobežojumus meža cūku blīvuma novērtēšanai. Tas apstiprina, ka zema blīvuma apstākļos, kad sagaidāms maz kontaktu vai populācija ir ļoti sadrumstalota (un līdz ar to arī kontaktu biežums ar kamerām), ir nepieciešams ievērojami lielāks fotokameru skaits un/vai garāks pētījums, lai iegūtu precīzas blīvuma aplēses, jo aprēķinātais variācijas koeficients (nenoteiktība) parasti ir liels (ENETWILD Consortium, 2022). Rezultātus iespējams uzlabot, ja zema blīvuma (0,7 līdz 6,99 dzīvnieki/km² meža teritorijās 250–450 ha platībā) apstākļos tiek izmantotas 9 kameras uz km² (Massei, 2017), taču tas nozīmētu 180 kameras 2000 ha teritorijai, kas ir nereāli un nepraktiski.

Fotokameru uzstādīšana prasa ievērojamu laiku un resursus, jo bieži nepieciešams attīrīt augsto veģetāciju, un katras kameras kalibrēšana aizņem apmēram 15 minūtes. Vidējais uzstādīšanas temps – ieskaitot iešanu vai braucienu līdz izvēlētajai vietai, veģetācijas attīrīšanu un kameras redzes lauka kalibrēšanu – ir aptuveni viena kamera 50 minūtēs. Pārvietošanās starp vietām var būt sarežģīta Latvijas biezo mežu dēļ. Divu cilvēku komandai 20 kameru uzstādīšana aizņem apmēram divas pilnas dienas, savukārt to pārvietošana divu dienu laikā ir gandrīz neiespējama un parasti aizņemtu trīs dienas. Nepieciešamo laiku iespējams samazināt, piesaistot vairāk cilvēku, taču tas prasa papildu resursus. Meža cūku populācijas blīvuma kontroli iespējams padarīt efektīvāku.

Pievilināšana ar ēsmu (Baiting at camera trap sites)

Peris u.c. (2019) centrālajā Spānijā veica gadu ilgu pētījumu, lai novērtētu, kā piebarošana ietekmē ar fotokamerām iegūtos meža cūku populācijas blīvuma novērtējumus. 36 kameras tika izvietotas 12 parauglaukumos, katru monitorējot aptuveni 60 dienas. Pusē vietu notika piebarošana ar aptuveni 5 kilogramiem kukurūzas, kas tika papildināta ik pēc 7– 10 dienām, bet pārējās vietas kalpoja kontrolei bez piebarošanas. Kā salīdzinoša uzskaites metode izmantota dzīvu meža cūku ķeršana, individuāla marķēšana ar ausu krotālijām un atbrīvošana (Peris et al., 2019).

Piebarošana vairāk nekā trīskāršoja fiksāciju skaitu kamerās – no 85 līdz 278 neatkarīgiem meža cūku novērojumiem – un būtiski samazināja sastapšanās biežuma variāciju. Barības pievienošana ne tikai palielināja fiksācijas varbūtību un samazināja sastapšanās biežuma variācijas koeficientu, bet arī ļāva iegūt uzticamus blīvuma novērtējumus, izmantojot mazāku kameru skaitu un īsākus uzstādīšanas periodus. Piebaroto vietu blīvuma aplēses sakrita ar atzīmēšanas-atkārtotas noķeršanas datiem, savukārt nepiebarotās vietas konsekventi uzrādīja zemu populācijas lielumu (Peris et al., 2019).

Latvijā, kur meža cūku blīvums Āfrikas cūku mēra dēļ ir samazinājies, kontrolēta piebarošana būtu efektīvs veids, kā palielināt detekcijas varbūtību un uzlabot blīvuma aplēšu precizitāti, īpaši mežainos apgabalos ar zemu dzīvnieku aktivitāti. Lai nodrošinātu rezultātu salīdzināmību un izvairītos no pārliekas uzvedības ietekmēšanas, piebarošana būtu jāstandartizē – gan barības veids, gan daudzums, gan papildināšanas intervāli (Peris et al., 2019).

Mednieku iesaiste novērojumos

Kopš 2024. gada visi nomedītie dzīvnieki tiek reģistrēti mobilajā lietotnē “Mednis”, kas aizstāj plastmasas marķierus un nodrošina Valsts meža dienestu ar precīziem telpiskiem un laika datiem par katru nomedījumu (Mobilā lietotne “Mednis”, 2024). Lietotni varētu izmantot arī kā ērtu un precīzu rīku mednieku novērojumu reģistrēšanai, piemēram, skatīt nākamo rindkopu.

Attālumu reģistrēšana (*Distance sampling*)

Uzskaite zināma garuma maršrutos, izmantojot termokameras, ir metode meža cūku blīvuma novērtēšanai, reģistrējot dzīvnieku novērojumus gar iepriekš izplānotiem transektiem un mērot attālumu līdz dzīvniekiem, lai izveidotu sastopamības funkciju. Termokameras uzlabo detekciju, īpaši naktī vai sliktas redzamības apstākļos, piemēram, miglā un sniegā, tādējādi risinot dažus vizuālās novērošanas ierobežojumus. Tomēr metodes efektivitāti būtiski ietekmē biotopa struktūra un populācijas blīvums. Vietās ar blīvu zemsedzi vai zemu meža cūku skaitu, it īpaši augstas medību intensitātes apstākļos metode prasa lielu uzskaites apjomu un rūpīgu kalibrēšanu. Lai gan tā veiksmīgi izmantota dažviet Eiropā, vislabāk tā darbojas atklātos biotopos vai reģionos ar lielāku meža cūku blīvumu. Latvijas biezo mežu apstākļos šīs metodes ieviešana visreālāk būtu iespējama atklātās vietās, piemēram, barošanas vietās, kuras pieejamas lielākajā daļā medību kolektīvu. Pieaugot termokameru pieejamībai un to lietošanai mednieku vidū, šī metode varētu būt vērtīgs papildinājums esošajām fotokameru metodēm (ENETWILD Consortium, 2018).

Uzskaite ar izdzīšanu (*Drive counts*)

Dzinējmedību uzskaite ir tradicionāla metode populācijas blīvuma noteikšanai, dzīvniekiem tiekot izdzītiem un saskaitītiem noteiktā teritorijā. Metode plaši izmantota pārnadžu populāciju novērtēšanai mežainās teritorijās, un to var veikt, izmantojot dzinējus ar vai bez suņiem, lai virzītu dzīvniekus uz medniekiem vai novērotājiem. Dzinējmedību laikā visi pamanītie indivīdi tiek reģistrēti īpaši norīkotu uzskaitītāju vai mednieku rindā. Metodes precizitāti ietekmē tādi faktori kā populācijas blīvums, dzīvnieku uzvedība, redzamība un dalībnieku koordinācija (ENETWILD Consortium, 2018).

Latvijā dzinējmedības ir bieži izmantota un labi izveidojusies prakse meža cūku un citu pārnadžu medībās rudens/ziemas sezonā. Šī iemesla dēļ dzinējmedību uzskaiti būtu salīdzinoši viegli integrēt esošajās medību aktivitātēs, padarot to par potenciāli izmaksu ziņā efektīvu populācijas datu ieguves metodi. Vecākās paaudzes mednieki to arī agrāk ir izmantojuši. Tomēr pastāv vairāki izaicinājumi, tostarp risks saskaitīt dzīvniekus divreiz, dzīvnieku iespējamā izvairīšanās no pamanīšanas un izteiktā cilvēka piepūles un laikapstākļu ietekme uz rezultātiem. Lai gan dzinējmedību uzskaite var sniegt noderīgus lokālus novērtējumus, īpaši augsta blīvuma apstākļos, metode prasa labu koordināciju un uzticamu datu ievadi no medniekiem, lai nodrošinātu precīzus populācijas novērtējumus (ENETWILD Consortium, 2018).

Pēdu uzskaite (*Track surveys*)

Pēdu uzskaite sniegā ietver dzīvnieku pēdu skaita vai biežuma reģistrēšanu gar iepriekš plānotiem transektiem, lai aprēķinātu vietējās populācijas relatīvās sastopamības indeksu. Šajā metodē pēdu skaits uz vienu uzskaites vienību var tikt izmantots populācijas lieluma novērtēšanai, un dažos gadījumos pēdu izmēri ļauj aptuveni noteikt populācijas struktūru. Metode ir vienkārša un lēta, taču to ietekmē vairāki kļūdu cēloņi, tostarp novērotāja pieredze, motivācija un laikapstākļi. Ilgstošs sals vai dziļš sniegs var samazināt dzīvnieku aktivitāti, izraisot populācijas pazeminātu novērtējumu.

Latvijā sniegā atstāto pēdu uzskaite būtu piemērota papildmetode ziemas sezonā, īpaši reģionos, kuros veidojas stabila sniega sega. Daudzi mednieki jau ņem vērā pirms medībām atrastās pēdas kā daļu no regulārajiem lauka novērojumiem, un šo prakšu integrēšana standartizētā monitoringa protokolā varētu uzlabot vietējo sastopamības novērtējumu. Lai šādi dati būtu uzticami, būtiski reģistrēt kopējo apsekoto teritoriju un laiku, kas pavadīts laukā, jo šie rādītāji raksturo novērošanas slodzi un ļauj salīdzināt datus starp dažādiem apgabaliem vai periodiem. Lai gan sniegā atstāto pēdu dati vieni paši nevar nodrošināt precīzus populācijas blīvuma aprēķinus, šīs metodes kombinēšana ar citām uz novērojumiem balstītām metodēm, piemēram, uzskaiti ar dzinējiem vai fotokamerām, būtu efektīvs veids, kā stiprināt meža cūku monitoringa sistēmu valstī (ENETWILD Consortium, 2018).

Nejaušas sastapšanās un uzturēšanās ilguma modelis *(Random Encounter and Staying Time (REST) model*)

Yokoyama u.c. (2020) izmantoja Beisija statistisko hierarhijas modeli, kas apvienoja fotokameru datus ar ķeršanas datiem, lai novērtētu sezonālo meža cūku blīvumu, biotopu izvēli un noķeršanas varbūtību. Modelis balstījās uz nejaušās sastapšanās un uzturēšanās ilguma metodi (REST), kas ir uzlabota nejaušās sastapšanās modeļa (REM) versija. Atšķirībā no REM, kas izmanto neatkarīgus dzīvnieku kustības datus, REST novērtē populācijas blīvumu, balstoties uz to, cik ilgi dzīvnieks uzturas kameras uztveršanas zonā, tādējādi modelis ir pilnībā balstīts uz fotokameru datiem (Yokoyama et al., 2020).

Autori analizēja mēneša novērojumu skaitu un uzturēšanās ilgumu 180 meža teritorijās, sasaistot tos ar dažādiem biotopiem, lai modelētu lokālos blīvumus un pēc tam tos pārrēķinātu uz 1 km² apsaimniekošanas vienībām. Ķeršanas rezultāti tika iegūti ar kastu un cilpu slazdiem – galvenajām ķeršanas metodēm šajā reģionā –, savukārt medības ar šaujamieročiem netika iekļautas, jo tās veidoja tikai ap 3% no kopējā medību apjoma. Modelī tika iekļauta ķeršanas slodze piepūle (aktīvo slazdu skaits mēnesī), līdz ar to noķerto indivīdu skaits atspoguļoja gan blīvumu, gan intensitāti, ļaujot atsevišķi novērtēt nozvejas varbūtību katram slazda tipam. Visi parametri tika novērtēti kopīgi, izmantojot Beisija pārbaudi (JAGS + R). Šāda integrēta pieeja samazināja nenoteiktību un ļāva identificēt sezonālas izmaiņas blīvumā, biotopu izmantošanā un noķeršanas varbūtībā, kas ziemā pieauga barības trūkuma un ēsmas efektivitātes dēļ. REST modelis tādējādi nodrošināja praktisku, tikai uz fotokamerām balstītu populācijas dinamika monitorēšanu un apsaimniekošanas pasākumu efektivitātes novērtēšanu (Yokoyama et al., 2020).

Līdzīgu pieeju varētu ieviest arī Latvijā, apvienojot ar fotokamerām iegūtos REST blīvuma novērtējumus, aizstājot fizisko slazdu izmantošanu ar medību statistiku. Medību slodze – piemēram, mednieku skaits, dzinējmedību dienas vai lauka darbs stundās – varētu aizstāt "slazdu slodzi", savukārt nomedīto vai pamanīto dzīvnieku skaits nodrošinātu ķeršanas vai novērojumu datus. Tas ļautu vienlaicīgi novērtēt gan nomedīšanas varbūtību, gan populācijas blīvumu, izmantojot Valsts meža dienesta esošos medību datus, bez nepieciešamības izvietot slazdus.

Darba drošības un dzīvnieku aizsardzības (labbūtības) prasības

Šis darbs neparedz meža cūku ķeršanu vai tiešu rīcību ar dzīviem indivīdiem, tomēr joprojām ir spēkā ētikas pamatprincipi dzīvnieku aizsardzībai. Visa darba gaitā nepieciešams ievērot Latvijas Dzīvnieku aizsardzības likumu un Eiropas Savienības Direktīvu 2010/63/ES par dzīvnieku aizsardzību, izmantojot tos zinātniskiem nolūkiem. Šie normatīvie akti nodrošina, ka dzīvniekiem netiek radītas liekas sāpes vai traucējumi. Šajā projektā izmantotās metodes – fotokameras, piebarošanas vietas un mednieku aptaujas – ir neinvazīvas, taču tās joprojām var ietekmēt dzīvnieku uzvedību. Lai to mazinātu, kameras un barotavas jāizvieto pārdomāti, bet lauka darbu apmeklējumu skaits jāsaglabā pēc iespējas mazāks. Projekts ievēro 3 R (3 pieeju) princips – aizstājamība, minimālisms un saudzīgums *(Replacement, Reduction, Refinement)*, lai samazinātu ietekmi uz savvaļas faunu. Medību dati (novērojumi un nomedījumi) tiks izmantoti tikai apkopotā veidā analīzei, un šī pētījuma ietvaros netiks organizētas papildu medības. Vietās, kur nepieciešams, pirms lauka darbu sākšanas tiks saņemta Dabas aizsardzības pārvaldes atļauja.

Lauka darbos nepieciešams ievērot drošības pasākumus pētnieku aizsardzībai. Tas ietver aizsargapģērba izmantošanu, lai pasargātu no ērču kodumiem, piesardzību, pārvietojoties pa nelīdzenu vai mežainu reljefu, kā arī drošu transportlīdzekļu izmantošanu izbraukumos. Lauka darbos vienmēr būs pieejama pirmās palīdzības aptieciņa.

Izpildes plāns

Projektu nepieciešams īstenot divu gadu periodā no 2026. gada janvāra līdz 2027. gada decembrim teritorijās, kur pēc līdzšinējās dzīvnieku uzskaites kārtības meža cūku populācijas blīvums nepārsniedz 1,5 uz 1000 ha un kur pēdējo 3 mēnešu laikā nav konstatēta ĀCM infekcija nomedītām vai atrastām bojāgājušām meža cūkām. 2026. gada vasaras sākumā jāorganizē īsa apmācība lauka komandai par fotokameru uzstādīšanu, kalibrēšanu un datu pārvaldību saskaņā ar ENETWILD protokoliem, izmantojot Eiropas Savvaļas observatorijas (EOW) platformu. Parauglaukumu izvēle un sagatavošana tiks pabeigta līdz jūnijam. Fotokameras tiks izvietotas uzskaites vietās jūlijā un augustā, un katrā vietā tās darbosies aptuveni sešas nedēļas pirms pārvietošanas.

Šo izvietojumu laikā līdztekus standarta nejaušās sastapšanās modelim (REM) jātestē alternatīvās monitoringa metodes. Jāapzina kameras, kas novietotas papildu piebarošanas un barošanas vietās, lai izvērtētu, vai to izvietojums uzlabo detekcijas biežumu zema blīvuma teritorijās. Paralēli visām monitorētajām vietām jāvāc mednieku aptauju dati, tostarp reģistrēti meža cūku novērojumi un nomedījumi. Šie dati tiks apvienoti ar fotokameru fiksācijām, lai testētu REST protokolu, kas pielāgots, izmantojot novērojumu un nomedījumu datus, nevis ķeršanas datus, un ļautu salīdzināt dažādu blīvuma novērtēšanas metožu rezultātus.

Datu ievākšana jāturpina līdz vēlam rudenim, kam sekos attēlu apstrāde un datu analīze no 2026. gada septembra līdz decembrim, izmantojot Agouti platformu. 2027. gadā tiks atkārtots tas pats sezonālais grafiks, lai iegūtu salīdzināmus datus un izvērtētu REM, REST un mednieku novērojumu savstarpējo atbilstību. 2027. gada noslēdzošie mēneši jāveltī padziļinātai analīzei, modeļu veiktspējas salīdzināšanai un galīgā ziņojuma sagatavošanai Zemkopības ministrijai.

Izmaksu aplēse

Šis pētījums tieši atbalsta Zemkopības ministrijas prioritātes savvaļas dzīvnieku slimību uzraudzībā, ilgtspējīgā medījamo dzīvnieku apsaimniekošanā un pārrobežu dzīvnieku infekciju izplatības novēršanā (Ministru kabineta noteikumi Nr. 59). Finansējums var segt pētnieku atalgojumu un ar to saistītos nodokļus, lauka darbu un datu ievākšanas izmaksas, materiālu iegādi vai nomu, analītiskos un laboratorijas pakalpojumus, programmatūru un aprīkojumu, ceļa izdevumus, kā arī administratīvās vai infrastruktūras izmaksas – kopumā līdz pat 100% no attiecināmajām izmaksām. Projekta rezultāti ir iesniegti Zemkopības ministrijai, glabāti Latvijas Biozinātņu un tehnoloģiju universitātes (LBTU) pētniecības datubāzē un būs brīvi pieejami vismaz piecus gadus (Ministru kabineta noteikumi Nr. 59).

Projekta budžets meža cūku populācijas blīvuma pārbaudei divās teritorijās ir sadalīts starp 2026. un 2027. gadu (7. tab.). Lielākā daļa izmaksu ir saistīta ar atalgojumu, lauka darbiem un aprīkojumu. Abus gadus projektā strādās divi lauka tehniķi un viens datu analītiķis, kurš vienlaikus pilda arī projekta koordinatora funkcijas. Ekspluatācijas izmaksas ietver ceļa izdevumus, naktsmītnes un degvielu lauka darbiem. Aprīkojuma izmaksas sedz fotokameras, uzlādējamās baterijas un tehnisko uzturēšanu, lai gan šīs izmaksas var būt zemākas, ja izpildītāja rīcībā jau ir pietiekams skaits fotokameru, kuras var atkārtoti izmantot, samazinot jaunu iekārtu iegādes nepieciešamību. Projekta budžetā nav iekļautas telpu izmaksas, transportlīdzekļi un noliktavas, kuras nodrošina darbu izpildītājs no netiešajām izmaksām (12%). Kopējās izmaksas ir plānotas 20 070 € apmērā 2026. gadā un 9 070 € 2027. gadā, kopējam budžetam sasniedzot 29 140 €. Tomēr izmaksas varētu samazināt līdz 19 140 €, ja tiktu izmantotas esošās fotokameras un nebūtu nepieciešami papildus inventāra iepirkumi.

7. tabula

Meža cūku kontroluzskaites izmaksas, veicot darbu vienlaicīgi divos objektos

Izmaksu veids	2026. g.	2027. g.
Darba samaksa, ieskaitot darba devēja sociālos maksājumus	5324	5324
Komandējumi, naktsmītnes, degviela	2334	2334
Iekārtas	11200	200
Biroja uzturēšana	0	0
Netiešās izmaksas	1212	1212
Kopā	20070	9070

2.3. Kritēriju izstrādei izmantotā literatūra

Allwin, B., Gokarn, N.S., Vedamanickan, S. and Gopal, S. (2016) The wild pig (*Sus scrofa*) behaviour – a retrospective study. *Journal of Dairy, Veterinary & Animal Research*, 3, 1–12.

Ballari, S.A. and Barrios-Garcia, M.N. (2014) A review of wild boar (*Sus scrofa*) diet and factors affecting food selection in native and introduced ranges. *Mammal Review*, 44, 124–134.

Barrios-Garcia, M.N. and Ballari, S.A. (2012) Impact of wild boar (*Sus scrofa*) in its introduced and native range: a review. *Biological Invasions*, 14, 2283–2300.

Campbell, T.A. and Long, D.B. (2009) Feral swine damage and damage management in forested ecosystems. *Forest Ecology and Management*, 257, 2319–2326.

Casaer, J., Milotic, T., Liefting, Y., Desmet, P. and Jansen, P. (2019) Agouti: A platform for processing and archiving of camera trap images. *Biodiversity Information Science and Standards*, 3; doi:10.3897/biss.3.46690.

Central Statistical Bureau of Latvia (2025) Agriculture of Latvia: Collection of Statistics. Rīga: Central Statistical Bureau of Latvia.

Dardaillon, M. (1988) Wild boar social groupings and their seasonal changes in the Camargue, southern France. *Zeitschrift für Säugetierkunde*, 53, 22–30.

Ditchkoff, S.S. and West, B.C. (2007) Ecology and management of feral hogs. *Human-Wildlife Conflicts*, 1, 149–151.

ENETWILD Consortium (2018) Guidance on estimation of wild boar population abundance and density: methods, challenges, possibilities. *EFSA Supporting Publications*, 15(7), EN-1449; doi:10.2903/sp.efsa.2018.EN-1449.

ENETWILD Consortium (2022) Wild boar density data generated by camera trapping in nineteen European areas. *EFSA Supporting Publications*, 19(3), EN-7214; doi:10.2903/sp.efsa.2022.EN-7214.

ENETWILD Consortium (2024) Generating wildlife density data across Europe in the framework of the European Observatory of Wildlife (EOW). *EFSA Supporting Publications*, 21(10); doi:10.2903/sp.efsa.2024.en-9084.

Enetwild Project / European Observatory of Wildlife (2022) *Camera trapping protocol for wild mammals density estimation.* Enetwild, June.

Fernández-Llario, P., Carranza, J. and Hidalgo de Trucios, S.J. (1996) Social organization of the wild boar (*Sus scrofa*) in Doñana National Park. *Mammalia*, 60(2), 273–278.

Gethöffer, F., Keuling, O., Maistrelli, C., Ludwig, T. and Siebert, U. (2023) Heavy youngsters – habitat and climate factors lead to a significant increase in body weight of wild boar females. *Animals*, 13(5), 898; doi:10.3390/ani13050898.

Keuling, O., Lauterbach, K., Stier, N. and Roth, M. (2010) Hunter feedback of individually marked wild boar (*Sus scrofa* L.): dispersal and efficiency in hunting in northeastern Germany. *European Journal of Wildlife Research*, 56, 159–167.

Keuling, O., Stier, N. and Roth, M. (2008) How does hunting influence activity and spatial usage in wild boar (*Sus scrofa* L.)? *European Journal of Wildlife Research*, 54, 729– 737.

Massei, G., Coats, J., Lambert, M., Pietravalle, S., Gill, R. and Cowan, D. (2017) Camera traps and activity signs to estimate wild boar density and derive abundance indices. *Pest Management Science;* doi:10.1002/ps.4763.

Medījamo dzīvnieku populācijas (2025) *Valsts meža dienests.* Pieejams: https://www.vmd.gov.lv/lv/medijamo-dzivnieku-populacijas (aplūkots 07.10.2025.).

Medījamo dzīvnieku populāciju stāvokļa novērtēšanas un pieļaujamā nomedīšanas apjoma noteikšanas metodika (2018). Rīga, Zemkopības ministrija.

Medību noteikumi (2014) Ministru kabineta noteikumi Nr. 421 "Medību noteikumi". *Latvijas Vēstnesis.*

Melis, C., Szafranska, P.A., Jedrzejewska, B. and Barton, K. (2006) Biogeographical variation in the population density of wild boar (*Sus scrofa*) in western Eurasia. *Journal of Biogeography*, 33, 803–811.

Ministru kabinets (2015) Noteikumi Nr. 59 "Valsts un Eiropas Savienības atbalsta piešķiršanas kārtība investīciju veicināšanai lauksaimniecībā". Pieejams: https://likumi.lv/ta/id/272094 (aplūkots 17.10.2025.).

Mobilā lietotne "Mednis" (2024) Valsts meža dienests. Pieejams: https://www.vmd.gov.lv/lv/mobila-lietotne-mednis (aplūkots 17.10.2025.).

Oļševskis, E., Guberti, V., Seržants, M., Westergaard, J., Gallardo, C., Rodze, I. and Depner, K. (2016) African swine fever virus introduction into the EU in 2014: Experience of Latvia. *Research in Veterinary Science*, 105, 28–30.

Oļševskis, E., Schulz, K., Staubach, C., Seržants, M., Lamberga, K., Pūle, D., Ozoliņš, J., Conraths, F.J. and Sauter-Louis, C. (2020) African swine fever in Latvian wild boar – a step closer to elimination. *Transboundary and Emerging Diseases*, 67(6), 2615–2629; doi:10.1111/tbed.13611.

Ozoliņš, J., Bagrade, G., Blūms, K., Done, G., Ornicāns, A., Pilāte, D., Stepanova, A., Šuba, J. and Žunna, A. (2024) Pārskats par valsts atbalsta programmas "Atbalsts lauksaimniecībā izmantojamam zinātnes pētījumam" izpildi pētījumā "Meža cūku skaita un populācijas blīvuma kontroles metodikas izstrāde un sistēmas ieviešana Latvijā, lai novērstu Āfrikas cūku mēra (ĀCM) izplatību". Salaspils, LVMI "Silava", 42 lpp.

Pārtikas un veterinārais dienests (2025) African swine fever outbreaks in Latvia. Pieejams: https://www.pvd.gov.lv/lv/afrikas-cuku-mera-uzliesmojumi-latvija (aplūkots 08.10.2025.).

Pautienius, A., Grigas, J., Pileviciene, S., Zagrabskaite, R., Buitkuviene, J., Pridotkas, G. and Stankevicius, A. (2018) Prevalence and spatiotemporal distribution of African swine fever in Lithuania, 2014–2017. *Virology Journal*, 15(1), 177; doi:10.1186/s12985-018-1090-8.

Peris, F., Closa-Sebastià, F., Marco, I., Serrano, E. and Casas-Díaz, E. (2019) Baiting improves wild boar population size estimates by camera trapping. *Mammalian Biology*, 98, 28– 35.

Podgórski, T., Fattorini, N., Augustsson, E., Baubet, E., Cagnacci, F., Fiderer, C., Fischer, C., Heurich, M., Ježek, M., Kjellander, P., Klamm, A., Licoppe, A., Morelle, K., Náhlik, A., Nivois, E., Olejarz, A., Said, S., Suter, S., Tari, T., … Focardi, S. (2025). Impact of hunting modality on social contacts in wild boar populations across Europe. *Journal of Applied Ecology,* e70230.; doi:10.1111/1365-2664.70230.

Schley, L. and Roper, T.J. (2003) Diet of wild boar (*Sus scrofa*) in Western Europe, with particular reference to consumption of agricultural crops. *Mammal Review*, 33, 43– 56.

Seward, N.W., VerCauteren, K.C., Witmer, G.W. and Engeman, R.M. (2004) Feral swine impacts on agriculture and the environment. *Sheep & Goat Research Journal*, 19, 34– 40.

Spitz, F. and Janeau, G. (1995) Daily selection of habitat in wild boar (*Sus scrofa*). *Journal of Zoology*, 237, 423–434.

Stahl, K., Sternberg-Lewerin, S., Blome, S., Viltrop, A., Penrith, M.L. and Chenais, E. (2019) Lack of evidence for long-term carriers of African swine fever virus: A systematic review. *Virus Research*, 272, 197725; doi:10.1016/j.virusres.2019.197725.

Tauriņš, E. (1982) *Latvijas zīdītājdzīvnieki.* Rīga: Zvaigzne, 252 lpp.

Valsts zemes dienests (2025) Zemes sadalījums zemes lietošanas veidos 2017–2025. Pieejams: https://data.gov.lv/dati/lv/dataset/zemes-sadalijums-zemes-lietosanas-veidos (aplūkots 17.10.2025.).

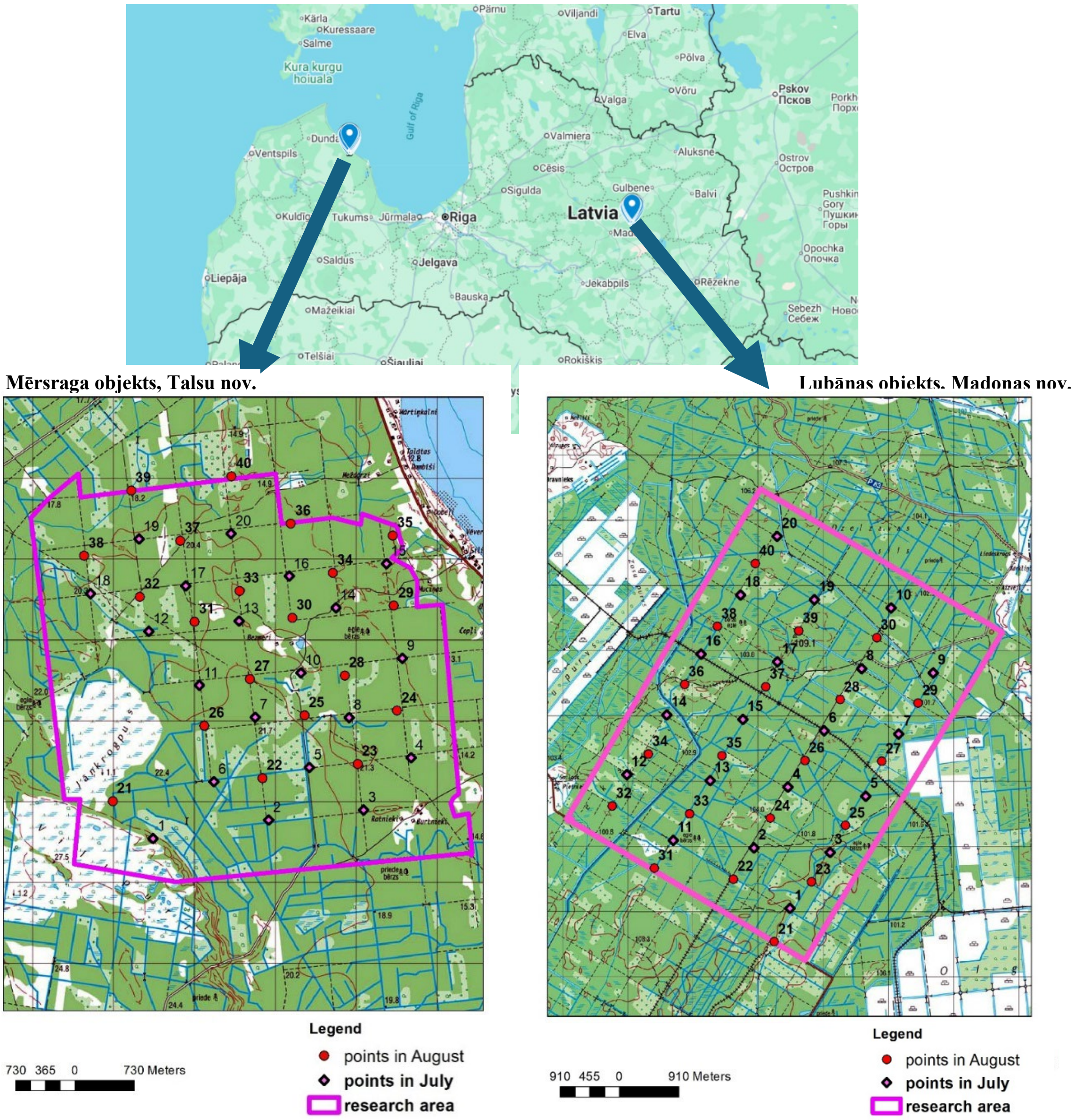
Yokoyama, Y., Nakashima, Y., Yajima, G. and Miyashita, T. (2020) Simultaneous estimation of seasonal population density, habitat preference and catchability of wild boars based on camera data and harvest records. *Royal Society Open Science*, 7(8), 200579; doi:10.1098/rsos.200579.

Zorenko, T. (2008) *Latvijas zīdītāju noteicējs.* Rīga: Gandrs, 95 lpp.

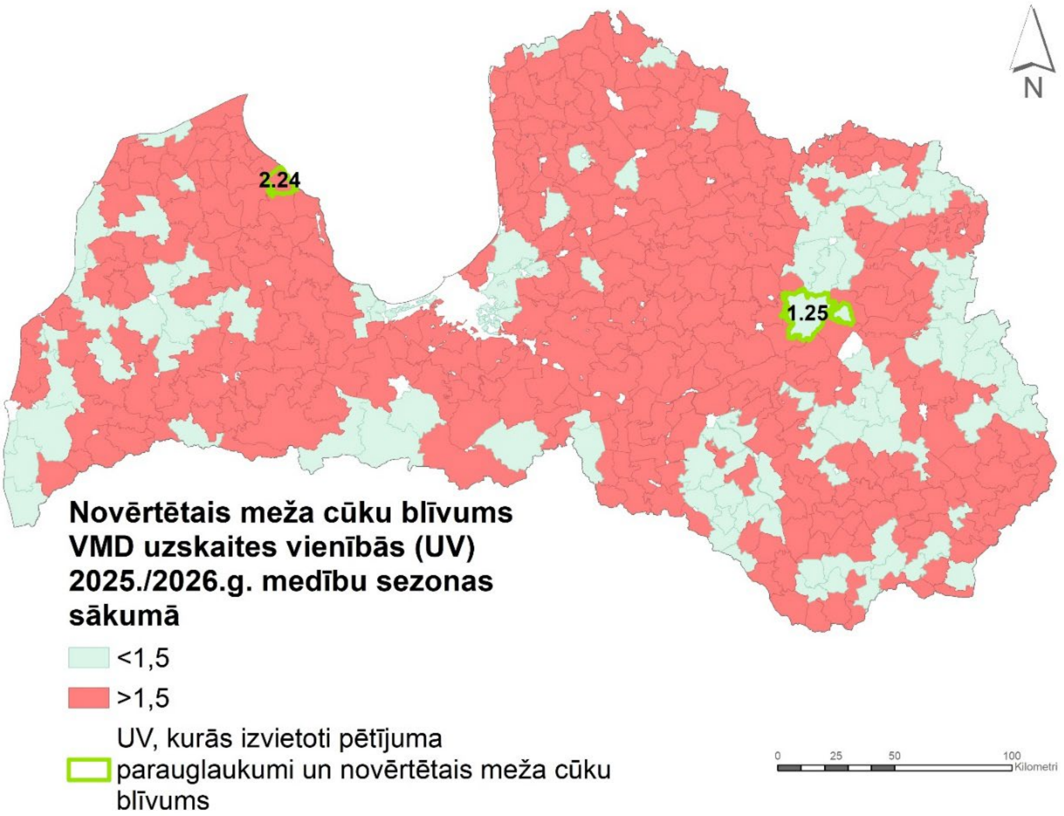
3. Uzskaites atbilstības pārbaude dabā izmēģinājuma teritorijās pēc meža cūku skaita samazināšanas līdz pieļaujamajam populācijas blīvumam

3.1. Metodika

2025. gada vasarā veikta meža cūku un pārējo medījamo dzīvnieku kontroluzskaite divos objektos: A/S “Latvijas valsts meži” Lubānas un Mērsraga meža iecirkņos (11. att.). Monitoringā tika izmantota kameru uzskaites pieeja, kas balstīta uz ENETWILD protokolu. Katra pētījuma teritorija bija apmēram 2500 hektārus liela. Lubānas iecirknī uzskaite notika atkārtoti, un, tāpat kā 2024. gadā, tajā pirms darbu uzsākšanas bija informācija par ļoti zemu populācijas blīvumu. Mērsraga iecirknī populācijas blīvums vērtēts kā vidēji augsts – 2,24 meža cūkas uz 1000 ha (12. att.). Katrā reģionā tika izvēlēti 40 parauglaukumi, kurus noteica sistemātiski. Kameras tika vienmērīgi sadalītas starp šiem punktiem, un vienlaicīgi tika monitorēti 20 parauglaukumi. Pēc četru nedēļu perioda kameras tika pārvietotas par vienu režģa vienību ziemeļu virzienā, lai nosegtu atlikušos 20 punktus un pabeigtu vienu monitoringa ciklu. Divu mēnešu laikā kopumā tika veikti 40 kameru izvietojumi katrā reģionā. Kameras tika uzstādītas meža ceļu un kvartālstigu krustpunktos, lai netraucētu mežsaimniecības darbiem. Koordinātas tika reģistrētas LKS-92 ģeodēziskajā koordinātu sistēmā, izmantojot LVM GEO lietotni, lai apliecinātu atbilstību ENETWILD protokola prasībām. Uzskaite tika pabeigta pirms sezonas dzinējmedību sākuma.



11. attēls. Meža cūku uzskaites teritoriju novietojums un uzstādīto slēpņa kameru tīkls pārbaudāmajos objektos.

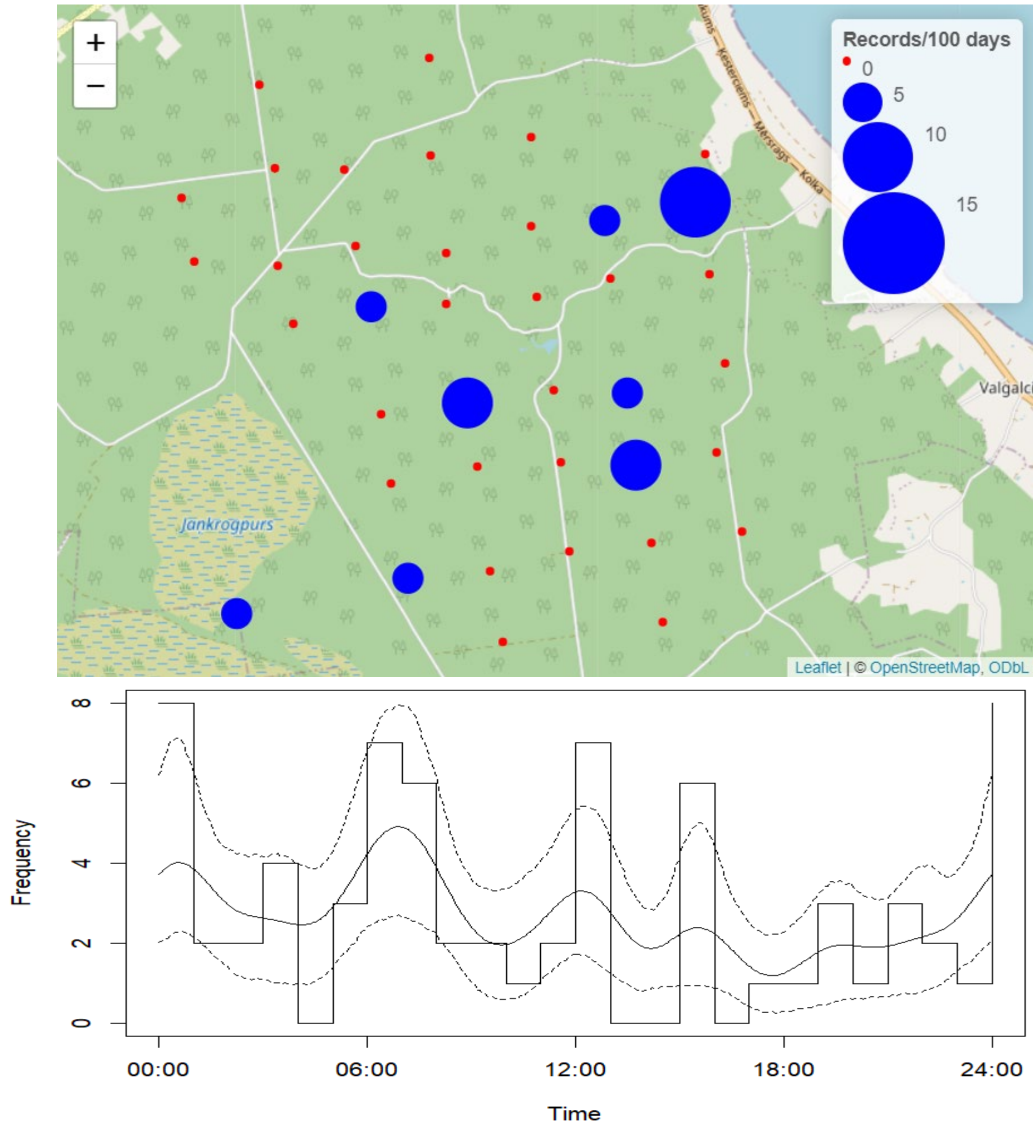


12. attēls. Meža cūku populācijas blīvums 1000 ha platībā Latvijā pēc VMD vērtējuma medījamo dzīvnieku uzskaites vienībās uz 2025. gada 1. aprīli un kontroluzskaitei izvēlēto parauglaukumu izvietojums.

3.2. Rezultāti

Lubānas mežu iecirkņa kontroluzskaitē ar slēpņa kamerām meža cūkas konstatētas nav, lai gan tās novērotas kameru uzstādīšanas laikā 2025. gada 8. jūlijā.

Mērsraga mežu iecirknī kamerās fiksēto meža cūku populācijas blīvums ir 0,61 indivīds uz km² jeb 6,1 meža cūka uz 1000 ha (13. att.), kas ievērojami pārsniedz ĀCM izplatības ierobežošanai pieļaujamo robežu un ir arī lielāks par vidējo blīvumu uzskaites vienībā (12. att.).



	estimate	se	cv	lcl95	ucl95	n	unit
radius	7.4462845	3.71175240	0.4984704	0.17124976	14.72131916	6	m
angle	51.7820459	17.21839243	0.3325166	18.03399674	85.53009506	7	degree
active_speed	1.1332930	0.47048780	0.4151511	0.21113689	2.05544908	7	km/hour
activity_level	0.2582600	0.04869718	0.1885588	0.16281350	0.35370643	39	none
overall_speed	7.0244210	3.20289579	0.4559658	0.74674522	13.30209670	NA	km/day
trap_rate	0.0294991	0.01056046	0.3579927	0.01128977	0.05138211	39	n/day
density	0.6101641	0.47075538	0.7715225	0.15986003	2.32891414	NA	n/km2

13. attēls. R-Studio aprēķinu un stirnu aktivitātes un blīvuma novērtējuma datu izvades grafiki un tabula. Tajā redzams kamerās fiksēto meža cūku novērojumu rādiuss (radius), leņķis (angle), pārvietošanās ātrums km/h (active_speed), aktivitātes biežums (activity_level), dzīvnieka noietā distance km/dienā (overall_speed), kamerās fiksēto dzīvnieku proporcija ind./dienā (trap_rate), kā arī novērtētais dzīvnieku blīvums ind./km2 (density). "Estimate" ir aprēķinātais novērtējums, "se" ir standartnovirze, "cv" ir variācijas koeficients, "lcl95" ir 95% ticamības intervāla leja, "ucl95" – augša, "n" ir novērojumu skaits un "unit" apzīmē mērvienību.

Slēpņa kameru izmantošana meža cūku uzskaitē apliecina šīs metodes atbilstību un uzticamību gan, lai pārbaudītu, vai meža cūku populācija lokāli ir samazināta zem 1,5 indivīdiem uz 1000 ha, gan, lai novērtētu populācijas blīvumu, kas ir augstāks par pieļaujamo robežu.

4. Meža cūku populācijas blīvuma un ĀCM epidemioloģisko datu analīze

4.1. Metodika

Meža cūku skaits, blīvums un saslimstība ar ĀCM

Pētījumā izmantota metodika, kas atbilst "Nacionālajā rīcības plānā attiecībā uz mežacūkām, lai nepieļautu Āfrikas cūku mēra izplatīšanos" noteiktajiem uzdevumiem – sasniegt un uzturēt mežacūku populāciju tādā daudzumā, kas nepārsniedz 0,15 dzīvnieku/km^2 visā Latvijas teritorijā, izstrādāt, cik vien iespējams, precīzu, praktiski izmantojamu un finansiāli īstenojamu uzskaites sistēmu mežacūku skaita noteikšanai un ieviest to medību uzskaites vienībās mežacūku skaita (mērķa blīvuma) kontrolei, attīstīt esošās informācijas sistēmas ĀCM uzraudzības un kontroles nodrošināšanai, kā arī nodrošināt iesaistīto personu un organizāciju apmācību un informēt sabiedrību par ĀCM un slimības izplatības risku. Veikta uzskatāma un viegli uztverama analīze ar datiem, kurus regulāri publisko Valsts meža dienests par meža cūku populācijas dinamiku (novērtētais populācijas lielums un sezonā nomedīto meža cūku skaits) un Pārtikas un veterinārais dienests (Pārtikas drošības, dzīvnieku veselības un vides zinātniskajā institūtā "BIOR" veiktie izmeklējumu rezultāti nomedītajām un atrastajām beigtajām meža cūkām, kuru paraugi ievākti atbilstoši PVD noteiktajām prasībām) (8. tab.). Šo datu ieguvē iesaistīti gan mednieki, gan atbildīgo dienestu darbinieki, tādēļ pētījums sniedz ieskatu tajā informācijā, kuras izcelsmi iespējams pārbaudīt ikvienam un kas veidojusies, vērtējot pieejamos skaitļus kopsakarībās. Populācijas blīvuma aprēķināšanai izmantota LR Valsts zemes dienesta, VMD informācija un oficiālās statistikas pārvaldes datu bāzes (https://stat.gov.lv/lv/statistikas-temas/noz/mezsaimnieciba).

8. tabula

Meža cūku skaita un ĀCM inficēto indivīdu dinamika, kopš slimības konstatēšanas Latvijas teritorijā

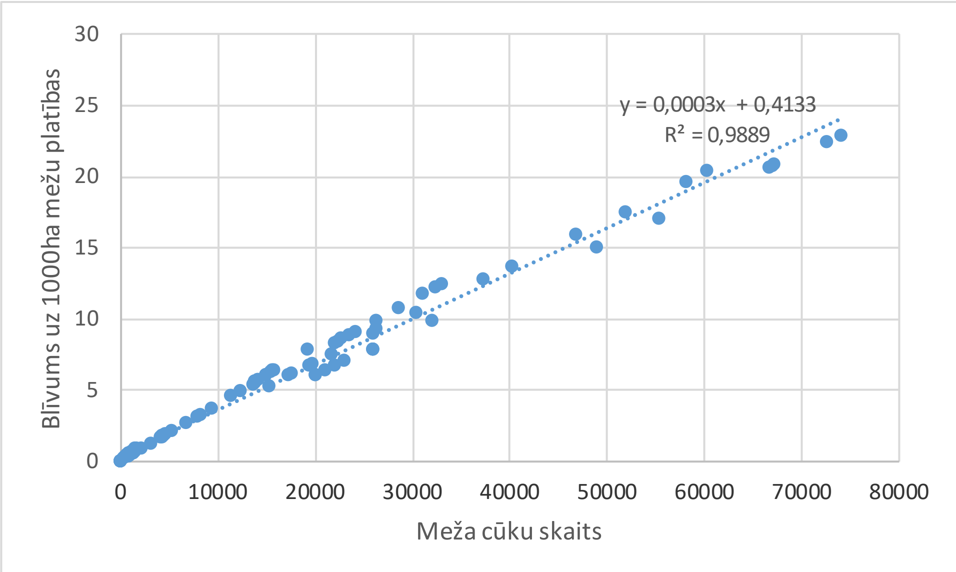
Gads	Kopējā skaita vērtējums valstī	Vidējais blīvums uz 1000 ha meža platību*	Sezonas laikā nomedītās meža cūkas	ĀCM pozitīvo meža cūku skaits
2014.	55354	17,04	44871	217
2015.	49000	15,04	50956	1048
2016.	32000	9,81	34084	1146
2017.	23000	7,02	25549	1431
2018.	20000	6,10	15238	905
2019.	20000	6,09	15279	430
2020.	22000	6,68	19262	377
2021.	26000	7,89	24485	448
2022.	26000	7,88	28006	1274
2023.	26000	7,87	30153	1002
2024.	21000	6,34	22284	1433
2025.	15000	4,52	**	1278

* meža kopplatība no: https://data.stat.gov.lv/pxweb/lv/OSP_PUB/START__NOZ__ME__MEP/MEM030/table/tableViewLayout1/;
** sezona noslēgsies 2026. gada 31. martā;
*** no gada sākuma līdz 2025. gada 15. novembrim

Darbā izmantota Windows 11 Pro Excel programmatūrā pieejamā grafiskā un statistisko funkciju analīze.

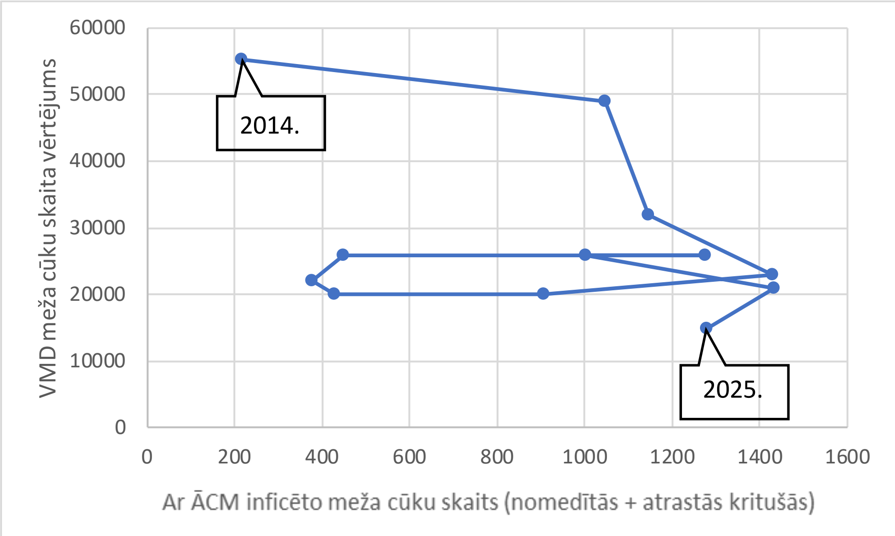
4.2. Rezultāti

Kā jau pētījuma 1. posmā veiktā vēsturisko datu analīze (Ozoliņš et al., 2024) apliecināja, augot meža cūku populācijai, palielinājās arī tās blīvums (14. att.).

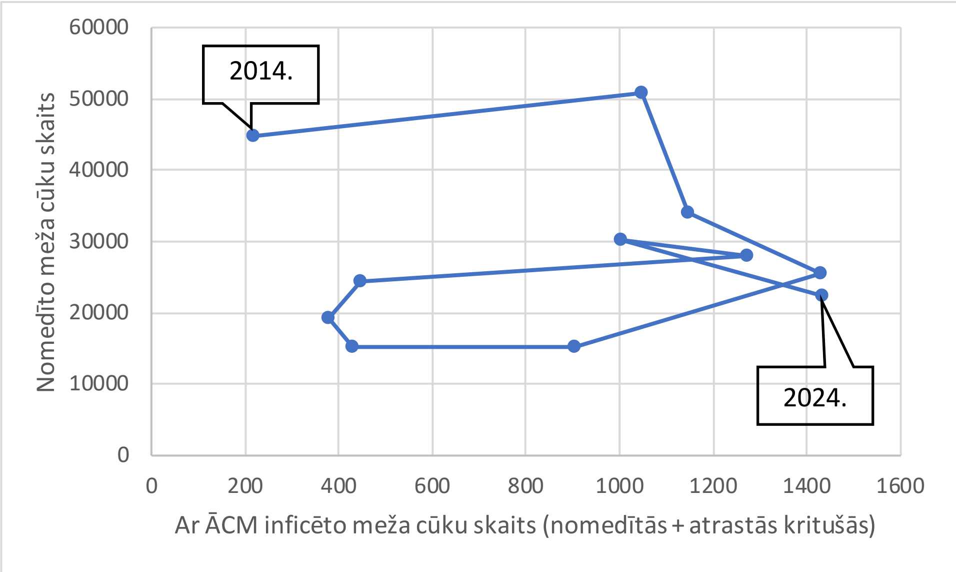


14. attēls. Meža cūku populācijas blīvuma atkarība no kopējā skaita 100 gadu periodā.

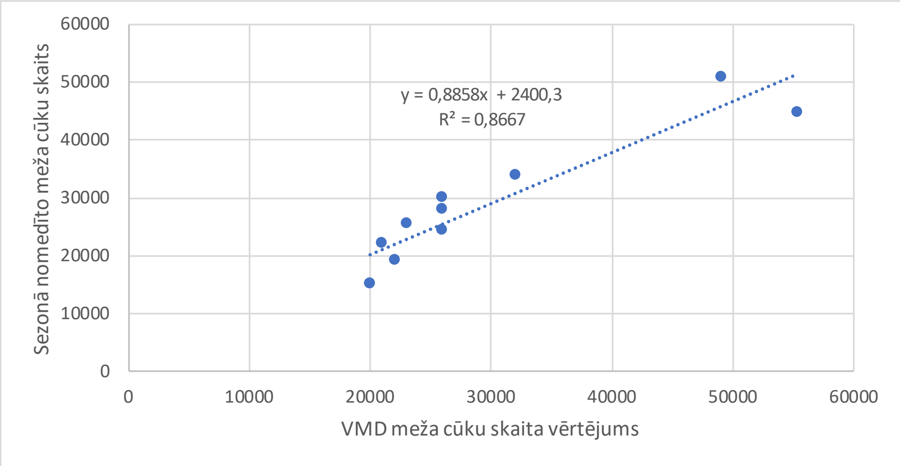
Kaut arī meža cūku populācijas blīvuma un saslimstības ar ĀCM saistības dinamika, izsekojot šim procesam pa gadiem, bijusi mainīga, piedzīvojusi kāpumu un kritumu, šobrīd tā šķiet apstājusies atkārtotā kāpumā, un infekcijas apturēšana ar medību paņēmieniem šķiet visai grūti īstenojama. Salīdzinot meža cūku novērtēto populācijas lielumu un ar ĀCM inficēto indivīdu kopskaitu, lineāra skaitļu sakritība nav konstatēta. Taču, izsekojot abu parametru saistību pa gadiem visā periodā (15. att.), redzams inficēto meža cūku skaita atkārtots pieaugums, kamēr to skaits nav samazinājies zem 20 000. Šāds populācijas lielums savā veidā kļuvis par pēdējās desmitgades atskaites punktu, jo nomedīto meža cūku skaits līdzinās vai pat pārsniedz dabā esošo skaitu, kas liecina, ka populācija spēj ātri atjaunoties. Pagaidām nav datu, kas liecinātu, ka valsts mērogā, saglabājoties šādam dzīvnieku skaitam, notiktu saslimstības samazināšanās, kaut gan populācijas vērtējums 2025. gadā ir nokrities par apmēram ceturtdaļu, salīdzot ar iepriekšējo. Ļoti līdzīgu izmaiņu gaitu uzrāda arī inficēto meža cūku skaita salīdzinājums ar nomedīto dzīvnieku daudzumu (16. att.). Tas arī nepārsteidz, jo starp meža cūku skaita vērtējumu un medību rezultātiem jau agrāk pastāvējusi un joprojām pastāv cieša korelācija (17. att.). Līdz ar to pagaidām nav nozīmes saistībā ar epidemioloģisko situāciju abus šos populācijas dinamikas rādītājus aplūkot atsevišķi. Tāpat nav nozīmes papildus skaita dinamikai analizēt valstī vidējā populācijas blīvuma izmaiņas, jo šī rādītāja izmantošana nesniegs atšķirīgu informāciju tādēļ, ka mežu platības pieaugums kopš 2014. gada bijis niecīgs un skaita un blīvuma izmaiņas notiek vienlaicīgi. Katrā ziņā abi grafiki rāda, ka kopš infekcijas sākuma turpmākos trīs gadus populācijas lielums samazinājies vairāk kā uz pusi, bet inficēto meža cūku skaits strauji pieaudzis. Tad sekojusi saslimstības samazināšanās pie trīs gadus gandrīz nemainīga populācijas lieluma un strauja atgriešanās agrākajā līmenī, kaut arī populācija pieaugusi nedaudz – tikai 20% robežās – kur pretī šajā gadā nokritusies pat līdz 15 000.



15. attēls. ĀCM epidemioloģisko datu un meža cūku populācijas lieluma savstarpējā saistība laika periodā, kopš vīrusa pirmās konstatēšanas Latvijā.

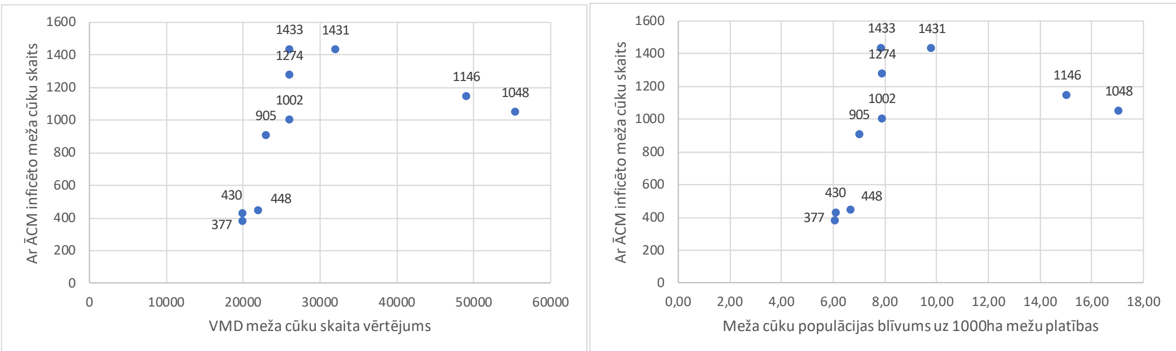


16. attēls. ĀCM epidemioloģisko datu un nomedīto meža cūku skaita savstarpējā saistība laika periodā, kopš vīrusa pirmās konstatēšanas Latvijā.

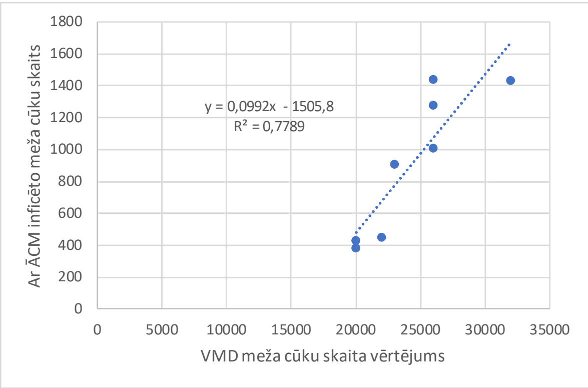


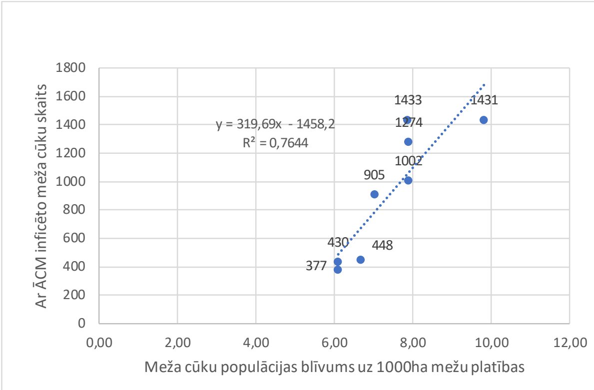
17. attēls. Nomedīto meža cūku skaita korelācija (r = 0,9309) ar meža cūku skaita vērtējumu Latvijā periodā no 2014. līdz 2024. gadam.

Pašreizējais inficēto meža cūku skaita palielinājums ir pārsniedzis to apjomu, kas tika konstatēts 2015. un 2016. gadā, kad slimība pārņēma vienīgi Latvijas austrumu daļu. Taču tagadējā aina skaidri parāda būtisku un ciešu korelāciju starp meža cūku populācijas lielumu, vidējo blīvumu un saslimstību (18., 19. att.). Šī saistība izpaužas apstākļos, kad vīruss valstī kļuvis par endēmisku saslimšanu, kas uz laiku noplok reizē ar meža cūku lokālu izmiršanu, bet tad atkal atgriežas agrākajās vietās, un meža cūku populācijas kopējais lielums vairs būtiski nepieaug, kaut arī uz laiku atjaunojas lokāli.



18. attēls. Gadījumu skaits, kad ĀCM saslimstība konstatēta nomedītām un atrastām kritušām meža cūkām salīdzinājumā ar attiecīgajā gadā VMD veikto meža cūku kopējā skaita un blīvuma vērtējumu Latvijā periodā no 2015. līdz 2024. gadam (attiecīgi r = 0,4230 skaitam un r = 0,4186 blīvumam).





19. attēls. Gadījumu skaits, kad ĀCM saslimstība konstatēta nomedītām un atrastām kritušām meža cūkām salīdzinājumā ar iepriekšējā gadā VMD veikto meža cūku kopējā skaita vērtējumu Latvijā periodā no 2017. līdz 2024. gadam (attiecīgi r = 0,8825 skaitam un r = 0,8743 blīvumam).

5. Manuskriptu sagatavošana publicēšanai SCOPUS līmeņa zinātniskā izdevumā

Sagatavots ziņojums 12. Baltijas Terioloģijas konferencei

"Wanted dead or alive – wild boar Sus scrofa control challenges concerning African swine fever outbreak in Latvia"

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Ozoliņš J., Bagrade G., Blūms K., Done G., Oļševskis E., Ornicāns A., Pilāte D., Seržants M., Stepanova A., Šuba J. 2025. In: Žunna A. (Ed.) Abstracts Book of 12th Baltic Theriological Conference "Baltic mammals in the turbulence of anthropogenic tensions", Jaundome, Latvia, March 27–29, 2025. Salaspils: LSFRI "Silava", p. 29, ISBN 978-9934-603-20-4

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"African swine fever vs. COVID-19: only one virus mattered for wild boar hunting bags in Europe"

Authors: Valentina Barukčić[1]*, Boštjan Pokorny[2], Jacopo Cerri[3], Klaus Hackländer[4], Ferdinand Bego[5], Alain Licoppe[6], Jim Casaer[7], Dalibor Ballian[8,9,10], Stoyan Stoyanov[11], Miloš Ježek[12], Mervi Kunnasranta[13], Elmo Miettinen[14], Eric Baubet[15], Oliver Keuling[16], Konstantinos Papakostas[17], András Náhlik[18], Andrea Monaco[19], Jānis Ozoliņš[20], Olgirda Belova[21], Sandra Cellina[22], Miloš Janković[23], Niels de Nijs[24], Barbara Zimmermann[25], Tomasz Podgórski[3,12], Carlos Fonseca[27], Attila Farkas[28], Nickolay Markov[29], Dragan Gačić[30], Petar Lazár[31], Joana Colomer[32], Göran Bergqvist[33], Claude Fischer[34], Giovanna Massei[35], Nikica Šprem[1].

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Manuskripta kopija pievienota 1. Pielikumā.

Līdzautoru statuss starptautiskas publikācijas 2. manuskriptam

"Trends of ungulate species in Europe: not all stories are equal"

Authors: Jacopo Cerri[1,2]*, Roberta Chirichella[2,3]*, Walter Arnold[5], Luděk Bartoš[6], Tomasz Borowik[2], Juan Carranza[7], Francesco Chianucci[8], Sándor Csányi[9], Göran Ericsson[10], Marco Heurich[11], Ilpo Kojola[12], Atle Mysterud[13], Boštján Pokorny[14], Krzysztof Schmidt[2], Nikica Šprem[15], Joaquín Vicente[16], Ajša Alagić[14], Linas Balčiauskas[17], Jim Casaer[18], Sandra

Cellina[19], Gundega Done[20], Slavomír Find'o[21], Carlos Fonseca[22], Dragan Gačić[23], Dime Melovski[24], Jānis Ozoliņš[20], Haritakis Papaioannou[25], Tiit Randveer[26], Vesa Ruusila[12], Christine Saint-Andrieux[27], Rauno Veeroja[28], Marco Apollonio[2,4].

Manuskripta kopija pievienota 2. Pielikumā.

African swine fever vs. COVID-19: only one virus mattered for wild boar hunting bags in Europe

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Abstract

Wild boar (*Sus scrofa*) populations have been steadily increasing across Europe in the last decades, due to the synergy between landscape modifications, the ecological plasticity of the species and global warming. However, since 2014, an increasing number of these populations have also been affected by African swine fever (ASF) and have experienced increased mortality. Moreover, in 2020 and 2021, wild boar hunting regimes were temporarily changed due to restrictions in response to COVID-19. There is therefore a need for a pan-European assessment of the long-term trend in wild boar populations. We analysed wild boar hunting bags from 21 European countries, as a proxy of population abundance, to estimate long-term trends between 2000 and 2022. We also identified possible changes in harvests due to COVID-19. Finally, we summarized changes in the number of hunters between 2018 and 2023 in 19 European countries. Wild boar harvest has increased steadily over the last two decades, peaking at over 3.6 million harvested individuals in 2019. Since the appearance of ASF in Europe, hunting bags in most affected countries decreased, i.e. either immediately after the first outbreak or following a short-term increase of the harvest after the outbreak. Restrictions due to COVID-19 did not have any clear impact on the total number of harvested wild boar. Over the past six years, in spite of mixed trends between the countries, the overall number of hunters has decreased across Europe.

Keywords: ASF; hunting management; mortality; population trend; SARS-CoV-2; *Sus scrofa*; ungulates

Highlights

Wild boar harvests increased 2.25-folds across Europe for two decades until 2019.

ASF outbreaks caused harvest declines in affected countries.

COVID-19 restrictions did not measurably affect wild boar harvest levels.

The overall number of hunters in Europe is decreasing (≈3.9 million), although some countries show slight increases.

In 2017, legal changes and the adoption of new hunting methods, such as night-vision devices and silencers, marked a key shift in hunting practices.

1. Introduction

Wild boar (*Sus scrofa*) is a highly adaptable species whose numbers have steadily increased throughout Europe in recent decades (Massei et al., 2015; Smith et al., 2025). This growth, along with the species' expansion into new areas, has made wild boar among the most widespread and commonly hunted ungulates in Europe (Jori et al., 2021). Hunting bag data further highlights this fact, showing an increase in the number of wild boar hunted, from almost 2.2 million in 2012 (Massei et al., 2015) to over 3 million in 2017 (Linnell et al., 2020), and almost 4 million in recent years (ENETWILD-consortium et al., 2024).

As wild boar populations have grown, conflicts with humans have also increased. Wild boar has high economic impact through damage to crops and forests, vehicle collisions, nuisance behaviour in urban areas, and disease transmission, with important consequences to public health (Šprem et al., 2013; Podgórski et al., 2018; Conejero et al., 2024). In addition, wild boar can also negatively affect other native species and biodiversity, sometimes leading to declines in the density and abundance of various plant and animal species (Barrios-Garcia and Ballari, 2012; Colomer et al., 2021). At the same time, wild boar are important ecosystem engineers, positively affecting the environment by shaping soil structure, promoting seed dispersal, and influencing nutrient cycling in many habitats (Barrios-Garcia and Ballarí, 2012).

The increase of the wild boar populations can be attributed to a combination of environmental and socio-economic factors, interacting with the biological and ecological plasticity of the species. For example, global warming has benefited wild boar populations in Central and Northern Europe by decreasing winter mortality and increasing food availability of high-energy food such as acorns and other forest seeds due to more frequent masting (Vetter et al., 2015). Landscape changes have also increased environmental suitability for the species. The afforestation and rural abandonment that characterized many marginal rural areas of Europe in the second half of the 20th century (Levers et al., 2018) have additionally increased the availability of food, and the fragmentation of semi-natural forests due to their conversion to arable land created mosaic landscapes that provided wild boar with both refuges and abundant resources (Ferens et al., 2025). Moreover, landscape anthropisation offered considerable and rich anthropogenic food resources (Colomer et al., 2024), without affecting individual fitness due to the ability of wild boar to avoid human disturbance (Johann et al., 2020). Reduced winter mortality and increased resource availability and accessibility alongside with supplementary feeding and baiting allowed wild boar populations to boom, due to a high reproductive rate of the species, which is the highest among wild ungulates (Barrios-Garcia and Ballari, 2012). Landscape anthropisation also promoted hybridization with domestic pigs (*Sus scrofa* f. *domesticus*), which may have further enhanced the reproductive capacity of wild boar (Iacolina et al., 2019).

Wild boar populations are greatly influenced by hunting which is still the main cause of the species' mortality (Bassi et al., 2020). Hunting is also believed to shift reproduction of wild boar to an earlier age (Gamelon et al., 2011), alter physiological state (Kelava-Ugarković et al., 2025), and affect the species' spatial behaviour (Olejarz et al., 2024). In some countries, hunters have been responsible for deliberate releases, which accelerated the spread of wild boar across Europe (Jori et al., 2021), and for extensive supplementary feeding which affects wild boar behaviour (Muthoka et al., 2023) and potentially also its survival rates (Oja et al., 2014).

In recent years, wild boar populations across Europe have been affected by African swine fever (onwards ASF) (Drimaj et al., 2020). In its latest outbreak on the continent, ASF was first detected in the (north)eastern part of the European Union (i.e., Poland and Baltic states) in 2014 and has since spread across several other European countries (Dixon et al., 2020). ASF causes high lethality among suids and in the absence of any treatment or vaccination, the disease represents a major threat to pig production and wild boar populations. Wild boar and its habitats are the sole reservoir of ASF virus (Chenais et al., 2018) and thus it is important to reduce wild boar numbers to help constrain the disease (Drimaj et al., 2020). Hunters play a key role in population control, alongside natural mortality sources such as starvation, disease, and predation (Massei et al., 2015). As hunting management strategies in Europe vary from country to country and are typically implemented at the local level, effectively controlling the spread of ASF in wild boar remains a significant challenge (Linnell et al., 2020; Sauter-Louis et al., 2021a). Various European countries have used a range of measures to combat ASF, including zoning, restricting wild boar movement with fencing, banning hunting in infected areas that are not physically contained, modifying habitat management, and prohibiting access to infected zones (EFSA et al., 2024a). Additionally, efforts to reduce wild boar numbers through intensive hunting and trapping have been introduced (Jori et al., 2021). The use of night vision equipment and silencers during wild boar hunts is also already permitted by law in some countries or under consideration in others (Sauter-Louis et al., 2021a). Despite these management efforts, ASF continues to spread among wild boar populations across Europe (Sauter-Louis et al., 2021a; EFSA et al., 2025). In most cases, the spread of the disease is not due to animal-to-animal transmission, but rather due to human activity (Bergmann et al., 2021); indeed, humans are responsible for all known long-distance transmissions of ASF in Europe.

In March 2020, the World Health Organization (WHO) declared the COVID-19 pandemic prompting countries worldwide to implement various forms of lockdown (Allen, 2022). These restrictions led to "anthropause", a period of reduced human activity which, in many cases, had a positive effect on wildlife (Rutz et al., 2020) with animals showing increased movement shortly after the lockdowns began (Pokorny et al., 2022). However, the pandemic also affected hunting and wildlife management. The number of hunting licenses issued during this period was lower than in previous years, indicating a decline in hunting activity (Cerri et al., 2024). Driven hunts with hounds, which rely heavily on group participation, may have been significantly affected by the restriction on gatherings in pandemic. Consequently, COVID-19 may have further reduced the number of active hunters, resulting in a decline in recreational hunting and a subsequent reduction in the control of wild ungulate populations (Cerri et al., 2024).

Collecting and analysing hunting statistics is essential for effective hunting management and the development of wildlife policies (Jori et al., 2021; Colomer et al., 2024). Data on hunting bags, ideally used in conjunction with the number of hunters or hunting effort, are an excellent tool for monitoring wildlife populations trends and for detecting factors such as disease outbreaks, poaching, and environmental changes that might affect these trends. Hunting bag data are primarily used in ecological research and wildlife management as indicators of population density (Carvalho et al., 2024).

The most recent pan-European study that used hunting bags to analyse wild boar and hunter population trends in 18 European countries from 1982 to 2012 was conducted by Massei et al. (2015). Therefore, our overall objective was to continue this data series and analyse trends in wild boar populations in Europe over the past two decades, a period marked by two major events – ASF outbreaks and COVID-19 lockdowns – that may have affected wild boar population numbers across the continent. Understanding the impact of these events is crucial for the future development of wild boar population management.

The specific aims of this study were: *i*) to present trends of wild boar hunting bag (as a proxy of the abundance) over the last two decades in Europe; *ii*) to explore how ASF outbreaks (i.e., its presence in a country) influenced wild boar hunting bags by comparing trends in ASF-infected and ASF-free countries; *iii*) to quantify potential changes in hunting bags due to COVID-19 associated restrictions and changes in recreational hunting; *iv*) to evaluate changes in the number of European hunters over the past six years.

2. Materials and methods

We collected wild boar hunting bag data from the last two decades in 29 European countries. To maintain the reliability of the manuscript and ensure accurate results, we excluded countries with missing or incomplete data (n = 8) from the analysis, leaving the following 21 countries: Austria, Belgium, Bulgaria, Croatia, Czech Republic, France, Germany, Hungary, Italy, Latvia, Lithuania, Luxembourg, the Netherlands, Poland, Portugal, Romania, Slovakia, Slovenia, Spain, Sweden, and Switzerland (Figure 1). It is important to emphasize that: *i*) in different countries wild boar are hunted with different techniques, *ii*) in some countries, numbers of hunted wild boar are defined through hunting quotas that are decided at the beginning of each hunting season based on population monitoring and a discussion of management objectives, and *iii*) this situation has changed through time. Regarding the hunting method, in countries such as Germany (Keuling et al., 2021) or Sweden (Thurfjell et al., 2013) a significant proportion of wild boar are stalked and culled from hides by individual hunters, whereas in other countries, most wild boar are harvested through driven hunts (e.g. Spain: Fernandez-de-Simon et al., 2023). In some countries, hunting quotas limit the number of wild boar that can be hunted (e.g. Slovakia: Goračova et al., 2025). In other countries, particularly those where drive hunts are common, such as Croatia, Czech Republic, Poland, and Spain there is no real limit to the number of wild boar hunted; moreover, in recent years hunters may even be financially motivated by the state to shoot as many wild boar as possible (e.g. Croatia, Slovenia). It is worth mentioning that, in the two decades, management regimes sometimes considerably changed within the same country.

Additional data on the number of hunters, hunting management of wild boar (Supplementary file 1) and on the COVID-19 lockdown periods and hunting management during these periods (Supplementary file 2), as well as data on the occurrence of ASF and the number of positive cases and hunting bans due to ASF were also provided by all included countries (Supplementary file 3).

As different countries had very different numbers of wild boar (harvest), either due to their size and the different range of the species or different hunting efforts and hunting intensities, we made hunting bag numbers between countries more comparable by calculating the hunting index, expressed as the total numbers of hunted individuals per km^2. Harvest densities (not population densities) represent the total number of wild boar that were hunted in each year, divided by the extension of the species range in 2022 in the respective country (ENETWILD-consortium et al., 2022). Although this value is an approximation, as the range of wild boar has likely expanded since 2000, we used data from 2022 as they were the only one with a pan-European coverage and an adequate resolution. We did not control for hunting effort, as data on overall hunting effort and the total number of hunters are not available for Europe over the study period. We used a Generalized Extreme Value distribution (Bali, 2003) for our response, and we used the year as a covariate. To account for country-specific trajectories, we fitted approximate Gaussian processes to each country (Wood, 2017). Moreover, we allowed the scale parameter of the Generalized Extreme Value distribution to vary between different countries (Bürkner, 2017a). The scale parameter captures the variability in the response; through this approach we managed to account for differences among countries in wild boar management, which could have resulted in higher or lower differences in the total number of wild boar that were harvested in different years. Models were fitted in STAN (Carpenter et al., 2017), through the brms package (Bürkner, 2017b) in R (R Core Team, 2025). Model selection was carried out through Bayesian leave-one-out cross validation (Vehtari et al., 2017) and posterior predictive checks and model residuals were used to assess the goodness of fit of the best candidate model. Continuous variables were standardized and centred before being included in the model.

To assess the variation in the number of wild boar that were hunted due to changes in hunting caused by COVID-19 restrictions, we used the approach proposed by Cerri et al. (2022; 2024). In this approach we: *i*) fitted a Bayesian Generalized Additive Model (GAM) to predict wild boar harvests between 2000 and 2019 in each country, *ii*) used the same model to forecast how many wild boar would have been harvested between 2020 and 2024, under the same temporal trend, and *iii*) compared the actual number of wild boar that were hunted between 2000 and 2024 against predictions for these five years from 2000-2019 data. We used a Bayesian Generalized Additive Model (GAM), because under the Bayesian inference framework values from the posterior distribution, even when included in credibility intervals, are not equally plausible (Kruschke and Liddell, 2018). Therefore, we could compare the number of wild boar that were hunted in 2020-2024 against the most plausible predicted value for each year. However, from the initial 21 countries included in the previous analysis, we had to exclude Latvia and Lithuania because wild boar numbers and harvests in these countries plummeted after 2014 due to ASF. Therefore, we trained our model with data that also reflected a rapid, generalized decrease in these two countries. As a result, we observe that post-COVID-19 predictions for the number of wild boar shot per km² are unrealistic: the 2014-2019 trend continues even for 2020-2023/2024, and in some cases, we even have negative values. Therefore, we removed these predicted values because they were not reliable.

We analysed the percentage change in hunter numbers by country, as well as the overall trend during the past six years, in 19 selected European countries (Austria, Belgium, Bulgaria, Croatia, Czech Republic, France, Germany, Hungary, Italy, Latvia, Luxembourg, Montenegro, Poland, Portugal, Slovakia, Slovenia, Spain, Sweden and Switzerland). Other countries were excluded from this analysis owing to incomplete data on hunter numbers.

3. Results

Our best candidate model showed that the Generalized Extreme Value distribution was a good approximation for wild boar harvest densities (Fig. S1) and explained a significant amount of variation in 2000-2019 data (Bayesian R^2 = 0.95). Model selection (Fig. S2) retained a model where the expected harvest density in each year was explained by a Gaussian process with 9 bases, and where variation in the harvest density differed between countries. Residuals (Fig. S3), the autocorrelation function (Fig. S4) as well as the exploration of country-specific trends showed that Gaussian processes were effective at capturing country-specific variation in wild boar harvests. However, the best candidate model still showed signs of overdispersion, when residuals were plotted against predicted values from the model (Fig. S3).

This probably depended upon the choice of quantifying hunting effort as the number of wild boar hunted, divided by the range of the species in each country, which did not entirely rule out differences among countries, in terms of the magnitude of hunting bags.

The total number of harvested wild boar in Europe has been steadily increasing over the last two decades, and in the period 2000-2022 total hunting bag in the 21 countries, included in our analysis, rose 2.25-folds, i.e. passing from approximately 1,297,500 individuals harvested in 2000 to 2,922,500 in 2022, with a peak of 3,663,500 individuals harvested in 2019. Data for 2023 and 2024 were not included in the analysis, as many countries had not yet published figures for those years. Moreover, for some countries included in the study, data were incomplete across the whole study period, although the number of harvested wild boar appears to be on the rise also there. Montenegro and Bosnia and Herzegovina have only recently begun recording wild boar hunting bag data, although the species has long been present and hunted in these two countries. Serbia publishes its official wild boar harvest data every two years, thus not providing reliable data. Finland and Norway have also only recently started to collect data on wild boar harvests following the species' recent expansion into these two countries. Greece and Russia had incomplete data, and Albania had no data recorded. To maintain consistency, these eight countries were excluded from the total harvest analysis, so only countries with continuous data from the year 2000 onward were included, as incorporating countries with shorter data records would distort the long-term trend (Figure 1). If the data from the eight countries with incomplete records are included, the number of harvested wild boar could potentially increase by approximately 177,000 individuals (see Supplementary file 4).

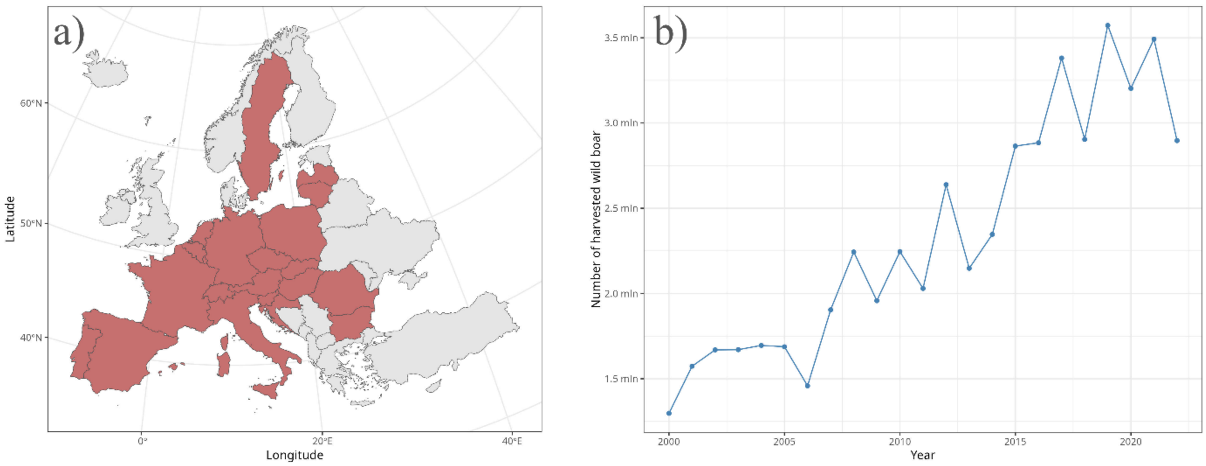

Figure 1. Complete datasets on wild boar hunting bags were available for 21 red-coloured countries (a) and were used to calculate overall hunting bag trends across Europe between 2000 and 2022 (b).

Since the first recent outbreak of ASF in the European Union in 2014, 18 of the 28 countries included in the study (i.e., those for which we collected any relevant data for this study, even when not included in the above analysis of temporal trends) have been affected by the disease (for more details, see Supplementary file 3). Hunting bags are showing different trends across 13 infected countries for which consistent data are available, but with the same ultimate outcome of a decline in the number of harvested animals (Figure 2a). In eight countries where ASF did not occur and for which relevant data are available, wild boar harvest generally continued to rise. The only exception is the Netherlands, where the number of harvested wild boar has declined sharply despite the absence of ASF (Figure 2b).

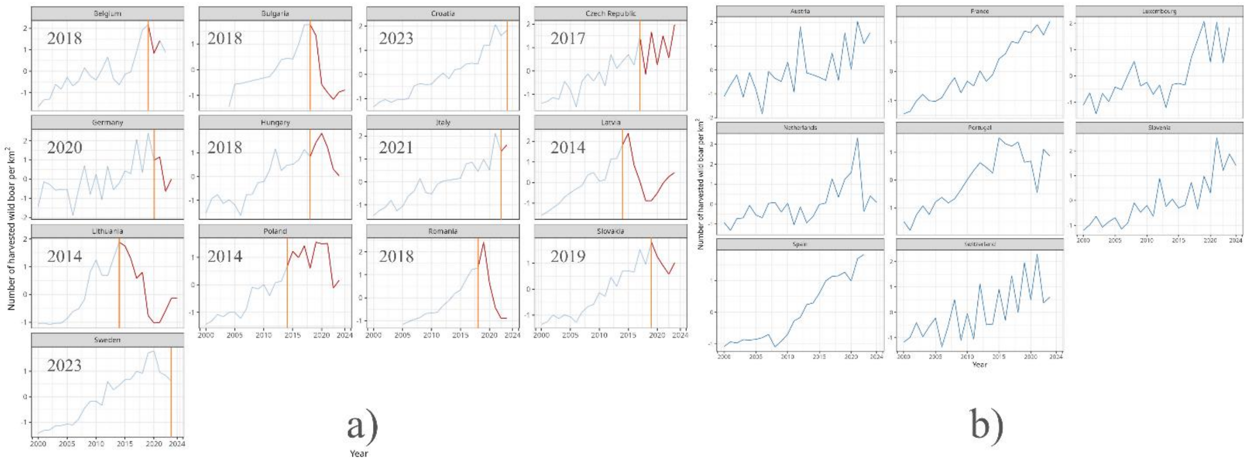

Figure 2. a) Wild boar hunting bags in 13 countries with African swine fever (ASF; years after outbreak in red lines, while vertical orange lines indicate the year in which ASF first appeared in each country; for more details, see Supplementary file 3). b) Wild boar hunting bags in eight countries without ASF. For Belgium and Spain, the dataset ends in 2022 as no official records for the last two years were published.

When assessing the impact of the COVID-19 lockdowns and the anthropause on the hunting activity through the total number of harvested wild boar, no clear pattern emerged, compared to the 2000-2019 period. When comparing the total number of wild boar that were hunted against the most likely values predicted by the posterior distribution of our candidate model, we found that in 2020, 13 out of 19 countries harvested a lower number of wild boar than expected, but 6 countries harvested more wild boar than expected. A similar pattern emerged in 2021 (8 and 11), 2022 (12 and 7) and 2023 (10 and 7), respectively. No clear pattern emerged even when considering values that fell outside of the 95% credibility interval (Figure 3). For 2023, Belgium and Spain are missing as we did not have data on wild boar hunting bags for that period in those two countries.

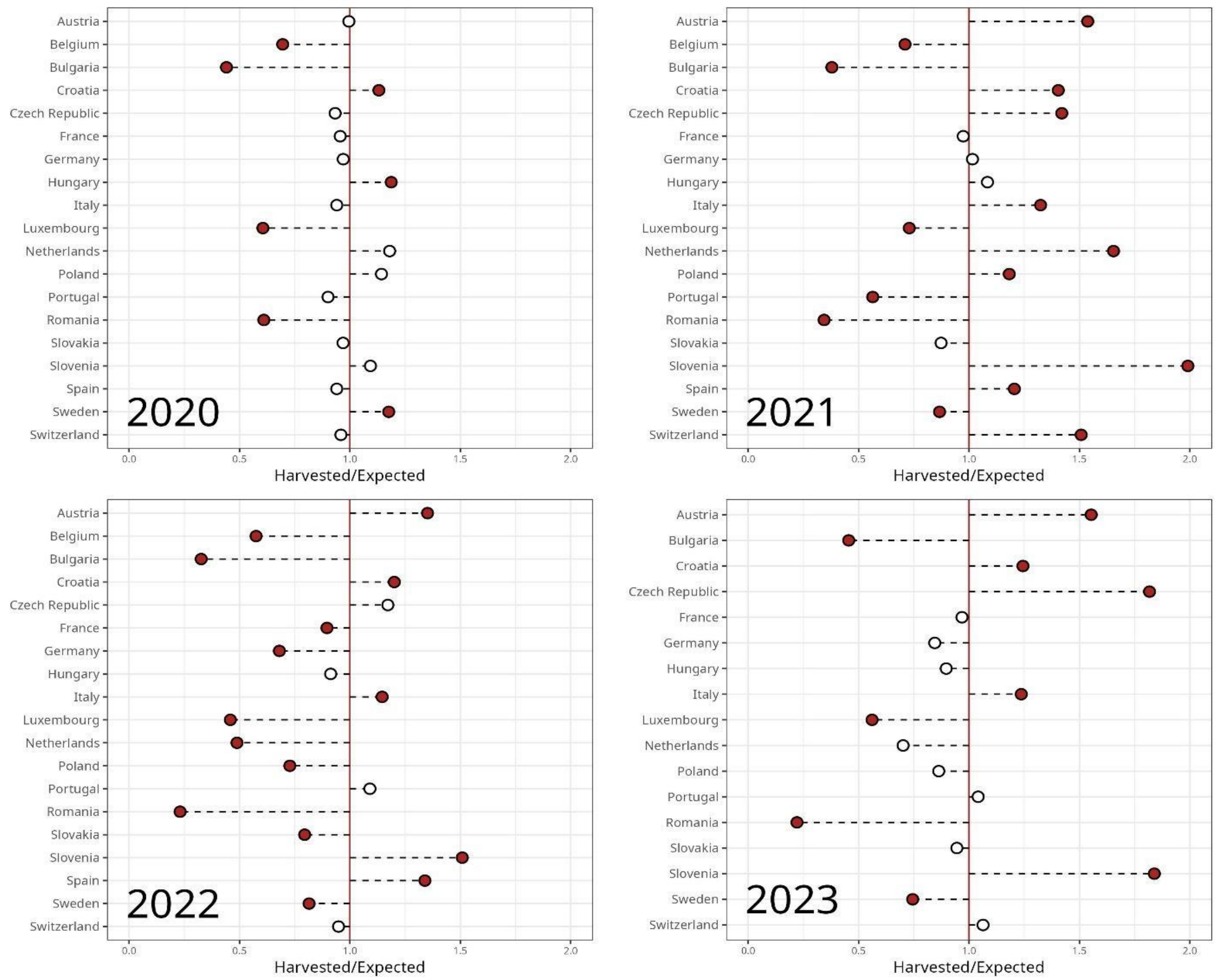

Figure 3. Impact of the COVID-19 restrictions on wild boar hunting bags in selected European countries, i.e. comparison between real and expected numbers of hunted individuals. Dots on the left side of the vertical lines indicate that the number of hunted individuals was lower than expected, while on the right side the number of hunted wild boar was higher than expected. Red dots indicate values that fell outside of the 95% credibility interval, reflecting harvests that deviated from the expected numbers, i.e. in scenario that COVID-19 restrictions did not occur.

The trend in hunter numbers varies among 19 European countries. While some countries have recently experienced an increase in the number of hunters, others have shown a marked decline (Figure 4). Overall, the total number of hunters in Europe demonstrates a substantial decrease over the past six years (Figure 5).

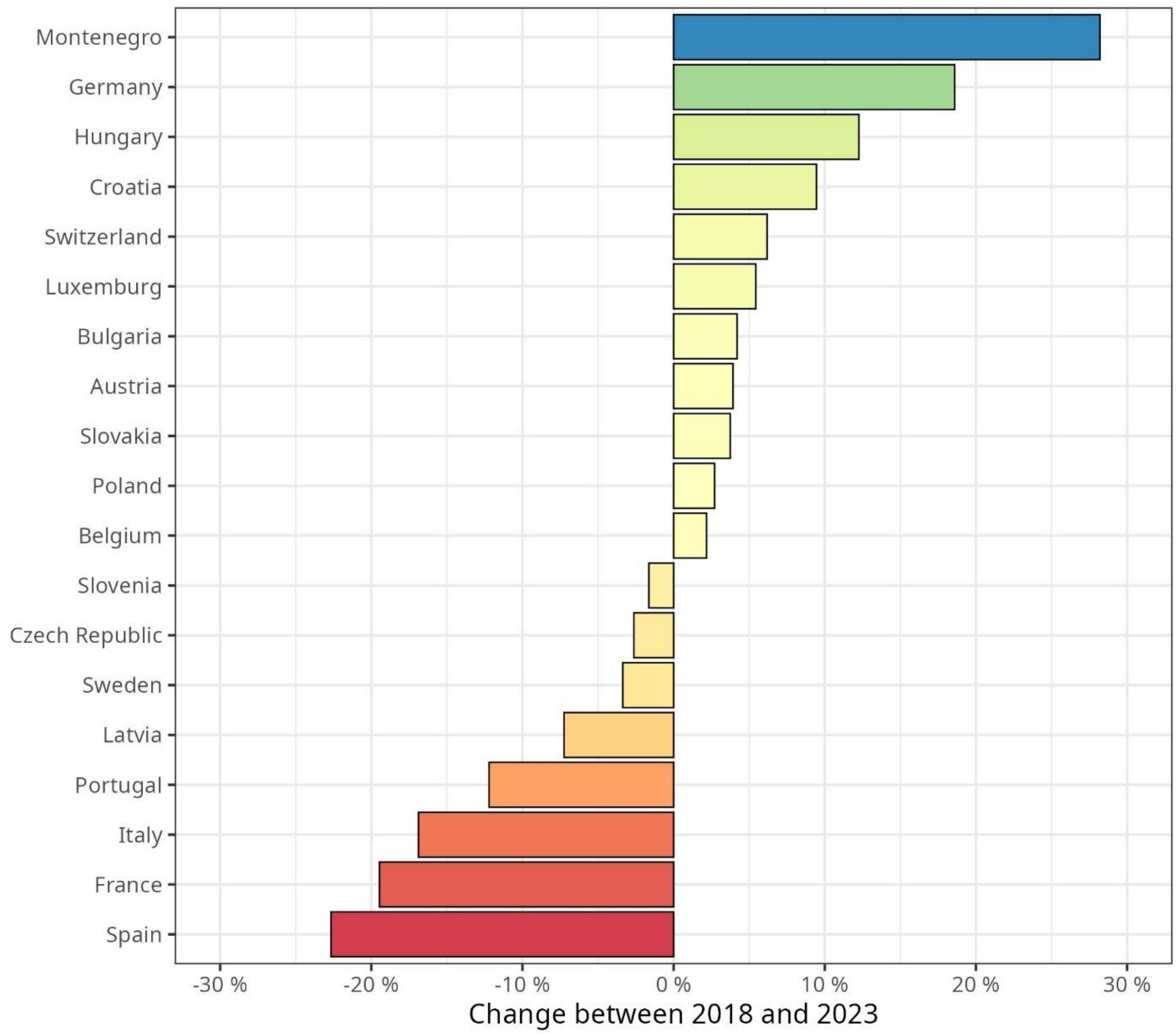

Figure 4. Percentage change between the number of hunters in 19 selected European countries that had the available data for the six-year period.

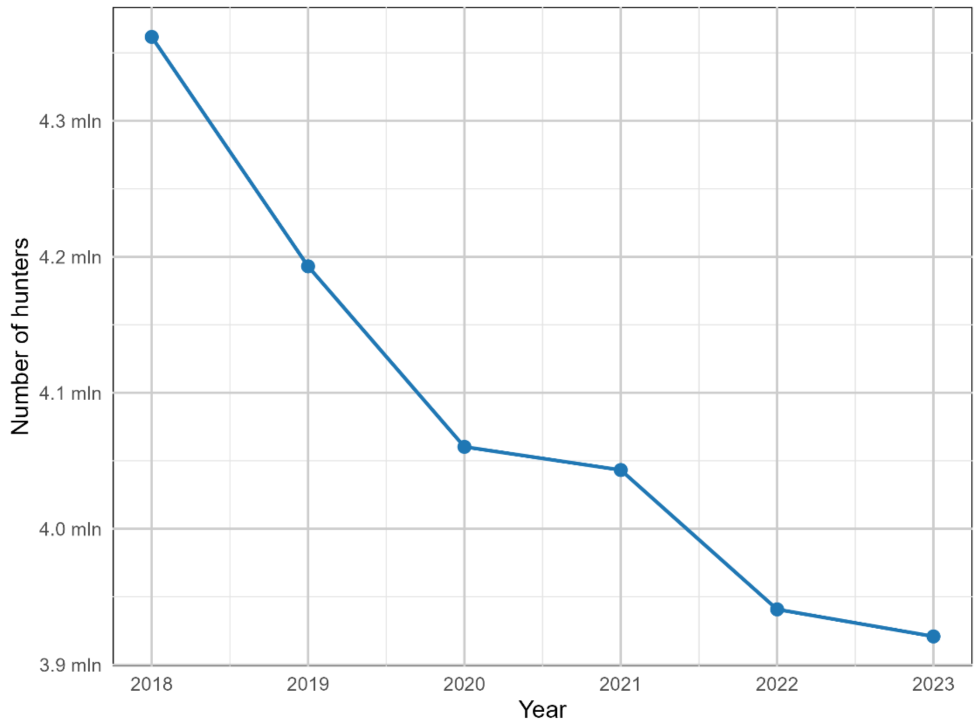

Figure 5. Overall trend in hunter numbers during the six-year period across 19 selected European countries.

4. Discussion

Accurate estimates of population abundance are essential for developing effective wildlife management strategies and for detecting changes in population trends (Soininen et al., 2016). In this respect, it is important to note that hunting data collection is not standardized across European countries, making it difficult to accurately estimate population densities and to precisely compare data among countries (EFSA et al., 2018). Nevertheless, in case of species such as wild boar, for which hunters are generally highly motivated to hunt and report the harvest, hunting data are good (and actually only broadly available) proxy/indicator for abundance as well as trends and interannual variability in population sizes (ENETWILD-consortium et al., 2018). Our analysis of wild boar hunting bag data reveals a significant increase in the number of wild boar harvested across Europe in the last two decades: since 2000, the number of hunted wild boar has increased 2.25-folds (Figure 1), passing from approximately 1.3 million individuals harvested in 2000 to 2.9 million in 2022, with a peak of 3.6 million wild boar harvested in 2019. This upward trend, previously observed by Sáaez-Royuela and Telleriia (1986) up to 1975, by Massei et al. (2015) up to 2012, and later by Linnell et al. (2020) up to 2017, has clearly continued in recent years, with a peak in 2019 after which the number of harvested wild boar in Europe began to slightly decrease, at least on a short term (i.e., last three year) basis. The rise in the number of wild boar harvested reflects the ongoing general increase of the abundance of the species in Europe, which is in accordance with increasing reports on the occurrence of urban individuals, crop damage and traffic collisions with wild boar (Conejero et al., 2024). Moreover, several factors can lead to underestimate the true number of wild boar mortality even in the countries with hunting data across the whole study period, for example illegal hunting and unreported roadkill (Massei et al., 2015; Bíl et al., 2025). The harvest/mortality of these animals is not documented, therefore the recorded hunting bags often reflect a lower count than the actual mortality rate, deviating by more than 30% in some countries (Massei et al., 2015). In some cases, hunting bag records typically rely on self-reported statistics, and their accuracy may be compromised by either over-reporting or under-reporting, further distorting population assessments (Massei et al., 2015; Soininen et al., 2016). In addition, hunting statistics sometimes do not include animals which are killed during wildlife control operations by non-hunters, such as police officers, whose numbers can be significant in some countries (Banti et al., 2021).

Understanding the impact of ASF on wild boar populations is crucial for designing evidence-based population management to combat ASF (Morelle et al., 2020), and to forecast future population trends. A recent model of ASF epidemics showed a decrease of the wild boar populations after an ASF outbreak (Salazar et al., 2022), which is consistent with our findings showing evident decline in wild boar hunting bags across most countries affected by ASF (Figure 2). Given that the hunting bag data reflect population trends and interannual variability of local wild boar numbers, our results indeed suggest that wild boar numbers declined in several European countries due to mortality caused by ASF.

When analysing how the outbreak of ASF in 2014 affected the hunting bags (as a proxy of the abundance) of wild boar, we found a difference in hunting bags after the ASF appearance in Latvia, Lithuania, and to a lesser extent in Poland. In Poland, unlike in Latvia and Lithuania, the hunting bags continued to rise until 2021 before declining. In both Latvia and Lithuania, after a sever drop immediately after the ASF outbreak, the hunting bag started to rise again in 2020, which may indicate either a recovery of the population or increased hunting pressure to stop the disease spreading (Figure 2). However, the European Food Safety Authority (EFSA) suggests that the growing hunting bags in the Baltic states reflect a genuine population recovery (EFSA et al., 2024b). Since 2014, ASF has continued to spread and in the following years (until 2022) it appeared in Belgium, Bulgaria, Czech Republic, Germany, Hungary, Italy, Romania, Serbia, and Slovakia (EFSA et al., 2020; Sauter-Louis et al., 2021b). In Belgium, the ASF epidemic lasted only one year and affected only 5-10% of the wild boar range. In this country, high hunting bag in 2018 and 2019 is linked to increased pressure imposed at the regional level to stop spreading of ASF as well as to the important mast production in 2018. Belgium effectively controlled ASF, reporting 833 cases in wild boar in 2018 (Sauter-Louis et al., 2021a), but the disease had no lasting impact on Belgian hunting bags, thanks to swift containment measures and small proportion of the country which had been affected. EFSA reported that the Bulgarian wild boar population followed a stabilising trend, but there was a decline in the abundance after the ASF outbreak (EFSA et al., 2025), which is consistent with our data (Figure 2). In countries where hunting bag trends did not decline immediately after the ASF outbreak, this could be due to the low percentage of the country affected by ASF. Further research should account for the percentage of country territory affected by ASF, i.e. with restriction zones, as a proxy of ASF spatial coverage. In 2023 and 2024, the first ASF outbreaks were recorded in several previously unaffected countries, such as Croatia and Sweden. The number of positive cases in these countries remains low, and hunting bags have not yet shown significant changes. ASF has only recently appeared in Sweden, and it has regained ASF-free status (EFSA et al., 2025), but the number of wild boar hunted had already decreased before the appearance of ASF. The effect of ASF on hunting bag should be closely monitored as previous work has shown that the density and abundance of wild boar decreased by 84% and 95%, respectively, within a year of the ASF outbreak (Morelle et al., 2020).

ASF poses a significant challenge for wildlife disease control (Jori et al., 2021). This is reflected in the fact that the number of reported ASF outbreaks in wild boar increased by 10 in 2023 in Europe compared to the previous year and remained at this level in the following year (EFSA et al., 2024b; 2025). In the inner zones of ASF occurrence, driven hunts were banned to contain the spread of the disease. In contrast, in the outer areas, targeted hunting for depopulation was promoted and intensified to reduce population density of wild boar (Sauter-Louis et al., 2021a). Many countries have also adopted sanitary culling and promoted the intensive harvesting of wild boar females whilst also revising regulations on wild boar hunting methods (see Supplementary file 3). Some studies argue that the decline in the wild boar population has been observed in the affected countries (Schulz et al., 2019; 2020), and the declines of the hunting bags confirmed by our results are a good indicator of this. However, from analysing solely the hunting bag data it is difficult to conclude whether the disease has affected the European wild boar populations due to its high mortality rate or whether the declines in hunting bags are rather due to the implemented hunting bans (Sauter-Louis et al., 2021a). Further research focusing on the impact of ASF on the demographic structure of wild boar populations could provide valuable insights into the resilience and long-term viability of populations as well as developing wild boar management strategies to combat ASF (Gočárová et al., 2025).

Due to the complexity of managing wild boar populations and the inability of hunters to achieve sufficient removal rates to control population growth, many countries have modified hunting regulations. These changes include the legalization of night hunting and the use of night vision or thermal imaging devices, with the year 2017 seemingly marking the starting point for making these changes legal (Supplementary file 1). Also, many countries have allowed the use of silencers, which has certainly contributed to better hunting success and a larger hunting bag. For example, a government decision in Sweden in 2019 to permit the use of movable lights and thermal imaging led to a significant increase in wild boar harvest and probably a decrease in population size. The observed up-following reduction in harvest is believed to result from this population decline. In addition, changes in supplementary feeding and baiting have been reported. In many countries where supplementary feeding used to be practiced, it has been banned in recent years. Following the spread of ASF, restrictions on the amount of feed used for baiting have been established and vary from country to country (Supplementary file 1). Moreover, monetary incentives for culling wild boar increased the hunting effort, with bounties again varying from country to country (Supplementary file 1). All these changes have influenced hunting effectiveness and may have affected hunting bag data, changing the association between hunting bags and population abundance throughout the study period.

In 2020, during the COVID-19 pandemic, the associated "anthropause" was widely reported to have positive impacts on wildlife due to reduced human activity and disturbance (Allen, 2022). Despite many studies emphasizing the potential transformation of existing wildlife management models due to COVID-19, little empirical research has been conducted on this topic (Cerri et al., 2024). Two studies examined the impact of COVID-19 lockdowns on the wild turkey (*Meleagris gallopavo*) hunting season in North America. One study observed an increase in hunting participation and effort in 2020 compared to previous years, resulting in a higher total reported harvest (Danks et al., 2022). The other study found no difference in harvest success compared to previous years despite an increase in the number of resident hunters (Chizinski et al., 2022). Our findings indicate that potential changes in wild boar hunting that could have followed COVID-19 restrictions did not significantly affect wild boar harvest (Figure 3). Indeed, analysis of the hunting bag data shows no major change in wild boar harvests during the COVID-19 lockdown period. This may be explained by the timing of lockdowns, which predominantly occurred in spring, a season that typically falls outside the main (driven) hunt period for wild boar, which in most European countries takes place in late autumn and winter. Furthermore, driven hunts on wild boar were not prohibited in most countries during the COVID-19 lockdowns and high alert periods, but were rather regulated with some restrictions, i.e. with the prescribed minimum distance and the maximum number of participants in the driven hunt varying from country to country (see Supplementary file 2). Due to the restrictions introduced during COVID-19 pandemic, many hunters may have shifted to single hunts, resulting in no significant changes in wild boar yields.

Controlling of the growing populations of wildlife can be achieved through recreational hunting (Šprem et al., 2024), and hunting is currently one of the widely employed tools for controlling overpopulated wildlife species, including wild boar (Gortázar and Fernandez-de-Simon, 2022). However, a significant shift from rural to urban lifestyles has contributed to a decline in the number of hunters across many European countries (Massei et al., 2015; Gaspar et al., 2025). One of the main challenges that the hunting communities are facing is the aging of the hunter population. Reports from the Iberian Peninsula and Denmark indicate that the hunting population is aging rapidly, with most hunters in the Iberian Peninsula falling between 61 and 70 years of age (Hansen et al., 2012; Gaspar et al., 2025). This older group of hunters is not being replaced by enough newcomers, leading to a demographic imbalance within the hunting community (Gaspar et al., 2025). It is also difficult to determine how many hunters specifically hunt wild boar, making it challenging to assess whether trends in wild boar hunters mirror those of the general hunting population (Massei et al., 2015).

Our findings indicate a heterogeneous situation about hunting in recent decades. In countries such as Czech Republic, France, Italy, Latvia, Portugal, Slovenia, Spain, and Sweden, hunter numbers are decreasing. On the other hand, several other European countries have seen growth in their hunting populations (Figure 4). Spain, for example, maintained a stable hunting population of around one million hunters for a decade until 2011, making it the largest in Europe at that time (Gaspar et al., 2025). However, this number has since declined dramatically, dropping by nearly half by 2022. Gaspar et al. (2025) reported that the Iberian Peninsula has experienced a 45% decline in its hunting population over the past 50 years. In contrast, Croatia has seen a recent increase in the number of hunters, possibly due to changes in education system (online lectures) and reduced licensing fees (80 euros), which have made hunting more accessible to younger generation. A similar trend was recorded in Bulgaria, where the cost of hunting permit was reduced to a symbolic 0.5 euros (see Supplementary file 1). Overall, the number of hunters during six-year period across 19 selected European countries has declined since 2018 (Figure 5), falling from 4.3 million to 3.9 million in 2023, although trends vary by country. Massei et al. (2015) reported the total number of hunters in 16 European countries to be around 7 million in 2011. This considerable difference in the number of hunters in these two studies could be a result of the fact that data on hunter numbers in Russia (over 3 million) were included in the study by Massei et al. (2015), but not in our one. However, the number of hunting license holders does not always reflect actual hunting activity (Gočárová et al., 2025), neither it reflects the effectiveness of (different) hunting practices. Given that wild boar harvest in Europe continue to rise while overall hunter numbers decline, it is likely that hunters in some countries have intensified their efforts to become more efficient in wild boar hunting (Massei et al., 2015; Gortázar and Fernandez-de-Simon, 2022), or this may also be a consequence of the implementation of more efficient hunting methods such as night vision devices (see above).

As the hunting population is aging rapidly, maintaining the high hunting effort to efficiently manage the wild boar population might become a problem in the future. Additionally, the implementation of measures to prevent the spread of ASF may also be hampered by the reduced number of hunters, e.g. when searching for carcasses, which is one of the most important measures to prevent the spread of ASF. This could potentially be solved by the establishment of professional hunters. Some countries, such as Austria and Belgium, have already established professional hunting units to help manage problematic wildlife populations (see Supplementary file 1).

5. Conclusions

Despite the continued spread of ASF across Europe, the overall wild boar population in the continent continues to grow until 2019. In several countries, however, the number of harvested animals has decreased following ASF outbreaks. This decline may be attributed either to the high mortality associated with the disease or to hunting bans and restrictions implemented as part of disease control measures. Other factors that may have reduced the number of animals harvested are the climate with occasional poor mast years and the spread of large predators such as wolves. In countries where ASF has only recently emerged, it is still too early to determine the long-term effects on wild boar harvests and population dynamics, which needs to be monitored in the future. As ASF continues its gradual expansion throughout Europe, many countries are adopting a range of control measures aimed at containing the disease and preventing its spread to unaffected regions. Our data suggest that COVID-19 had no impact on wild boar harvests. Given that (recreational) hunting remains the primary method for wild boar population control, it is essential to ensure a stable and active population of hunters or to implement additional options (i.e., activation of professional hunters, implementation of capturing/trapping) as well as to potentially explore alternative methods such as fertility control that might complement culling. Importantly, in countries experiencing a decline in hunter numbers, systemic changes to the registration and training processes for new hunters should be considered. Additionally, establishing and supporting professional hunting units could be an effective strategy for managing overabundant or problematic wildlife species, thereby enhancing disease control efforts and contributing to sustainable wildlife management.

CRediT authorship contribution statement

Valentina Barukčić: Writing – original draft, Data curation, Visualization; **Boštjan Pokorny:** Conceptualization, Writing – review & editing, Data curation; **Jacopo Cerri:** Writing – original draft, Formal analysis, Visualization; **Klaus Hackländer:** Investigation, Data curation; **Ferdinand Bego:** Writing – review & editing**,** Investigation, Data curation; **Alain Licoppe:** Writing – review & editing, Investigation, Data curation; **Jim Casaer:** Writing – review & editing**,** Investigation, Data curation; **Dalibor Ballian:** Investigation, Data curation; **Stoyan Stoyanov:** Investigation, Data curation; **Miloš Ježek:** Investigation, Data curation; **Mervi Kunnasranta:** Writing – review & editing**,** Investigation, Data curation; **Elmo Miettinen:** Writing – review & editing**,** Investigation, Data curation; **Eric Baubet:** Investigation, Data curation; **Oliver Keuling:** Writing – review & editing, Investigation, Data curation; **Konstantinos Papakostas:** Investigation, Data curation; **András Náhlik:** Writing – review & editing, Investigation, Data curation; **Andrea Monaco:** Investigation, Data curation; **Jānis Ozoliņš:** Writing –

review & editing, Investigation, Data curation; **Olgirda Belova:** Investigation, Data curation; **Sandra Cellina:** Investigation, Data curation; **Miloš Janković:** Investigation, Data curation; **Niels de Nijs:** Writing – review & editing, Investigation, Data curation; **Barbara Zimmermann:** Investigation, Data curation; **Tomasz Podgórski:** Writing – review & editing, Investigation, Data curation; **Carlos Fonseca:** Investigation, Data curation; **Attila Farkas:** Writing – review & editing, Investigation, Data curation; **Nickolay Markov:** Investigation, Data curation; **Dragan Gačić:** Investigation, Data curation; **Petar Lazár:** Investigation, Data curation; **Joana Colomer:** Writing – review & editing, Investigation, Data curation; **Göran Bergqvist:** Investigation, Data curation; **Claude Fischer:** Investigation, Data curation; **Giovanna Massei:** Writing – review & editing, Investigation, Data curation; **Nikica Šprem:** Conceptualization, Writing – review & editing, Supervision.

Declaration of generative AI use

During the preparation of this manuscript, the author(s) did not use AI tools.

Conflict of Interest Declaration

The authors declare no conflict of interest.

Data availability statement

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

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Supporting information

Supporting information may be found in the online version of this article.

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References

Allen, D.W., 2022. Covid-19 lockdown cost/benefits: A critical assessment of the literature. Int. J. Econ. Bus. 29, 1-32. https://doi.org/10.1080/13571516.2021.1976051

Bali, T.G., 2003. The generalized extreme value distribution. Econ. Lett. 79, 423-427. https://doi.org/10.1016/S0165-1765(03)00035-1

Banti, P., Mazzarone, V., Mattioli, L., Ferretti, M., Lenuzza, A., Lopresti, R., Zaccaroni, M., Taddei, M., 2021. A step change in wild boar management in Tuscany region, Central Italy. In Managing wildlife in a changing world. IntechOpen. https://doi.org/10.5772/intechopen.100012

Barrios-Garcia, M.N., Ballari, S.A., 2012. Impact of wild boar (*Sus scrofa*) in its introduced and native range: a review. Biol. Invasions. 14, 2283-2300. https://doi.org/10.1007/s10530-012-0229-6

Bassi, E., Gazzola, A., Bongi, P., Scandura, M., Apollonio, M., 2020. Relative impact of human harvest and wolf predation on two ungulate species in Central Italy. Ecol. Res. 35, 662-674. https://doi.org/10.1111/1440-1703.12130

Bergmann, H., Schulz, K., Conraths, F.J., Sauter-Louis, C., 2021. A review of environmental risk factors for African swine fever in European wild boar. Anim. 11, 2692. https://doi.org/10.3390/ani11092692

Bíl, M., Balčiauskas, L., Bílová, M., Cellina, S., Favilli, F., Gačić, D., Guinard, E., Heurich, M., Ivanova, N., Junghardt, J., Keuling, O., Kruuse, M., Kukalaj, Q., Langbein, J., Laube, P., Licoppe, A., Masaryk, P., Maślanko, W., Mayer, M., Moroney, A., Moţ, R., Mrđenović, D., Náhlik, A., Nebunu Nezval, V., Niemi, M., Pokorny, B., Psaralexi, M., Ralevic, S., Ricci, S., Rolandsen, Ch.M., Rosell, C., Santos, S.M., Seiler, A., Steiner, W., Swinnen, K.R.R., Šprem, N., Trajçe, A., Trpeski, V., van der Grift, E.A., Vogiatzakis, I. Zihmanis, I., 2025. Wildlife-vehicle collision liability in Europe: A review of existing approaches and their implications. J. Environ. Manag. 380, 124986. https://doi.org/10.1016/j.jenvman.2025.124986

Bürkner, P.C., (2017b). brms: An R package for Bayesian multilevel models using Stan. J. Stat. Softw. 80, 1-28. https://doi.org/10.18637/jss.v080.i01

Bürkner, P.C., 2017a. Advanced Bayesian multilevel modeling with the R package brms. arXiv preprint arXiv:1705.11123. https://doi.org/10.48550/arXiv.1705.11123

Carpenter, B., Gelman, A., Hoffman, M.D., Lee, D., Goodrich, B., Betancourt, M., Brubaker, M., Guo, J., Li.P., Riddell, A., 2017. Stan: A probabilistic programming language. J. Stat. Softw. 76, 1-32. https://doi.org/10.18637/jss.v076.i01

Carvalho, J., Hipólito, D., Teixeira, D., Fonseca, C., Torres, R.T., 2024. Hunting bag statistics of wild mammals in Portugal (1989–2022): on the need to improve data report and compilation. Eur. J. Wildl. Res. 70, 96. https://doi.org/10.1007/s10344-024-01850-y

Cerri, J., Mori, E., Ancillotto, L., Russo, D., Bertolino, S., 2022. COVID-19, media coverage of bats and related Web searches: a turning point for bat conservation? Mammal. Rev. 52, 16-25. https://doi.org/10.1111/mam.12261

Cerri, J., Musto, C., Ferretti, M., Delogu, M., Bertolino, S., Martinoli, A., Bisi, F., Preatoni, D., Tattoni, C. Apollonio, M., 2024. COVID-19 could accelerate the decline in recreational hunting: A natural experiment from Northern Italy. PLoS One 19, e0309017. https://doi.org/10.1371/journal.pone.0309017

Chenais, E., Ståhl, K., Guberti, V., Depner, K., 2018. Identification of wild boar–habitat epidemiologic cycle in African swine fever epizootic. Emerg. Infect. Dis. 24, 810–812. https://doi.org/10.3201/eid2404.172127

Chizinski, C.J., Gruntorad, M.P., Lusk, J.J., Meduna, L.R., Inselman, W.M., Fontaine, J.J., 2022. The influence of the COVID-19 pandemic on spring turkey hunting. J. Wildl. Manag. 86, e22202. https://doi.org/10.1002/jwmg.22202

Colomer, J., Massei, G., Roos, D., Rosell, C., Rodríguez-Teijeiro, J.D., 2024. What drives wild boar density and population growth in Mediterranean environments? Sci. Total. Environ. 931, 172739. https://doi.org/10.1016/j.scitotenv.2024.172739

Colomer, J., Rosell, C., Rodriguez-Teijeiro, J.D., Massei, G., 2021. ‘Reserve effect’: An opportunity to mitigate human-wild boar conflicts. Sci. Total. Environ. 795, 148721. https://doi.org/10.1016/j.scitotenv.2021.148721

Conejero, C., González-Crespo, C., Fatjó, J., Castillo-Contreras, R., Serrano, E., Lavín, S., Mentaberre, G., López-Olvera, J.R., 2024. Between conflict and reciprocal habituation: Human-wild boar coexistence in urban areas. Sci. Total. Environ. 936, 173258. https://doi.org/10.1016/j.scitotenv.2024.173258

Danks, Z.D., Schiavone, M.V., Butler, A.B., Fricke, K., Davis, A., Cobb, D.T., 2022. Effects of the COVID-19 pandemic on 2020 spring turkey hunting across the United States. Wildl. Soc. Bull. 46, e1294. https://doi.org/10.1002/wsb.1294

Dixon, L.K., Stahl, K., Jori, F., Vial, L., Pfeiffer, D.U., 2020. African swine fever epidemiology and control. Annu. Rev. Anim. Biosci. 8, 221-246. https://doi.org/10.1146/annurev-animal-021419-083741

Drimaj, J., Kamler, J., Hošek, M., Plhal, R., Mikulka, O., Zeman, J., Drápela, K., 2020. Reproductive potential of free-living wild boar in Central Europe. Eur. J. Wildl. Res. 66, 1-11. https://doi.org/10.1007/s10344-020-01416-8

ENETWILD-consortium, Guerrasio, T., Carniato, D., Acevedo, P., Apollonio, M., Arakelyan, M., Arnon, A., Beatham, S., Belova, O., Berde, L., Berdión, O., Blanco-Aguiar, J.A., Bleier, N., Burgui Oltra, J.M., Carvalho, J., Casaer, J., Dijkhuis, L., Duniš, L., Ertuk, A., Dal Mas, M., Ferroglio, E., Forti, A., Gačić, D., Gavashelishvili, A., Hillstöm, L., Janječić, M., Ježek, M., Keuling, O., Licoppe, A., Liefting, Y., Martinez-Carrasco Olano, I., Palencia, P., Plis, K., Podgorski, T., Pokorny, B., Rowcliffe, M., Santos, J., Smith, G.C., Sola de la Torre, J., Stoyanov, S., Zanet, S., Vicente, J., Scandura, M., 2024. Generating wildlife density data across Europe in the framework of the European Observatory of Wildlife (EOW). EFSA Supporting Publications 21, 9084E. https://doi.org/10.2903/sp.efsa.2024.EN-9084

ENETWILD-consortium, Illanas, S., Croft, S., Smith, G.C., López-Padilla, S., Vicente, J., Blanco-Aguiar, J.A., Scandura, M., Apollonio, M., Ferroglio, E., Zanet, S., Vada, R., Keuling, O., Plis, K., Podgorski, T., Brivio, F., Fernández-López, J., Ruiz-Rodríguez, C., Soriguer, R.C., Acevedo, P., 2022. New models for wild ungulates occurrence and hunting yield abundance at European scale. EFSA Supporting Publications 19, 7631E. https://doi.org/10.2903/sp.efsa.2022.EN-7631

ENETWILD-consortium, Keuling, O., Sange, M., Acevedo, P., Podgorski, T., Smith, G., Scandura, M., Apollonio, M., Ferroglio, E., Vicente, J., 2018. Guidance on estimation of wild boar population abundance and density: methods, challenges, possibilities. EFSA Supporting Publications 15, 1449E. https://doi.org/10.2903/sp.efsa.2018.EN-1449

European Food Safety Authority (EFSA), Boklund, A., Cay, B., Depner, K., Földi, Z., Guberti, V., Masiulis, M., Miteva, A., More, S., Olsevskis, E., Šatrán, P., Spiridon, M., Stahl, K., Thulke, H.H., Viltrop, A., Wozniakowski, G., Broglia, A., Abrahantes, J.C., Dhollander, S., Gogin, A., Verdonck, F., Amato, L., Papanikolaou, A., Gortázar, C., 2018. Epidemiological analyses of African swine fever in the European Union (November 2017 until November 2018). EFSA J. 16, e05494. https://doi.org/10.2903/j.efsa.2018.5494

European Food Safety Authority (EFSA), Boklund, A., Bøtner, A., Chesnoiu, V.T., Depner, K., Desmecht, D., Guberti, V., Helyes, G., Korytarova, D., Linden, A., Miteva, A., More, S., Olsevskis, E., Ostojic, S., Roberts, H., Spiridon, M., Ståhl, K., Thulke, H.H., Vilija, G., Viltrop, A., Wallo, R., Wozniakowski, G., Abrahantes, C.J., Dhollander, S., Gogin, A., Ivanciu, C., Papanikolaou, A., Villeta, L.C.G., Gortázar, C., 2020. Epidemiological analyses of African swine fever in the European Union (November 2018 to October 2019). EFSA J. 18, e05996. https://doi.org/10.2903/j.efsa.2020.5996

European Food Safety Authority (EFSA), Boklund, A.E., Ståhl, K., Miranda Chueca, M.Á., Podgórski, T., Vergne, T., 2024a. Risk and protective factors for ASF in domestic pigs and wild boar in the EU, and mitigation measures for managing the disease in wild boar. EFSA J. 22, e9095. https://doi.org/10.2903/j.efsa.2024.9095

European Food Safety Authority (EFSA), Ståhl, K., Boklund, A.E., Podgórski, T., Vergne, T., Abrahantes, J.C., Cattaneo, E., Papanikolaou, A., Mur, L., 2024b. Epidemiological analysis of African swine fever in the European Union during 2023. EFSA J. 22, e8809. https://doi.org/10.2903/j.efsa.2024.8809

European Food Safety Authority (EFSA), Ståhl, K., Boklund, A.E., Podgórski, T., Vergne, T., Aminalragia-Giamini, R., Abrahantes, J.C., Papaleo, S., Mur, L., 2025. Epidemiological analysis of African swine fever in the European Union during 2024. EFSA J. 23, e9436. https://doi.org/10.2903/j.efsa.2025.9436

Ferens, M., Załuski, D., Borkowski, J., 2025. Landscape features affecting wild boar use of agricultural fields: Implications for wild boar management. J. Environ. Manag. 389, 126157. https://doi.org/10.1016/j.jenvman.2025.126157

Fernandez-de-Simon, J., Ferreres, J., Gortázar, C., 2023. The number of hunters and wild boar group size drive wild boar control efficacy in driven hunts. Eur. J. Wildl. Res. 69, 35. https://doi.org/10.1007/s10344-023-01661-7

Gamelon, M., Besnard, A., Gaillard, J.M., Servanty, S., Baubet, E., Brandt, S., Gimenez, O., 2011. High hunting pressure selects for earlier birth date: wild boar as a case study. Evolution 65, 3100-3112. https://doi.org/10.1111/j.1558-5646.2011.01366.x

Gaspar, M., Acevedo, P., Arrondo, E., García-Martínez, I., Herrero, J., Pascual-Rico, R., Sánchez-Zapata, J.A., Anadón, J.D., 2025. The demographic collapse of hunting in the Iberian Peninsula. People Nat. 7, 765-776. https://doi.org/10.1002/pan3.10770

Gočárová, M., Moravčíková, N., Molnár, L., Fik, M., Kasarda, R., 2025. The impact of biometeorological, demographic, and ecological factors on the population density of wild boar in Slovakia. Sustainability 17, 4516. https://doi.org/10.3390/su17104516

Gortázar, C., Fernandez-de-Simon, J., 2022. One tool in the box: the role of hunters in mitigating the damages associated to abundant wildlife. Eur. J. Wildl. Res. 68, 28. https://doi.org/10.1007/s10344-022-01578-7

Hansen, H.P., Peterson, M.N., Jensen, C., 2012. Demographic transition among hunters: a temporal analysis of hunter recruitment dedication and motives in Denmark. Wildl. Res. 39, 446-451. https://doi.org/10.1071/WR12028

Iacolina, L., Corlatti, L., Buzan, E., Safner, T., Šprem, N., 2019. Hybridisation in European ungulates: an overview of the current status, causes, and consequences. Mammal. Rev. 49, 45-59. https://doi.org/10.1111/mam.12140

Johann, F., Handschuh, M., Linderoth, P., Dormann, C.F., Arnold, J., 2020. Adaptation of wild boar (*Sus scrofa*) activity in a human-dominated landscape. BMC Ecol. 20, 4. https://doi.org/10.1186/s12898-019-0271-7

Jori, F., Massei, G., Licoppe, A., Ruiz-Fons, F., Linden, A., Václavek, P., Chenais, E., Rosell, C., 2021. Management of wild boar populations in the European Union before and during the ASF crisis. In Understanding and combatting African swine fever: A European perspective. Wageningen Academic Publishers, pp. 263-271. https://doi.org/10.3920/978-90-8686-910-7_8

Kelava Ugarković, N., Fabijanić, N., Barić Rafaj, R., Konjačić, M., Šprem, N., 2025. Fear of hunt in wild boar; stress response and meat quality. Eur. J. Wildl. Res. (in press) DOI: 10.1007/s10344-025-02032-0

Keuling, O., Strauß, E., Siebert, U., 2021. How do hunters hunt wild boar? Survey on wild boar hunting methods in the Federal State of Lower Saxony. Animals 11, 2658. https://doi.org/10.3390/ani11092658

Kruschke, J.K., Liddell, T.M., 2018. The Bayesian New Statistics: Hypothesis testing, estimation, meta-analysis, and power analysis from a Bayesian perspective. Psychon. Bull. Rev. 25, 178-206. https://doi.org/10.3758/s13423-016-1221-4

Levers, C., Schneider, M., Prishchepov, A.V., Estel, S., Kuemmerle, T., 2018. Spatial variation in determinants of agricultural land abandonment in Europe. Sci. Total. Environ. 644, 95-111. https://doi.org/10.1016/j.scitotenv.2018.06.326

Linnell, J.D., Cretois, B., Nilsen, E.B., Rolandsen, C.M., Solberg, E.J., Veiberg, V., Kaczenksy, P., Van Moortew, B., Panzacchi, M., Rauset, G.R., Kaltenborn, B., 2020. The challenges and opportunities of coexisting with wild ungulates in the human-dominated landscapes of Europe's Anthropocene. Biol. Conserv. 244, 108500. https://doi.org/10.1016/j.biocon.2020.108500

Massei, G., Kindberg, J., Licoppe, A., Gačić, D., Šprem, N., Kamler, J., Baubet, E., Hohman, U., Monaco, A., Ozolinš, J., Cellina, S., Podgórski, T., Fonseca, C., Markov, N., Pokorny, B., Rosell, C., Náhlik, A., 2015. Wild boar populations up, numbers of hunters down? A review of trends and implications for Europe. Pest. Manag. Sci. 71, 492-500. https://doi.org/10.1002/ps.3965

Muthoka, C.M., Andren, H., Nyaga, J., Augustsson, E., Kjellander, P., 2023. Effect of supplemental feeding on habitat and crop selection by wild boar in Sweden. Ethol. Ecol. Evol. 35, 106-124. https://doi.org/10.1080/03949370.2021.2024265

Oja, R., Kaasik, A., Valdmann, H., 2014. Winter severity or supplementary feeding—which matters more for wild boar? Acta. Theriol. 59, 553-559. https://doi.org/10.1007/s13364-014-0190-0

Olejarz, A., Augustsson, E., Kjellander, P., Ježek, M., Podgórski, T., 2024. Experience shapes wild boar spatial response to drive hunts. Sci. Rep. 14, 19930. https://doi.org/10.1038/s41598-024-71098-8

Podgórski, T., Apollonio, M., Keuling, O., 2018. Contact rates in wild boar populations: implications for disease transmission. J. Wildl. Manage. 82, 1210-1218. https://doi.org/10.1002/jwmg.21480

Pokorny, B., Cerri, J., Bužan, E., 2022. Wildlife roadkill and COVID-19: A biologically significant, but heterogeneous, reduction. J. Appl. Ecol. 59, 1291-1301. https://doi.org/10.1111/1365-2664.14140

Rutz, C., Loretto, M.C., Bates, A.E., Davidson, S.C., Duarte, C.M., Jetz, W., Johnson, M., Kato, A., Kays, R., Mueller, T., Primack, R.B., Ropert-Coudert, Y., Tucker, M.A., Wikelski, M., Cagnacci, F., 2020. COVID-19 lockdown allows researchers to quantify the effects of human activity on wildlife. Nat. Ecol. Evol. 4, 1156-1159. https://doi.org/10.1038/s41559-020-1237-z

Sáaez-Royuela, C., Telleriia, J.L., 1986. The increased population of the wild boar (*Sus scrofa* L.) in Europe. Mamm. Rev. 16, 97-101. https://doi.org/10.1111/j.1365-2907.1986.tb00027.x

Salazar, L.G., Rose, N., Hayes, B., Hammami, P., Baubet, E., Desvaux, S., Andraud, M., 2022. Effects of habitat fragmentation and hunting activities on African swine fever dynamics among wild boar populations. Prev. Vet. Med. 208, 105750. https://doi.org/10.1016/j.prevetmed.2022.105750

Sauter-Louis, C., Conraths, F.J., Probst, C., Blohm, U., Schulz, K., Sehl, J., Fischer, M., Hendrik Forth, J., Zani, L., Depner, K., Mettenleiter, T.C., Beer, M., Blome, S., 2021a. African swine fever in wild boar in Europe—A review. Viruses 13, 1717. https://doi.org/10.3390/v13091717

Sauter-Louis, C., Forth, J.H., Probst, C., Staubach, C., Hlinak, A., Rudovsky, A., Blome, S., 2021b. Joining the club: First detection of African swine fever in wild boar in Germany. Transbound. Emerg. Dis. 68, 1744-1752. https://doi.org/10.1111/tbed.13890

Schulz, K., Olsevskis, E., Staubach, C., Lamberga, K., Serzants, M., Cvetkova, S., Conraths, F.J., Sauter-Louis, C., 2019. Epidemiological evaluation of Latvian control measures for African swine fever in wild boar on the basis of surveillance data. Sci. Rep. 9, 4189. https://doi.org/10.1038/s41598-019-40962-3

Schulz, K., Staubach, C., Blome, S., Nurmoja, I., Viltrop, A., Conraths, F.J., Kristian, M., Sauter-Louis, C., 2020. How to demonstrate freedom from African swine fever in wild boars—Estonia as an example. Vaccines 8, 336. https://doi.org/10.3390/vaccines8020336

Smith, C.G., Vicente, J., Croft, S., Warren, D., Blanco-Aguiar, J.A., Acevedo, P., Guerrasio, T., Scandura, M., Apollonio, M., Carvalho, J., Torres, R.T., Pinto, N., Ares-Pereira, G., Fonesca, C., Keuling, O., Šprem, N., Gavashelis, A., Kerdikoshvili, N., Shakun, V., De Waele, V., Licoppe, A., Plhal, R., Bicho, C., Gutiérrez, I., Santos, J., Buzan, E., Pokorny, B., Gačić, D., Ertürk, A., Soyumert, A., Stoyanov, S., Gruychev, G., Illanas, S., Fernandez-Lopez, J., Csányi, S., Plis, K., Podgórski, T., Zanet, S., Ferroglio, E., 2025. Mapping wild boar density across Europe: combining spatial models and density estimates. Preprint https://doi.org/10.21203/rs.3.rs-7526029/v1

Soininen, E.M., Fuglei, E., Pedersen, Å.Ø., 2016. Complementary use of density estimates and hunting statistics: different sides of the same story? Eur. J. Wildl. Res. 62, 151-160. https://doi.org/10.1007/s10344-016-0987-z

Šprem, N., Barukčić, V., Jazbec, A., Ugarković, D., Ilić, I., Pokorny, B., 2024. Factors affecting hunting efficiency in the case of golden jackal. Eur. J. Wildl. Res. 70, 19. https://doi.org/10.1007/s10344-024-01770-x

Šprem, N., Duduković, D., Keros, T., Konjević, D., 2013. Wildlife- vehicle collisions in Croatia – A hazard for humans and animals. Coll. Antropol. 37, 531-535. https://hrcak.srce.hr/104610

Thurfjell, H., Spong, G., Ericsson, G., 2013. Effects of hunting on wild boar *Sus scrofa* behaviour. Wildl. Biol. 19, 87-93. https://doi.org/10.2981/12-027

Vehtari, A., Gelman, A., Gabry, J., 2017. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. Stat. Comput. 27, 1413-1432. https://doi.org/10.1007/s11222-016-9696-4

Vetter, S.G., Ruf, T., Bieber, C., Arnold, W., 2015. What is a mild winter? Regional differences in within-species responses to climate change. PLoS One 10, e0132178. https://doi.org/10.1371/journal.pone.0132178

Wood, S.N., 2017. Generalized additive models: an introduction with R. Boca Raton: Chapman and Hall/CRC. https://doi.org/10.1201/9781315370279

Title: Trends of ungulate species in Europe: not all stories are equal

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Abstract

Wild ungulates have deep impacts on socio-ecological systems, and analyzing large-scale population trends in a multispecies set can identify their environmental and socio-economic drivers. We collected annual hunting bags (n = 11,046, period 1975-2018) of 7 wild ungulates of high management interest across 25 European countries. We identified different temporal trends in hunting bags and for roe deer, red deer, wild boar, fallow deer, and mouflon, we also evaluated the social and environmental drivers of their abundances.

Number of harvested red deer, fallow deer, and wild boar increased steadily across Europe, with minor differences among countries, despite variations in land use and climate. On the contrary, roe deer harvest has decreased in six European countries since the late 1990s, probably due to reduced ecotone areas and locally also due to predation, intraspecific competition, and/or climate severity. Northern chamois harvests in Austria and Switzerland have decreased markedly, probably due to increasing temperatures, which decrease the survival of kids at high altitudes. Wild boar harvests have decreased in Poland, Estonia, Latvia, and Lithuania since the African Swine Fever outbreak in 2013-2014. Minor differences emerged between countries adopting different management regimes for wild ungulates.

While many studies pointed out landscape changes as the cornerstone for the increase in wild ungulates across Europe, our research emphasizes important species-specific differences. There is a need to predict how landscape and climate change and the growing presence of large carnivores, will affect populations of species already showing signs of decline, like European roe deer and northern chamois.

Keywords: wild ungulates; hunting bags; time-series analysis; wildlife management; reforestation; rural abandonment.

Introduction

The cumulative impact of human activities had driven most large mammals into severe declines and regional extinctions by the end of the Holocene (i.e., in late 19th and early 20th centuries; Ripple et al. 2015). As for wild ungulates living in the Global North, particularly in Europe, a prolonged decrease started in the 18th century and lasted until the end of the II World War (Linnell and Zachos 2010; Putman et al. 2011; Beguin et al. 2016; Carpio et al. 2021). Some Central European countries like Austria experienced a different trend in the XIX century but the shared the marked decrease from the beginning of the XX century till the end of the War (Schwenk 1985). Since then, wild ungulates have increased their geographical range and numbers, being nowadays generally abundant and widespread (Apollonio et al. 2010).

The members of the Cervidae family, such as red deer (*Cervus elaphus*) and European roe deer (*Capreolus capreolus*), as well as wild boar (*Sus scrofa*) are increasingly ubiquitous and abundant in most European countries, accounting for over 90% of total wild ungulate biomass (Milner et al. 2006; Apollonio et al. 2010). These species can have strong ecological impacts (Fuller and Gill 2001; Carpio et al. 2021), as they can damage soil properties (Harada et al. 2020) and remove plant biomass (Marchiori et al. 2012) or curtail forest regeneration (Côté et al. 2004; Pépin et al. 2006), thus affecting also animal communities (Barasona et al. 2021; Dawson et al. 2024; Mori et al. 2020; Oja 2017; Palmer et al. 2015; Rae et al. 2014) and ecological successions (Perea et al. 2014; Suzuki 2024). Moreover, wild ungulates transmit diseases to other wildlife, domestic ungulates and humans (Gortazar et al. 2007), sometimes with major economic impacts, like in the case of the African swine fever (hereinafter ASF; Bergmann et al. 2021). However, (native) wild ungulates are also very important compositional part and key species of terrestrial ecosystems, where they have several important ecological roles/functions which are essential for existence and functionality of those ecosystems (Chiriboga et al. 2019; Pokorny and Jelenko 2014; Pokorny et al. 2017; Smit and

Putman 2011), but they also have several important values for humans (Csanyi et al. 2014; Pascual-Rico et al. 2021).

In the respect of global changes that may influence population dynamics of wild ungulates, the current situation in Europe stemmed from the synergy between three large-scale processes of human land-use that started in the late 1940s: the exodus from rural to urban areas (Baudin and Stelter 2022), which reduced human disturbance, increased the amount of land available to wild ungulates and fostered a shift in wildlife value orientations that allowed the subsequent emergence of conservation policies (Manfredo et al. 2020); the decrease in the amount of land used for agricultural production and livestock breeding (Jepsen et al. 2015), which eased human pressures on the environment and progressively increased biomass available to wild ungulates; the development of institutions and laws that govern the reforestation of rural areas, the creation of protected areas, the implementation of intensive wildlife management systems, and the reintroduction or translocation of wild ungulates (Fuchs et al. 2015).

Understanding how these processes have influenced the population trends of different wild ungulates, across European countries, is needed to manage them adequately. However, differences between European countries, in terms of their environment and society, make it hard to completely generalize the numerical and geographical expansion of wild ungulates.

In this study, we summarized large-scale population dynamics of wild ungulates, by using annual hunting bags as a proxy of different species abundances across Europe and identified their most relevant environmental and socio-economic drivers in a framework of human-wildlife coexistence (Carpio et al. 2021). In particular, over the last few decades, wildlife agencies in Europe have: *i*) managed common and widespread species with relevant hunting and commercial interest, such as red deer, roe deer and wild boar, *ii*) conserved species with limited distribution but abundant local populations such as moose (*Alces alces*) and northern chamois (*Rupicapra rupicapra*), *iii*) taken decisions about controlling emerging diseases, like in the case of ASF in wild boar, or chronic wasting disease in deer species, and *iv*) controlled introduced species with widespread (i.e., fallow deer, *Dama dama*) or local (i.e., mouflon, *Ovis gmelini musimon*) distribution. In consequence, these diverse practices could have had contrasting effects on the population demography of different species.

This paper analyzes the population dynamics of seven ungulate species to identify species-specific or species-country-specific differences in their trends and highlight their environmental and socio-economic drivers. The results of this study can contribute to build a background to predict how emerging factors like climate change as well as the recovery of large carnivores and (imported) diseases could add to their influence in affecting populations of more widespread species.

2. Methods

2.1 Data collection

To quantify long-term trends in wild ungulate populations, we collected data about annual harvests of wild ungulates across 25 European countries. Among these countries we selected the 19 countries that had hunting bag dataset starting from 1975 till 2018 for ungulate species. Although some studies highlighted the potential limitations of hunting bags in reflecting the population densities and temporal dynamics of wild ungulates (Pettorelli et al. 2007; Imperio et al. 2010), we used this data as they were the only figures available for such a long-time span. In this paper, we do not consider hunting bags as a direct indicator of population biological parameters but rather as an index representing the interaction between environmental factors and the harvest rate of different ungulate species, which can reflect long-term changes in populations (Massei et al. 2015; Aebischer 2019).

Data collection focuses on seven species that are regularly harvested or controlled to reduce their impacts on human activities and ecosystems: European roe deer (17 countries), red deer (17), wild boar (15), fallow deer (6), mouflon (6), northern chamois (6), and moose (6). For all these 7 species, we collected hunting bags from 1975 to 2018. Moreover, we also compared the 1948 – 2018 trends in roe and red deer hunting bags in Austria, Denmark, Sweden, and Switzerland to better understand their simultaneous temporal evolution concerning forest structure (see the Discussion section). Because individual countries have different living conditions and, therefore, very different ungulate populations, we standardized counts in each country, by subtracting the mean and dividing by the standard deviation. This allowed us to compare time series from different countries, represented as standardized values of each time series, that would have been on different scales otherwise. We did not divide hunting bags according to the area of each country (calculated bag densities), as this value was larger than the distribution range of the various species, which for decades ago was often unknown.

2.2 Statistical analysis

For each species, we used longitudinal cluster analysis (Den Teuling et al. 2021), based on Dynamic Time Warping (DTW; Sardá-Espinosa 2019), to identify groups of countries with similar long-term trends. The optimal number of clusters was identified by inspecting the silhouette index. As DTW clustering does not allow us to compare a solution with two clusters against a solution with a single cluster, we used a cutoff of 0.5 for the silhouette index: in case there were groups with truly diverging long-term trends in each species, the silhouette index would have been higher than this cutoff (for an explanation of these metrics, see Den Teuling et al. 2021).

Then, we also used the random forests algorithm (Breiman 2001) to quantify the effect of different landscape and socio-economic dynamics on the temporal evolution of hunting bags. Wild ungulates are generally deemed to be favored by forest cover, which can provide regular (Spitzer et al, 2020) and pulsed (Bisi et al. 2018; Barrere et al. 2020; Touzot et al. 2020) food resources, a refuge against human disturbance (Bonnot et al. 2013; Carbillet et al. 2020; Jasińska et al. 2021; Salvatori et al. 2023; Dupke et al. 2017), and shelter from temperatures above critical thresholds (van Beest et al.

2012; Ewald et al. 2014; Reiner et al. 2021, 2022; Kramer et al. 2022). Therefore, we also included changes (1975-2018) in the proportion of forested areas of each country as a covariate in the model. The amount of forest cover in each country was obtained by combining official data from the Food and Agriculture Organization with data from forestry inventories of the various countries. Moreover, as some ungulate species are also affected by the availability of understory and secondary successions (Hewison et al. 2009; Reiner et al. 2023; Vannini et al. 2021; Zong et al. 2023), we also calculated the percentage of forests that in 1975 were less than 20 years of age. This value was obtained from Vilén et al. (2012) and aimed to identify countries subjected to intense afforestation policies in the 1950s and the 1960s. Moreover, in Europe, forest expansion followed agricultural land abandonment, particularly in mountainous or marginal areas (MacDonald et al. 2000; Levers et al. 2018). Therefore, we also used changes in the percentage of the population living in rural areas (https://data.worldbank.org/indicator/SP.RUR.TOTL.ZS) and changes in the proportion of surface that was covered by croplands (https://data.worldbank.org/indicator/AG.LND.AGRI.ZS) in individual countries as predictors in our model.

In most cases, rural abandonment also corresponded to a decrease in the presence of livestock in the environment, which can compete with wild ungulates for resources and transmit infectious and parasitic diseases (Martin et al. 2011; Chirichella et al. 2014). Therefore, we also controlled for differences in livestock units of each country (https://ec.europa.eu/eurostat/statistics-explained/index.php?title=Glossary:Livestock_unit_(LSU)) between 1975 and 2018.

Finally, as European countries differ in their game management systems, we also controlled different management policies' effects on wild ungulates. Namely, following Apollonio et al. (2010) and Putman et al. (2011), we compared countries *i*) with a centralized, top-down approach, where overall hunting quotas are established by national agencies and subsequently divided across regions, *ii*) with a decentralized top-down approach, where national wildlife agencies fix overall quotas, but their implementation is up to management districts, *iii*) where wildlife agencies define the boundaries of management units, but these units are then entirely responsible for the determination of hunting quotas, *iv*) countries with a “bottom-up” approach, where hunting quotas are determined by each district and where districts could aggregate between them, and *v*) countries with a “libertarian” approach, where hunting quotas are entirely up to landowners.

In random forests, we also controlled for the year of each hunting bag in each country to model overall temporal trends, which could have been caused by unmeasured factors, such as climate change (Mysterud et al. 2010) or numerical increase of large carnivores (Chapron et al. 2014).

In random forest modeling, we did not model either the hunting bags of moose nor those of the chamois, as we had too few countries and, therefore, little variation in model covariates. Moreover, our analyses did not include variables representing climatic conditions. Although climate is a key factor affecting the population dynamics of wild ungulates (Apollonio and Chirichella 2023; Malpeli et al. 2024), which can be represented by indexes such as the North Atlantic Oscillation (Mysterud et al. 2003), climate conditions in Europe are not homogeneous either between, or within countries. For example, they vary according to the latitude, elevation, or distance from the coast of different areas. However, aggregating these gradients at the national scale would have resulted in the so-called “ecological fallacy” and biased our findings (Salkeld and Antolin 2020).

All continuous predictors were converted to z-scores. As random forests average between multiple regression trees, the relative importance of each predictor was measured as the decrease in node impurities through the residual sum of squares. Statistical analyses were carried out using R (R Core Team 2024).

3. Results

Between 1975 and 2018, Europe-wide hunting bags increased for all 7 studied species of ungulates (Table 1, Fig. 1). This increase was considerable and yet quite heterogeneous among countries. Even when excluding particularly extreme increases (Table 1), the median increase of harvest per species during the 43-year study period was as follows: European roe deer (1.97 folds), red deer (10.95), wild boar (10.20), fallow deer (5.58), mouflon (14.58), northern chamois (2.27), and moose (1.33), respectively. In case of wild boar, it is worth mentioning that the species was absent from Sweden until its accidental introduction in the wild during the late 1970s, but in 2018 a total of 112,352 wild boar were harvested (Fig. 2). Moreover, in Finland, approx. 1,000 roe deer were culled in 2013; in 2023/2024, this number has risen to 16,555 individuals (Ilpo Kojola, personal communication).

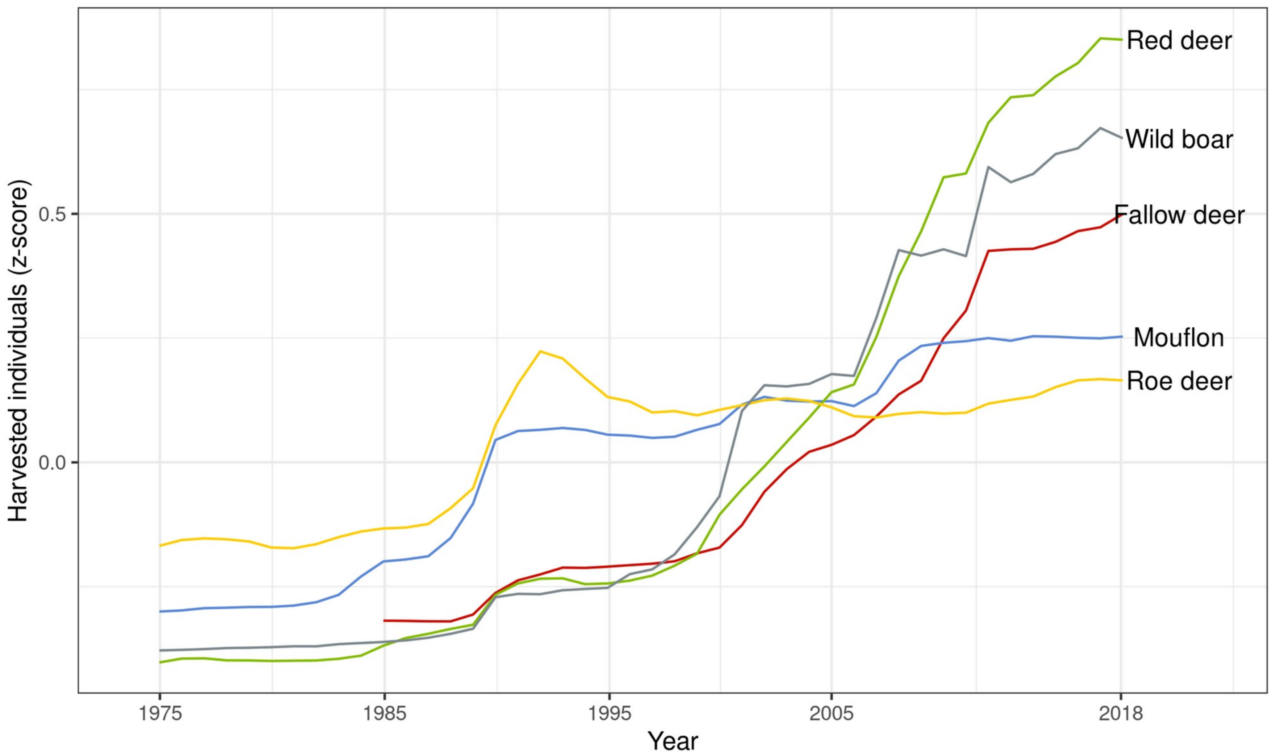


Fig. 1. Conditional effects plots, representing the evolution in the average number of harvested individuals, across the different species, according to random forests. The number of harvested individuals was transformed to a Z-score and is represented in terms of standard deviations, from the mean value of each country.

The only ungulates with an overall decrease in their harvests were northern chamois in Austria and Switzerland, and moose in Lithuania (Table 1). Furthermore, in Poland, 560 moose were hunted in 1975, with harvests peaking in 1989 (1,670 individuals), but hunting was suspended in 2001 due to the dramatic decline of the population (Bobek et al. 2005).

Longitudinal cluster analysis confirmed the pan-European, long-term increase in hunting bags. Except for northern chamois, for which two groups of countries with clearly diverging trends emerged, the Silhouette Index (hereinafter, SI) for a two-cluster solution was always below the cutoff of 0.5 (Fig. 3). This indicates that clusters had poorly distinguished long-term trends, with hunting bags in 2018 being consistently higher than those in 1975. However, the graphical inspection of cluster centroids sometimes revealed different groups of countries concerning short-term fluctuations or emerging differences.

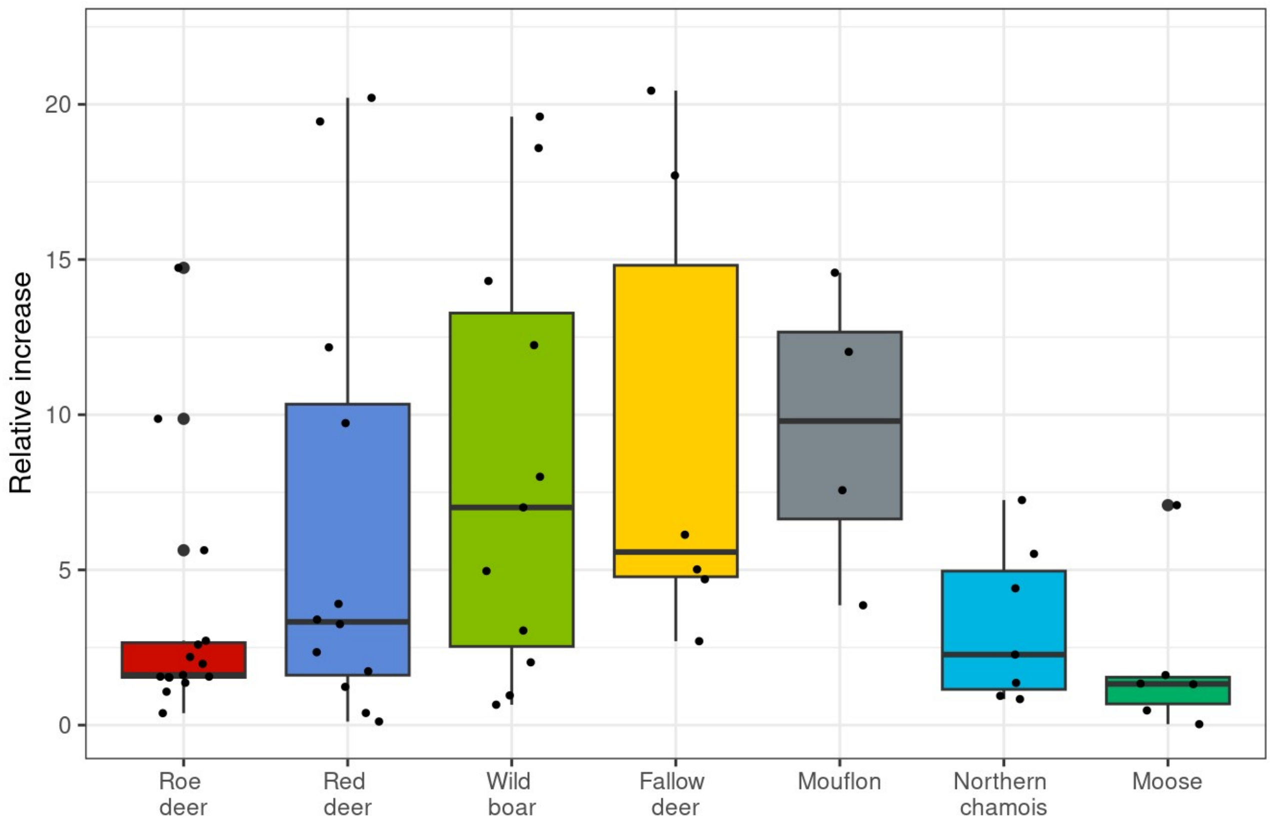


Fig. 2. Relative increase in the number of wild ungulates, across European countries (see Table 1 for detailed data in particular countries). The relative increase indicates how larger the number of harvested individuals was in 2018, compared to 1975. To make comparisons clearer, we omitted those countries where harvests had increased more than 25 times (see the Results section).

When considering roe deer (SI = 0.37; Fig. 3), hunting bags have decreased since the late 1990s in Luxembourg, Norway, Switzerland, Slovenia, Sweden, and the autonomous province of Trento (Italy). On the other hand, in the rest of Europe, after a decrease in the late 1990s, roe deer harvests have boomed.

Harvests increased steadily across most of Europe in case of red deer (SI = 0.37; Fig. 3). However, in Estonia, Latvia, Lithuania, Poland, Slovakia, and Slovenia, harvests of this species peaked in the early 1990s, then decreased and subsequently increased again with a change point around 2010. In some Eastern European countries, these patterns might occur at different levels due to the political changes after the collapse of socialism (1989/1990), as shown by Bragina et al. (2018).

Wild boar experienced a steady increase across most of Europe. However, the increase in wild boar harvests was temporally lagged in Croatia, Poland, Estonia, Latvia, Lithuania, and Sweden, where it started after 1995. Noteworthy, in Poland and Baltic countries, wild boar harvests also decreased after 2013-2014, when an outbreak of ASF occurred in this area (Cwynar et al. 2019).

Fallow deer had even less pronounced differences in long-term trends of its harvests (SI = 0.23; Fig. 3), which increased homogeneously across Europe. Homogeneity also characterized mouflon (SI = 0.34), whose harvests also increased markedly across the 6 European countries for which we had data. Luxembourg was the only country with a different trajectory, where harvests of mouflon boomed in the 1990s and then dropped in 2015.

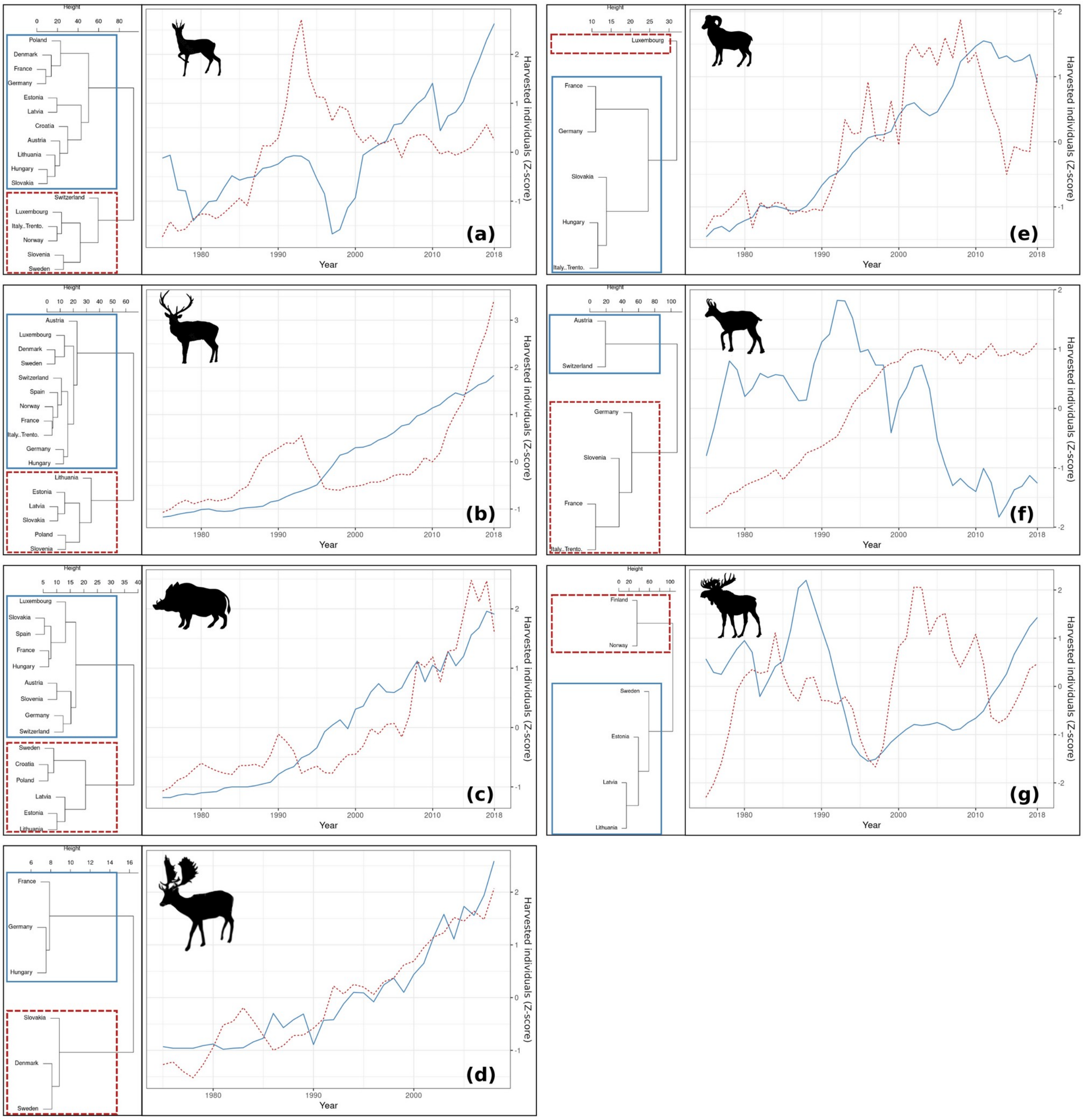
The only species characterized by well-distinguished opposite harvest trends in two groups of countries was northern chamois (SI = 0.61; Fig. 3). Harvests increased between 1975 and the early 1990s in Austria and Switzerland, where they subsequently declined in recent years. On the other hand, the number of harvested individuals continuously increased in France, Germany, Slovenia, and the autonomous province of Trento (Italy).

As for moose harvests (SI = 0.44; Fig. 3), two groups of countries emerged. In Sweden, Estonia, Latvia and Lithuania, harvests increased until the late 1980s, declined until the mid-1990s, and increased again. Norway and Finland instead constituted a second group of countries with somewhat different temporal dynamics. In Norway, moose harvests increased until the late 1990s, then slightly declined. In Finland, on the other hand, harvests fluctuated highly, with two peaks, i.e. from 1980 to the mid-1990s and from 2000 to 2010, with two sharp declines in between (Fig. S2).

Random forests predicted well hunting bags of roe deer (R^2 = 0.81; MSE = 0.18), red deer (R^2 = 0.92; MSE = 0.07), fallow deer (R^2 = 0.94; MSE = 0.06), wild boar (R^2 = 0.90; MSE = 0.09), and mouflon (R^2 = 0.92; MSE = 0.08). However, random forests also revealed species-specific differences in the most important correlates of hunting bags (Table 2). Overall, hunting bags were positively associated with the years within the time series, which aligns with the fact that each species increased in the number of harvested individuals over time. The year of each hunting bag was the most important predictor for red deer and wild boar.

However, the temporal component was not the most predictive factor for roe deer, mouflon, and fallow deer. The change in % of forest cover of each country was the most important predictor for roe deer and mouflon: hunting bags for these two species were much higher in those countries with a marked increase in forest cover. The change in the percentage of the human population that lived in rural areas was the most crucial factor predicting hunting bags in fallow deer, with peak in countries with little rural depopulation. Other predictors seemed to have a comparatively smaller effect (Table 2).

When comparing the trends of roe deer and red deer harvests with data from 1948 in Austria, Denmark, Sweden, and Switzerland, we noticed that the two species exhibited two types of connected trends. In the first case, there were years when roe deer harvests started stagnating or declining, corresponding with a marked increase in red deer harvests. This happened in Switzerland in 1980, Austria in the mid-1990s, and Denmark in the early 2010s. On the other hand, sometimes the peak in roe deer harvests largely anticipated that of red deer. This was the case for Sweden, where roe deer harvests started booming in the mid-1980s and those of red deer increased in the 2010s, and in Denmark, where roe deer harvests increased around 1980 and red deer in the early 2000s (Fig. 5).



318 Fig. 3. Cluster centroids and dendrograms for the various species: roe deer (a), red deer (b), wild boar (c), fallow deer (d), mouflon (e), northern chamois (f), moose (g). For temporal changes in moose harvests in Finland and Norway, see Fig. S2. The number of harvested individuals was transformed to a Z-score and is represented in terms of standard deviations, from the mean value of each country.

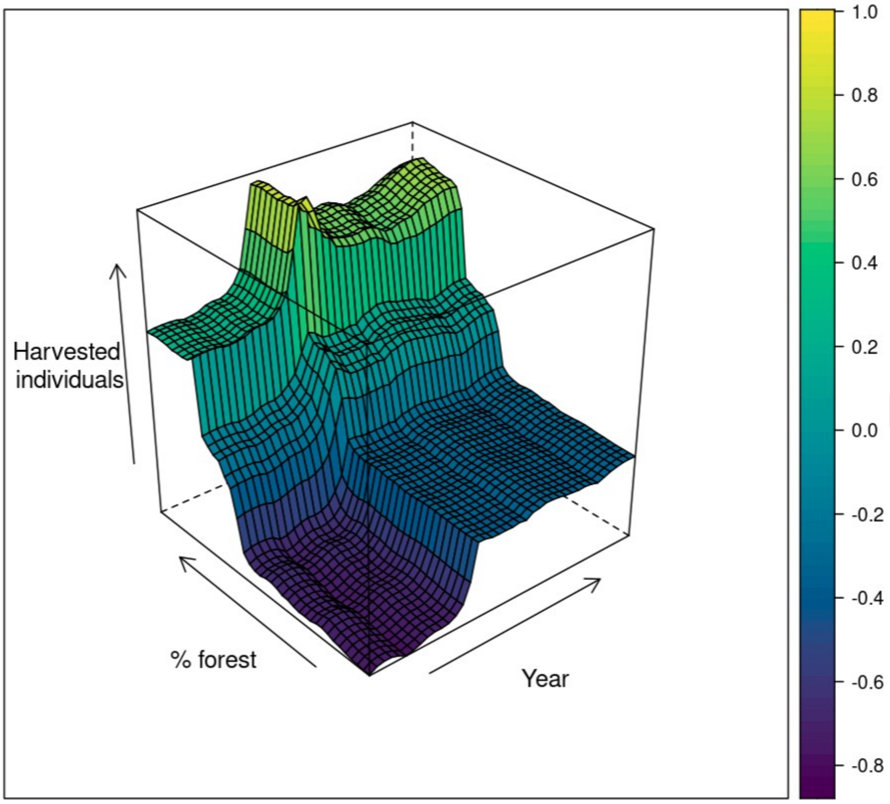


Fig. 4. Conditional effect plot, representing the change in the number of harvested roe deer according to time and relative change in forest cover.

4. Discussion

If we compare changes in large mammal distribution and abundance in Europe, we can appreciate a difference between ungulates and large carnivores. Chapron et al. (2014) reported that the success of large carnivores in Europe stemmed from coordinated legislation shared by many European countries (e.g., Council Directive 92/43/EEC; Bern Convention), context-specific management practices, and institutional arrangements. Instead, the general picture about wild ungulates in Europe suggests that these species could regain a landscape that had significantly changed when human pressure shifted towards urbanized areas, while at the same time being intensively managed all over the continent. Our study shows that in the last decades, the trends of European ungulates' harvest (which is also a proxy of their abundance) increased, following socio-economic changes associated with the shift from rural economies, characterized by low production applied to large areas, to industrial and post-industrial economies. Indeed, according to our results, ungulates have experienced a significant increase in abundance in Europe, with a correspondent change in management issues like those related to the development of locally overabundant populations (Carpio et al. 2021; Valente et al. 2020).

Many previous studies have already confirmed that human development shapes wildlife populations (Tucker et al. 2021; Johnson et al. 2023), and in this context our approach revealed: *i*) marked country-specific differences in the long-term trend of cold-adapted species, *ii*) country based emerging differences for European roe deer and wild boar, *iii*) the complementary and sometimes opposite temporal development for deer species with a different ecology, *iv*) similarities and differences in the overall weight of environmental factors across different species or among different population of the same species. These results can be helpful in predicting how landscape, climate change, and emerging diseases could affect the dynamics of future wild ungulate populations.

First, for Alpine/boreal species like northern chamois and moose, we found evident variations in the temporal trend of their harvests between countries. In the case of northern chamois (*Rupicapra rupicapra rupicapra*), while harvests increased between 1975 and the early 1990s in Austria and Switzerland, where they subsequently declined, a permanent increase was revealed in France, Germany, Slovenia, and autonomous province of Trento (Italy). Indeed, the future of northern chamois conservation will further depend on several different environmental factors, with impacts on demography and life history traits that still need to be fully clarified (Chirichella et al. 2021; Corlatti et al. 2022). Available data and studies revealed the importance of environmental heterogeneity in shaping the population dynamics of wild ungulates, especially in response to ongoing climatic and land use changes (Mason et al. 2014; Chirichella et al. 2021; Hoste et al. 2024; Reiner et al. 2021), concerning the expansion and increase of potential competitors (e.g., red deer: Corlatti et al. 2019; Donini et al. 2021), and predators (Chapron et al. 2014; Vogt et al. 2024). Another species with limited distribution but abundant local populations, i.e. moose, revealed country-specific patterns in dynamics (e.g., Bobek et al. 2005; Kojola et al. 2021). These results confirmed the importance of site-specific management/conservation issues to maintain sustainable populations of a species susceptible to human-caused disturbance, vehicle collisions, illegal killings, and rising temperatures (Janík et al. 2021). The best example of this is the moose population in Poland, where it –in spite of the lowest harvest rate in Europe– has faced almost complete extermination and where recovering populations are still limited by low environmental connectivity (Bluhm et al. 2023).

On the other hand, although our findings highlighted a long-term increase in the harvests of roe deer and wild boar, we also found emerging short-term differences. In the case of wild boar, some countries experienced an average reduction in hunting bags between 2013 and 2014. This differentiation could have been due to the impact of ASF in Poland, Estonia, Latvia, and Lithuania (Cwynar et al. 2019), Recent data collected by the *ENETWILD* Consortium indicates a recovery of wild boar populations in the Baltic countries affected by ASF since 2019/2020 (ENETWILD-consortium, 2023; EFSA 2024). It will be interesting evaluating the effect of the impact wild boar abundance fluctuations due to ASF on habitats and communities, included other wild ungulates species (and their hunting and predation by large carnivores).

Another differentiation of harvest rates among countries occurred in the case of roe deer, whose hunting bags in 5 countries have declined since a peak in the early 1990s. This decline in roe deer harvests is likely to have been driven by changes in forest structures at the landscape scale (Fig. 4), and locally by the recovery of large carnivores as in the case of Eurasian lynx *Lynx lynx*; in Sweden

(Andrén and Liberg 2015). This point might be clarified when simultaneously considering the harvests of roe and red deer over a long period. However, roe deer is still expanding its distribution range in certain regions, like central and southern Iberia (Virgós and Telleria 1998). In Austria, Denmark, Sweden, and Switzerland, where the harvest of these two species had been recorded from 1948, we noticed that the change points of the time series of the two species coincided and then exhibited a symmetrical pattern: harvests of red deer always increased when those of roe deer reached a plateau or even started declining (Fig. 5). Moreover, roe deer did not show an increase comparable to that of red deer despite the steady increase of forest cover in Europe. The former is, in fact, typical of pioneer species, linked to the early stages of forest development that provide important resources like access to cover (Mysterud and Ostbye 1999) and high quality and diversity forage, particularly at ecotones in proximity to open areas (Andersen et al. 1998; Saïd and Servanty 2005). On the contrary, red deer is more adapted to live among all different environments occupied, in mature forests, forest-agriculture mosaics, and even in artificial conifer plantations, being a mixed feeder with a better capacity to exploit poor quality forage (Hoffman 1989; Gordon and Prins 2019). A comparative analysis of the trends of the two species for the countries with available pre-1975 data has shown a greater growth rate in roe deer in the pre-1975 period with a subsequent slowdown. On the contrary, faster growth in the post-1975 period is noted for red deer, a species able to benefit from the late successional stages of forests deriving from post-WW2 agriculture decline (Mattioli et al. 2022). These symmetrical trends were already noticed in the Italian Alps (Chirichella et al. 2017). Finding them in four countries indicates that similar dynamics could be widespread across Europe and might produce a decline in roe deer populations over the next few years. Moreover, locally, other factors like, for example, the influence of golden jackal (*Canis aureus*) in the Balkans and Hungary (Bijl et al. 2024) or, in the case of the Danube and its tributaries and in Central Europe, the increase of American liver fluke (*Fascioloides magna*), a non-native liver parasite, could be important factor in the decline of roe deer (Csivincsik et al. 2023).

This shows that multifactorial processes are influencing single ungulate species distribution and abundance in Europe.

The increase in forest area partially contributed to explaining red deer harvest dynamics, as reported in other studies (e.g., Heurich et al. 2015; Chirichella et al. 2017). While in the case of wild boar, due to the ecological adaptability and invasive potential of this species, it is more difficult to find a primary driver of expansion and increase, the changes in the percentage of area covered by croplands were found in our study to be most important after the temporal component. Indeed, many studies reported the effect of different drivers (i.e., climate, both harshness, and warming; habitat, agriculture, both current diversity and possible change; large carnivore presence and abundance; hunting management practices; supplementary feeding) as limiting or promoting factors in shaping wild boar populations dynamics (for a review, see Melis et al. 2006 and Scandura et al. 2022).

In our analysis, the temporal component was not the most predictive factor for roe deer, mouflon, and fallow deer. The change in the percentage of forest area was the most relevant driver for roe deer and mouflon: hunting bags for mouflon were much higher in those countries with a marked increase in forest cover. Moreover, the percentage of area covered by croplands was also an important factor driving the abundance of mouflon (see Garel et al. 2022, for a review about mouflon).

Similarly, the change in the percentage of the human population that lived in rural areas was the most important factor in predicting hunting bags in fallow deer. As De Marinis et al. (2022) reported, fallow deer is one of the most widespread introduced mammals in Europe as it has been established in most European countries; if they are not present in the wild, then they are kept in farms, reserves, or parks (Bijl and Csányi 2022). Its distribution/density is, therefore, a direct consequence of human activity (Bijl and Csányi, 2022; Masseti 1996, 2002; Sykes et al. 2011).

However, to date, the population dynamics of this species (and their drivers) have received poor attention, especially in northern/central Europe and for free-ranging populations.

Climate shaped the distribution of European mammals (Santos et al. 2020), and its effects are foreseen to become increasingly important (Levinsky et al. 2007). However, in this study we did not investigate the effect of climatic factors over the population dynamics of European ungulates. This choice was motivated by the mismatch between local climatic conditions in each country and our country-level Nevertheless, considered that climate affects the distribution and dynamics of cold-adapted ungulates (i.e. species with a low thermal neutral zone) (Lovari et al. 2020), as well as those of species with a wide distribution (e.g., wild boar: Markov et al. 2022; deer species: Apollonio and Chirichella 2023), we believe that it is important to address this gap to guide the management of wild ungulates in European landscapes facing climate change.

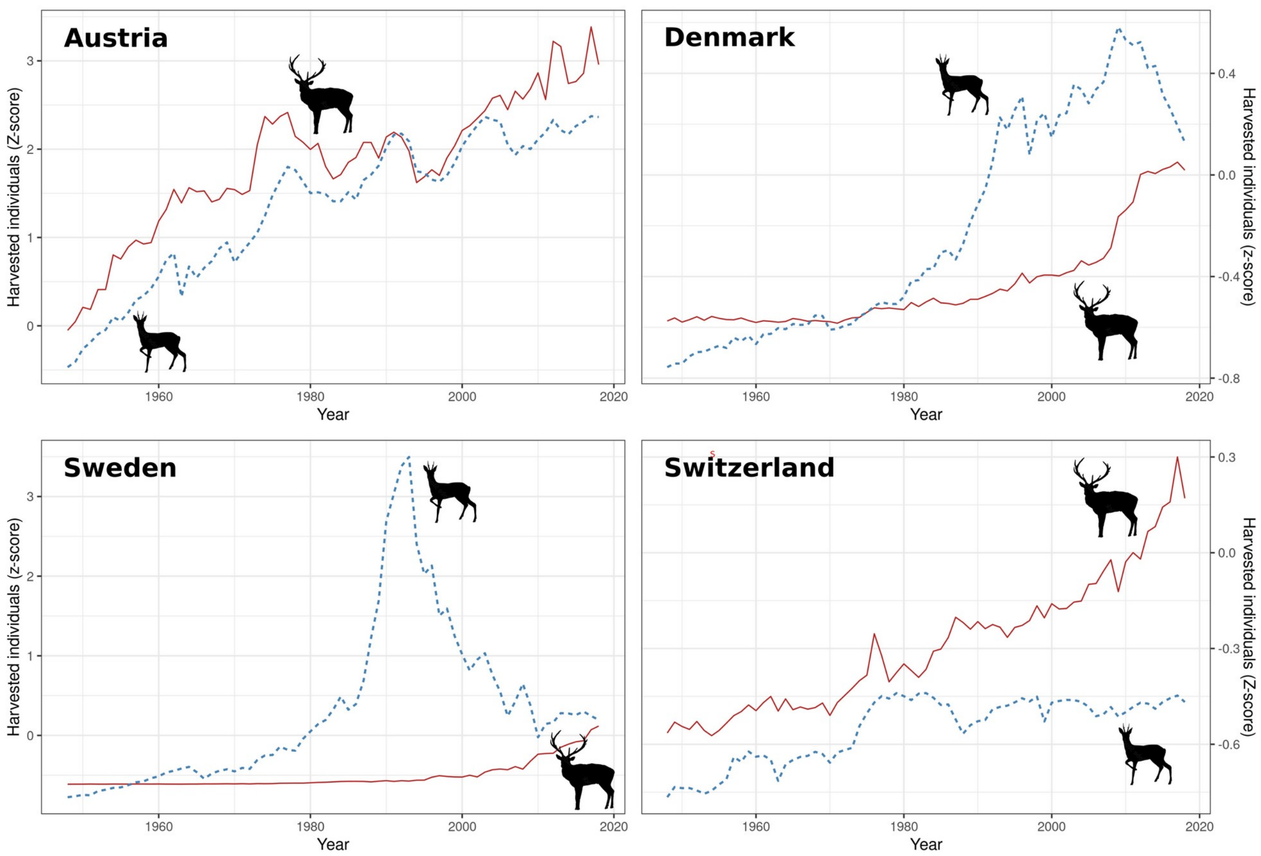


Fig. 5. Temporal trends of roe deer (dashed line) and red deer (solid line) harvests, between 1948 and 2018, in four countries: Austria (top-left), Denmark (top-right), Sweden (bottom-left), and Switzerland (top-right). The number of harvested individuals was transformed to a Z-score and is represented in terms of standard deviations, from the mean value of each country.

5. Conclusion

A combination of reforestation, agricultural abandonment, and rural-urban migration has led to a situation where wild ungulates are widespread across Europe. Nevertheless, the main drivers of change differ among species, as well as between different socio-economic and environmental contexts. Wild ungulates are hunted in virtually all parts of their distributional range, including most protected areas (van Beeck Calkoen et al. 2020), with major differences between and within countries. Hunting seems to be the major source of mortality in wild ungulates and therefore the main anthropogenic driver of population density (Bassi et al. 2020; van Beeck Calkoen et al. 2023). In this context, it is extremely important not to generalize the increase in ungulates but to consider their local status and short-term fluctuations, to support proper management strategies for the different species. Our findings confirm the need for long-term national and international monitoring schemes, aiming to better understand the demography of wild ungulates (Carpio et al. 2021; ENETWILD consortium, 2023), which is essential to implement and/or improve policies for their science-based management and conservation.

CRediT authorship contribution statement

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Jacopo Cerri, Marco Apollonio, Roberta Chirichella, Francesco Chianucci - **Methodology**

Jacopo Cerri, Roberta Chirichella - **Software**

Walter Arnold, Luděk Bartoš, Tomasz Borowik, Juan Carranza, Sándor Csányi, Göran Ericsson, Marco Heurich, Ilpo Kojola, Atle Mysterud, Boštján Pokorny, Krzysztof Schmidt, Nikica Šprem, Joaquín Vicente, Ajša Alagić, Linas Balčiauskas, Jim Casaer, Sandra Cellina, Gundega Done, Slavomír Find'o, Carlos Fonseca, Dragan Gačić, Dime Melovski, Jānis Ozoliņš, Haritakis Papaioannou, Tiit Randveer, Vesa Ruusila, Christine Saint-Andrieux, Rauno Veeroja - **Validation**

Jacopo Cerri, Roberta Chirichella, Francesco Chianucci - **Formal analysis**

Juan Carranza, Sándor Csányi, Göran Ericsson, Marco Heurich, Ilpo Kojola, Atle Mysterud, Boštján Pokorny, Krzysztof Schmidt, Nikica Šprem, Joaquín Vicente - **Investigation**

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Jacopo Cerri, Marco Apollonio, Roberta Chirichella, Walter Arnold, Juan Carranza, Sándor Csányi, Göran Ericsson, Marco Heurich, Ilpo Kojola, Atle Mysterud, Boštján Pokorny, Krzysztof Schmidt, Nikica Šprem, Joaquín Vicente **Writing – Original Draft**

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Jacopo Cerri, Roberta Chirichella – **Visualization**

Marco Apollonio - **Supervision**

Marco Apollonio, Roberta Chirichella - **Project administration**

Marco Apollonio - **Funding acquisition**

Data availability

Data and software code are available from the Open Science Framework, at the following link:

https://osf.io/uvfcs/

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Conflict of interest

The authors declare that they have no competing interests.

Ethical approval

Not applicable

References

Aebischer NJ (2019) Fifty-year trends in UK hunting bags of birds and mammals, and calibrated estimation of national bag size, using GWCT's National Gamebag Census. Eur J Wildl Res 65: 64. https://doi.org/10.1007/s10344-019-1299-x

Andersen R, *et al*. (1998) The European roe deer: the biology of success. Scandinavian University Press, Oslo.

Andrén H, Liberg O (2015) Large impact of Eurasian lynx predation on roe deer population dynamics. *PloS One* 10*:* e0120570. https://doi.org/10.1371/journal.pone.0120570

Apollonio M, *et al*. (2010) *European ungulates and their management in the 21st century*. Cambridge University Press.

Apollonio M, Chirichella R (2023) Deer and climate change: impacts and perspectives. *Anim. Prod. Sci.* 63: 1573-1582. https://doi.org/10.1071/AN22296

Barasona JA, *et al*. (2021) Expansion of native wild boar populations is a new threat for semi-arid wetland areas. Ecol. Indic. 125: 107563. https://doi.org/10.1016/j.ecolind.2021.107563

Barrere J, *et al*. (2020) How does oak mast seeding affect the feeding behavior of sympatric red and roe deer? Basic Appl. Ecol. 47: 83-94. https://doi.org/10.1016/j.baae.2020.04.006

Bassi E, *et al*. (2020) Relative impact of human harvest and wolf predation on two ungulate species in Central Italy. Ecol. Res. 35: 662-674. https://doi.org/10.1111/1440-1703.12130

Baudin T, Stelter R (2022) The rural exodus and the rise of Europe. J. Econ. Growth 27: 365-414. https://doi.org/10.1007/s10887-022-09206-4

Beguin J, *et al*. (2016) Management of forest regeneration in boreal and temperate deer–forest systems: challenges, guidelines, and research gaps. Ecosphere 7: e01488. https://doi.org/10.1002/ecs2.1488

Bergmann H, *et al*. (2021) A review of environmental risk factors for African Swine Fever in European wild boar. Animals 11: 2692. https://doi.org/10.3390/ani11092692

Bijl H, Csányi S (2022) Fallow deer (*Dama dama*) population and harvest changes in Europe since the early 1980s. Sustainability 14: 12198. https://doi.org/10.3390/su141912198

Bijl H, *et al*. (2024) From invaders to residents: The golden jackal (*Canis aureus*) expansion in Hungary since the mid-1990s. PLoS One 19, e0306489 https://doi.org/10.1371/journal.pone.0306489

Bisi F, *et al*. (2018) Climate, tree masting and spatial behaviour in wild boar (*Sus scrofa* L.): insight from a long-term study. Ann. For. Sci. 75: 1-9. https://doi.org/10.1007/s13595-018-0726-6

Bluhm H, *et al*. (2023) Widespread habitat for Europe's largest herbivores, but poor connectivity limits recolonization. Divers. Distrib. 29: 423-437. https://doi.org/10.1111/ddi.13671

Bobek B, *et al*. (2005) A moose recovery plan for Poland: main objectives and tasks. Alces: A Journal Devoted to the Biology and Management of Moose 41: 129-138. https://www.alcesjournal.org/index.php/alces/article/view/417/499

Bonnot N, *et al*. (2013) Habitat use under predation risk: hunting, roads and human dwellings influence the spatial behaviour of roe deer. Eur J Wildl Res 59: 185-193. https://doi.org/10.1007/s10344-012-0665-8

Bragina EV, *et al*. (2018) Wildlife population changes across Eastern Europe after the collapse of socialism. Front. Ecol. Environ. 16: 77-81. https://doi.org/10.1002/fee.1770

Breiman L (2001) Random forests. Mach. Learn. 45: 5-32. https://doi.org/10.1023/A:1010933404324

Carbillet J, *et al*. (2020) Under cover of the night: Context-dependency of anthropogenic disturbance on stress levels of wild roe deer *Capreolus capreolus*. Conserv. Physiol. 8: coaa086. https://doi.org/10.1093/conphys/coaa086

Carpio AJ, *et al*. (2021) Wild ungulate overabundance in Europe: contexts, causes, monitoring and management recommendations. Mamm. Rev. 51: 95-108. https://doi.org/10.1111/mam.12221

Chapron G, *et al*. (2014) Recovery of large carnivores in Europe's modern human-dominated landscapes. Science 346: 1517-1519. https://doi.org/10.1126/science.1257553

Ramirez JI, *et al*. (2019) Long-term effects of wild ungulates on the structure, composition and succession of temperate forests. Forest Ecol. Manag. 432: 478-488. https://doi.org/10.1016/j.foreco.2018.09.049

Chirichella R, *et al*. (2014) Competition between domestic and wild ungulates. Behaviour and Management of European Ungulates Caithness Whittles Publishing, 110-23.

Chirichella R, *et al*. (2017) Alpine landscape and canopy cover from 1973 to 2011: are roe and red deer population dynamics linked? Wildl. Res. 44: 504-513. https://doi.org/10.1071/WR16232

Chirichella R, *et al*. (2021) Contrasting effects of climate change on Alpine chamois. J. Wildl. Manag. 85: 109-120. https://doi.org/10.1002/jwmg.21962

Corlatti L, *et al*. (2019) Long-term dynamics of Alpine ungulates suggest interspecific competition. J. Zool. 309: 241-249. https://doi.org/10.1111/jzo.12716

Corlatti L, *et al*. (2022) Past, present, and future of chamois science. Wildl. Biol. 2022: e01025. https://doi.org/10.1002/wlb3.01025

Côté SD, *et al*. (2004) Ecological impacts of deer overabundance. Annual Rev. Ecol. Evol. S. 35: 113-147. https://doi.org/10.1146/annurev.ecolsys.35.021103.105725

Csányi S, *et al*. (2014) Valuing ungulates in Europe. In: Putman, R., Apollonio, M. (Eds.). *Behaviour and Management of European Ungulates*. Dunbeath: Whittles Publishing, pp. 13-45.

Csivincsik Á, *et al*. (2023) The Large American Liver Fluke (*Fascioloides magna*): A Survivor's Journey through a Constantly Changing World. Parasitologia 3: 300-326. https://doi.org/10.3390/parasitologia3040031

Cwynar P, *et al*. (2019) African swine fever status in Europe. *Viruses* 11: 310. https://doi.org/10.3390/v11040310

Dawson BM, *et al*. (2024). Drastic changes in ground-dwelling beetle communities following high-intensity deer culling: insights from an island ecosystem. Environ. Entomol. 53: 223-229. https://doi.org/10.1093/ee/nvae013

De Marinis AM, *et al*. (2002). European fallow deer *Dama dama* Linnaeus, 1758. In Hackländer, K., and F. E. Zachos (eds.) Handbook of the Mammals of Europe. Terrestrial Cetartiodactyla (Section Editors: F. E. Zachos, L. Corlatti). Springer, Cham. 2022, 115.

Den Teuling N, *et al*. (2021). Clustering of longitudinal data: A tutorial on a variety of approaches. *arXiv preprint arXiv:2111.05469*. https://doi.org/10.48550/arXiv.2111.05469

Donini V, et al. (2021) Disentangling demographic effects of red deer on chamois population dynamics. Ecol. Evol. 11: 8264-8280. https://doi.org/10.1002/ece3.7657

Dupke C, *et al*. (2017) Habitat selection by a large herbivore at multiple spatial and temporal scales is primarily governed by food resources. Ecography 40: 1014-1027. https://doi.org/10.1111/ecog.02152

ENETWILD-consortium, *et al*. (2023) A guidance on how to start up a national wildlife population monitoring program harmonizable at European level. *EFSA Supporting Publications* 20: 8218E. https://doi.org/10.2903/sp.efsa.2023.EN-8218

European Food Safety Authority, *et al*. (2024) Epidemiological analysis of African swine fever in the European Union during 2023. EFSA Journal 22: e8809. https://doi.org/10.2903/j.efsa.2024.8809

Ewald M, *et al*. (2014) LiDAR remote sensing of forest structure and GPS telemetry data provide insights on winter habitat selection of European roe deer. Forests 5: 1374-1390. https://doi.org/10.3390/f5061374

Fuchs R, *et al*. (2015) Gross changes in reconstructions of historic land cover/use for Europe between 1900 and 2010. Glob. Cange Biol. 21: 299-313. https://doi.org/10.1111/gcb.12714

Fuller RJ, Gill RM (2001) Ecological impacts of increasing numbers of deer in British woodland. Forestry 74: 193-199. https://doi.org/10.1093/forestry/74.3.193

Garel M, *et al*. (2022). Mouflon *Ovis gmelini* Blyth, 1841. In Handbook of the Mammals of Europe (pp. 1-35). Cham: Springer International Publishing.

Gordon IJ, Prins HH (2019) Browsers and grazers drive the dynamics of ecosystems. The ecology of browsing and grazing II, 405-445. https://doi.org/10.1007/978-3-030-25865-8_16

Gortázar C, *et al*. (2007) Diseases shared between wildlife and livestock: a European perspective. Eur J Wildl Res 53: 241-256. https://doi.org/10.1007/s10344-007-0098-y

Harada K, *et al*. (2020). Legacy effects of sika deer overpopulation on ground vegetation and soil physical properties. Forest Ecol. Manag. 474: 118346. https://doi.org/10.1016/j.foreco.2020.118346

Heurich M, *et al*. (2015) Country, cover or protection: What shapes the distribution of red deer and roe deer in the Bohemian forest ecosystem? PLoS One 10: e0120960. https://doi.org/10.1371/journal.pone.0120960

Hewison AM, *et al*. (2009). Landscape fragmentation influences winter body mass of roe deer. Ecography 32: 1062-1070. https://doi.org/10.1111/j.1600-0587.2009.05888.x

Hofmann RR (1989) Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. Oecologia 78: 443-457. https://doi.org/10.1007/BF00378733

Hoste A, *et al*. (2024) Projection of current and future distribution of adaptive genetic units in an alpine ungulate. Heredity 132: 54-66. https://doi.org/10.1038/s41437-023-00661-2

Imperio S, *et al*. (2010) Investigating population dynamics in ungulates: do hunting statistics make up a good index of population abundance? Wildl. Biol. 16: 205-214. https://doi.org/10.2981/08-051

Janík T, *et al*. (2021) The declining occurrence of moose (*Alces alces*) at the southernmost edge of its range raise conservation concerns. Ecol. Evol. 11: 5468-5483. https://doi.org/10.1002/ece3.7441

Jasińska KD, *et al*. (2021). Habitat-Related Differences in Winter Presence and Spring—Summer Activity of Roe Deer in Warsaw. Forests, 12: 970. https://doi.org/10.3390/f12080970

Jepsen MR, *et al*. (2015) Transitions in European land-management regimes between 1800 and 2010. Land use policy 49: 53-64. https://doi.org/10.1016/j.landusepol.2015.07.003

Johnson TF, *et al*. (2023) Socioeconomic factors predict population changes of large carnivores better than climate change or habitat loss. Nat. Commun., 14: 74. https://doi.org/10.1038/s41467-022-35665-9

Kojola I, *et al*. (2021) Calf/female ratio and population dynamics of wild forest reindeer in relation to wolf and moose abundances in a managed European ecosystem. Plos one 16: e0259246. https://doi.org/10.1371/journal.pone.0259246

Kramer CJ, *et al*. (2022) Summer habitat use and movements of invasive wild pigs (*Sus scrofa*) in Canadian agro-ecosystems. Can. J. Zool. 100: 494-506. http://dx.doi.org/10.1139/cjz-2021-0116

Levers C, *et al*.. 2018. Spatial variation in determinants of agricultural land abandonment in Europe. Sci. Tot. Environ. 644: 95-111. https://doi.org/10.1016/j.scitotenv.2018.06.326

Levinsky I, *et al*. (2007) Potential impacts of climate change on the distributions and diversity patterns of European mammals. Biodiv. Conserv. 16: 3803-3816. https://doi.org/10.1007/s10531-007-9181-7

Linnell J, Zachos F (2010) Status and distribution patterns of European ungulates: genetics, population history and conservation. In: Ungulate Management in Europe: Problems and Practices, pp 12–53.

Lovari S, *et al*. (2020). Climatic changes and the fate of mountain herbivores. Clim. Change 162: 2319-2337. https://doi.org/10.1007/s10584-020-02801-7

MacDonald D, *et al*. (2000) Agricultural abandonment in mountain areas of Europe: environmental consequences and policy response. J. Environ. Manag. 59: 47-69. https://doi.org/10.1006/jema.1999.0335

Malpeli KC, *et al*. (2024) Existing evidence on the effects of climate variability and climate change on ungulates in North America: a systematic map. Environ. Evid. 13, 8. https://doi.org/10.1186/s13750-024-00331-8

Manfredo MJ, *et al*. (2020) The changing sociocultural context of wildlife conservation. Conserv. Biol. 34: 1549-1559. https://doi.org/10.1111/cobi.13493

Marchiori E, *et al*. (2012) Wild red deer (*Cervus elaphus* L.) grazing may seriously reduce forage production in mountain meadows. Ital. J. Anim. Sci. 11: e9 https://doi.org/10.4081/ijas.2012.e9

Markov N, *et al*. (2022). The wild boar Sus scrofa in northern Eurasia: a review of range expansion history, current distribution, factors affecting the northern distributional limit, and management strategies. Mamm. Rev. 52: 519-537. https://doi.org/10.1111/mam.12301

Martin C, *et al*. (2011) A survey of the transmission of infectious diseases/infections between wild and domestic ungulates in Europe. Vet. Res. 42: 1-16. https://doi.org/10.1186/1297-9716-42-70

Mason TH, *et al*. (2014) Environmental change and long-term body mass declines in an alpine mammal. Front. Zool. 11: 1-14. https://doi.org/10.1186/s12983-014-0069-6

Massei G, *et al*. (2015) Wild boar populations up, numbers of hunters down? A review of trends and implications for Europe. *Pest Manag Sci* 71: 492-500. https://doi.org/10.1002/ps.3965

Masseti M (1996) The postglacial diffusion of the genus Dama Frisch, 1775, in the Mediterranean region. Ricerche Biologia Selvaggina 25: 7-29.

Masseti M (2002) Island of deer. Natural history of the fallow deer of Rhodes and of the terrestrial and fresh water vertebrates of the Dodecanese, 2nd edn. Municipality of Rhodes, Greece.

Mattioli S, *et al*. (2022) Red deer *Cervus elaphus* Linnaeus, 1758. In Handbook of the Mammals of Europe. Cham: Springer International Publishing.

Melis C, *et al*. (2006) Biogeographical variation in the population density of wild boar (*Sus scrofa*) in western Eurasia. J. Biogeogr. 33: 803-811. https://doi.org/10.1111/j.1365-2699.2006.01434.x

Milner JM, *et al*. (2006) Temporal and spatial development of red deer harvesting in Europe: biological and cultural factors. J. Appl. Ecol. 43: 721-734. https://doi.org/10.1111/j.1365-2664.2006.01183.x

Mori E, *et al*. (2020) Impact of wild boar rooting on small forest-dwelling rodents. Ecol. Res. 35: 675-681. https://doi.org/10.1111/1440-1703.12113

Mysterud A, Østbye E (1999) Cover as a habitat element for temperate ungulates: effects on habitat selection and demography. *Wildl. Soc. Bull*, 385-394. https://www.jstor.org/stable/3783905

Mysterud A, Sæther BE (2010) Climate change and implications for the future distribution and management of ungulates in Europe. *Ungulate management in Europe: problems and practices*, 349-375.

Mysterud A, *et al*. (2003) The response of terrestrial ecosystems to climate variability associated with the North Atlantic Oscillation. *Geoph. Monog. Series* 134: 235-262. https://doi.org/10.1029/134GM11

Oja, R (2017) Consequences of supplementary feeding of wild boar: concern for ground-nesting birds and endoparasite infection (Doctoral dissertation, Universitatis Tartuensis). https://dspace.ut.ee/server/api/core/bitstreams/46377fb9-0523-40cc-a109-fb279c3624d0/content

Palmer G, *et al*. (2015). Nationwide trophic cascades: changes in avian community structure driven by ungulates. Sci. Rep. 5: 15601. https://doi.org/10.1038/srep15601

Pascual-Rico R, *et al*. (2021) Usually hated, sometimes loved: A review of wild ungulates' contributions to people. Sci. Tot. Env. 801: 149652. https://doi.org/10.1016/j.scitotenv.2021.14965

Pépin D, *et al*. (2006) Relative impact of browsing by red deer on mixed coniferous and broad-leaved seedlings—an enclosure-based experiment. Forest Ecol. Manag. 222: 302-313. https://doi.org/10.1016/j.foreco.2005.10.034

Perea R, *et al*. (2014) Big game or big loss? High deer densities are threatening woody plant diversity and vegetation dynamics. Biodiv. Cons. 23: 1303-1318. https://doi.org/10.1007/s10531-014-0666-x

Pettorelli N, *et al*. (2007) Aerial surveys vs hunting statistics to monitor deer density: the example of Anticosti Island, Quebec, Canada. Wildl. Biol. 13: 321-327. https://doi.org/10.2981/0909-6396(2007)13[321:ASVHST]2.0.CO;2

Pokorny B, *et al*. (2017) Ecological value, importance and impacts of wild ruminants. Gozdarski Vestnik 75: 360-372. http://dirros.openscience.si/IzpisGradiva.php?id=8108

Pokorny B, Jelenko I (2014) Ecological importance and impacts of wild boar (*Sus scrofa* L.). Zlatorogov Zbornik. 2: 2-30. https://clan.lovska-zveza.si/userfiles/Lovstvo/pdf/Zlatorogov_zbornik_2013.pdf

Putman R, Apollonio M, Andersen R (Eds., 2011) *Ungulate management in Europe: problems and practices*. Cambridge University Press.

Rae LF, *et al*. (2014) Multiscale impacts of forest degradation through browsing by hyperabundant moose (*Alces alces*) on songbird assemblages. Diversi. Distrib. 20: 382-395. https://doi.org/10.1111/ddi.12133

R Core Team (2024) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Reiner R, *et al*. (2023) Forest disturbances increase the body mass of two contrasting ungulates. J. Appl. Ecol. 60: 2177-2187. https://doi.org/10.1111/1365-2664.14481

Reiner R, *et al*. (2021) Forests buffer the climate-induced decline of body mass in a mountain herbivore. Glob. Change Biol. 2716: 3741-3752. https://doi.org/10.1111/gcb.15711

Reiner R, *et al*. (2022) Habitat and climate shape growth patterns in a mountain ungulate. Ecol. Evol. 12: e8650. https://doi.org/10.1002/ece3.8650

Ripple WJ, *et al*. (2015) Collapse of the world's largest herbivores. Sci. Adv., 1: e1400103. https://doi.org/10.1126/sciadv.1400103

Saïd S, Servanty S (2005) The influence of landscape structure on female roe deer home-range size. Landscape Ecol. 20: 1003-1012. https://doi.org/10.1007/s10980-005-7518-8

Salkeld DJ, Antolin MF (2020) Ecological fallacy and aggregated data: a case study of fried chicken restaurants, obesity and Lyme disease. Ecohealth 17: 4-12. https://doi.org/10.1007/s10393-020-01472-1

Salvatori M, *et al*. (2023) Crowded mountains: Long-term effects of human outdoor recreation on a community of wild mammals monitored with systematic camera trapping. Ambio 52: 1085-1097. https://doi.org/10.1007/s13280-022-01825-w

Santos AM, *et al*. (2020) Current climate, but also long-term climate changes and human impacts, determine the geographic distribution of European mammal diversity. Global Ecol. Biogeogr. 29: 1758-1769. https://doi.org/10.1111/geb.13148

Sardá-Espinosa A (2017) Comparing time-series clustering algorithms in r using the dtwclust package. R package vignette, 12**,** 41. https://cran.r-hub.io/web/packages/dtwclust/vignettes/dtwclust.pdf

Scandura M, *et al*. (2022) Wild Boar *Sus scrofa* Linnaeus, 1758. In Terrestrial Cetartiodactyla. Cham: Springer International Publishing.

Smit C, Putman R (2011) Large herbivores as 'environmental engineers.' In: Putman R, Apollonio M, Andersen R, eds. *Ungulate Management in Europe: Problems and Practices*. Cambridge University Press; 2011:260-283. https://doi.org/10.1017/CBO9780511974137.010

Spitzer R, *et al*. (2020) Fifty years of European ungulate dietary studies: a synthesis. Oikos 129: 1668-1680. https://doi.org/10.1111/oik.07435

Suzuki M (2024) Ecosystem transition due to deer overabundance: Insights from long-term studies and future considerations. *Ecol. Res*. 40: 3-19 https://doi.org/10.1111/1440-1703.12537

Sykes NJ, *et al*. (2011) New evidence for the establishment and management of the European fallow deer (*Dama dama dama*) in Roman Britain. J. Archaeol. Sci. 38 156–165 https://doi.org/10.1016/j.jas.2010.08.024

Touzot L, *et al*. (2020). How does increasing mast seeding frequency affect population dynamics of seed consumers? Wild boar as a case study. Ecol. Appl., 30: e02134. https://doi.org/10.1002/eap.2134

Tucker MA, *et al*. (2021) Mammal population densities at a global scale are higher in human-modified areas. Ecography 44: 1-13. https://doi.org/10.1111/ecog.05126

Valente AM, *et al*. (2020) Overabundant wild ungulate populations in Europe: management with consideration of socio-ecological consequences. Mammm. Rev. 50: 353-366. https://doi.org/10.1111/mam.12202

van Beeck Calkoen ST, *et al*. (2023) Numerical top-down effects on red deer (*Cervus elaphus*) are mainly shaped by humans rather than large carnivores across Europe J. Appl. Ecol. 60: 2625-2635. https://doi.org/10.1111/1365-2664.14526

van Beeck Calkoen ST, *et al*. (2020) Ungulate management in European national parks: Why a more integrated European policy is needed. *J. Environ. Manag*. 260: 110068. https://doi.org/10.1016/j.jenvman.2020.110068

van Beest FM, *et al*. (2012) Temperature-mediated habitat use and selection by a heat-sensitive northern ungulate. Anim. Behav. 84: 723-735. https://doi.org/10.1016/j.anbehav.2012.06.032

Vannini C, *et al*. (2021) Land cover and weather jointly predict biometric indicators of phenotypic quality in a large herbivore. Ecol. Ind. 128: 107818. https://doi.org/10.1016/j.ecolind.2021.107818

Vilén T, *et al*. (2012) Reconstructed forest age structure in Europe 1950–2010. Forest Ecol. Manag. 286: 203-218. http://dx.doi.org/10.1016/j.foreco.2012.08.048

Virgós E., Tellería JL (1998) Roe deer habitat selection in Spain: constraints on the distribution of a species. Can. J. Zool. 76: 1294-1299. https://doi.org/10.1139/z98-065

Vogt K, *et al*. (2024) Estimating kill intervals for a specific prey species using location clusters from GPS-collared Eurasian lynx (*Lynx lynx*). Eur. J. Wildl. Res. 70: 52. https://doi.org/10.1007/s10344-024-01804-4

Zong X, *et al*. (2023) Habitat visibility affects the behavioral response of a large herbivore to human disturbance in forest landscapes. J. Env. Manag. 348: 119244. https://doi.org/10.1016/j.jenvman.2023.119244

Supplementary figures

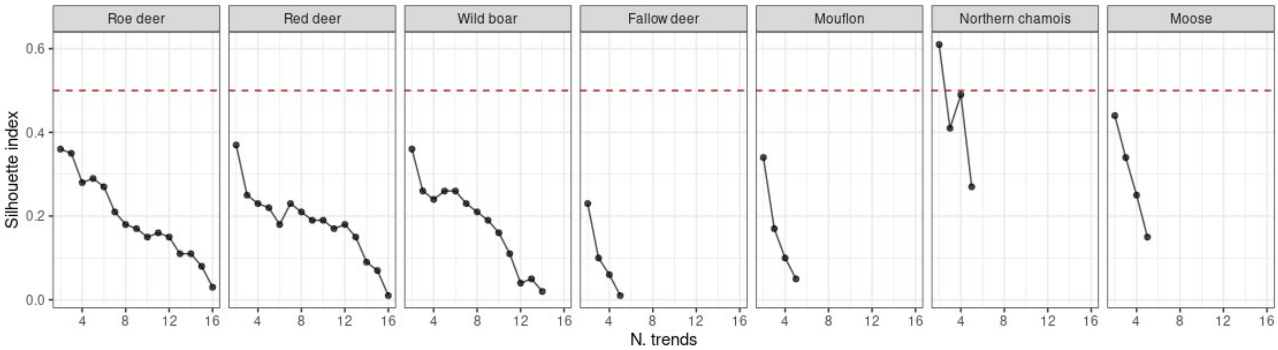

Fig. S1. Evolution of the Silhouette index for a growing number of temporal trends, in each species. Higher value of the index reflects more pronounced differences between long-term trends of cluster centroids. The horizontal line represents the cutoff value of 0.5, which is the threshold to identify clusters with different long-term trends according to Den Teuling et al. (2021).

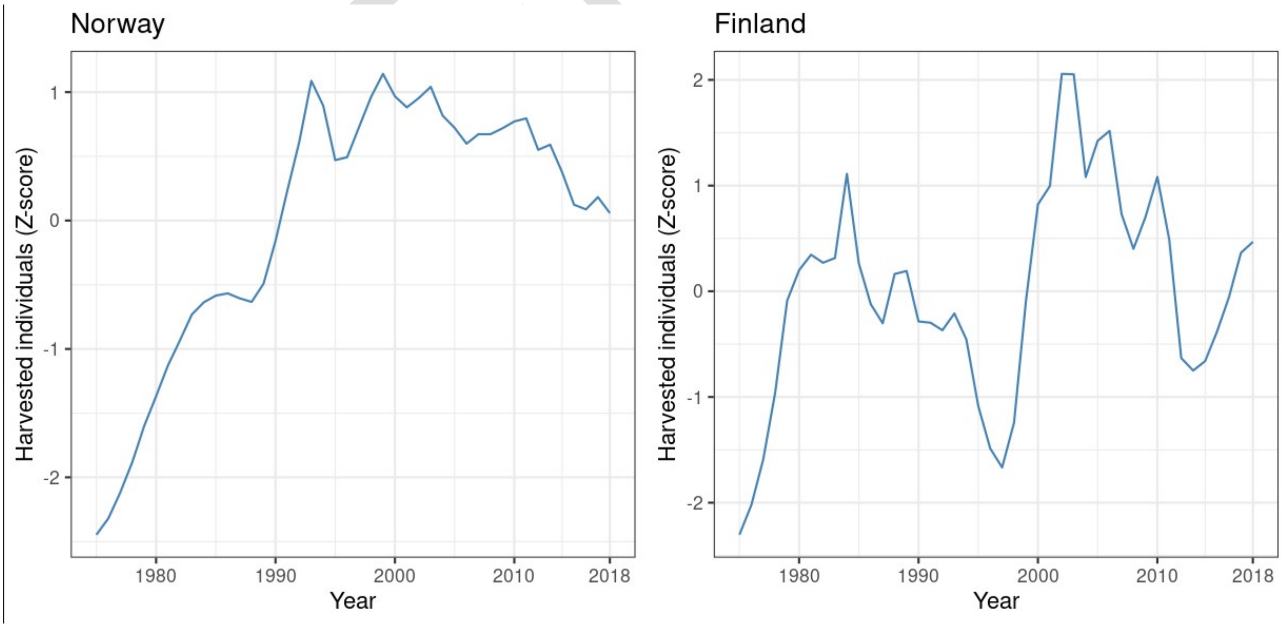

Fig. S2. Temporal trends in harvested moose in Norway and Finland. The number of harvested individuals was transformed to a Z-score and is represented in terms of standard deviations, from the mean value of each country.

Tables

Table 1. Number of harvested individuals, for each species per country, in 1975 and 2018 (- = no data or not considered; / = no presence). For fallow deer, data started in 1985. For moose in Poland, data were not considered as hunting was suspended in 2001. We also did not consider wild boar in Sweden, whose population originated from a reintroduction in the late 1970s and was not hunted for years.

Species/year	Roe deer		Red deer		Wild boar		Fallow deer		Mouflon		Northern chamois		Moose	
Country	1975	2018	1975	2018	1975	2018	1985	2018	1975	2018	1975	2018	1975	2018
Austria	208,886	284,916	44,598	54977	4,355	30,542	-	-	-	-	21,953	20,685	/	/
Croatia	4,204	16,160	1,674	3,933	2,418	29,599	-	971	-	497	12	87	/	/
Denmark	36,044	93,477	1,130	9,745	-	-	1,901	9,537	-	-	/	/	/	/
Estonia	16,390	24,146	5	2,757	4,977	4,761	-	-	-	-	/	/	5,441	7,163
Finland	-	-	-	-	/	/	-	-	-	-	/	/	12,285	58,190
France	59,426	586,464	6,709	65,275	45,830	747,367	217	1,331	191	2,784	2,815	12,407	/	/
Germany	787,806	1,206,445	44,517	77,212	120,831	599,862	24,127	65,226	1,869	7,214	2,131	4,843	/	/
Hungary	54,337	119,287	16,642	65,040	14,050	159,855	3,394	15,949	583	4,412	/	/	/	/
Italy (Trento)	2,119	4,185	9	2,287	-	-	/	/	2	270	541	2,985	/	/
Latvia	10,086	27,422	882	17,825	7,535	15,238	-	-	-	-	/	/	5,583	7,474
Lithuania	10,400	28,931	405	7,876	9,690	18,016	/	/	/	/	/	/	3,270	2,317
Luxembourg	4,493	7,016	131	426	972	7,777	-	-	2	119	/	/	/	/
Norway	5,240	29,520	3,807	43,800	/	/	/	/	/	/	/	/	10,218	30,600
Poland	47,100	210,133	10,200	95,365	40,400	266,047	-	-	-	-	-	-	-	-
Slovakia	16,557	25,856	10,993	42,937	13,696	41,723	718	14,677	461	5,544	-	-	-	-
Slovenia	19,969	30,875	1,600	6,268	1,257	8,250	70	275	50	459	1,625	2,212	/	/
Spain	-	-	11,843	144,134	19,038	373,225	-	-	-	-	/	/	/	/
Sweden	61,349	99,165	138	11,267	-	112,352	2,849	50,449	-	-	/	/	51,544	83,059
Switzerland	39,377	42,389	3,552	12,081	489	6,997	/	/	-	-	13,358	11,192	/	/

Table 2. Relative importance of the various predictors, expressed as the decrease in node impurities through the residual sum of squares. This value tells how well trees can split variables (the higher the better).

	Year	Changes in % of area covered by forests	Changes in livestock density	Changes in % of population in countryside	Changes in % of area covered by croplands	% of forests which had 20 years of age or less in 1975	Management regime
Roe deer	0.19	0.65	0.07	0.12	0.12	0.13	0.04
Red deer	0.58	0.16	0.03	0.05	0.06	0.01	0.01
Wild boar	0.45	0.06	0.02	0.01	0.15	0.01	0.01
Fallow deer	0.22	0.03	0.01	0.33	0.08	0.01	0.01
Mouflon	0.14	0.26	0.01	0.04	0.17	0.00	0.00