

Proposta de resolució de conflicte entre l'humà i el senglar a Collserola

Grup per a la conservació de la biodiversitat de Collserola



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Des de LIBERA! i DEPANA, volen proposar un nou enfocament pel que fa a la resolució del conflicte existent entre l'ésser humà i el porc senglar.

Fins al moment, després de més de 24 temporades de caça, com a mínim, s'ha tractat de controlar el creixement de la població amb la finalitat d'intentar solucionar el conflicte, reduint-la mitjançant una taxa de mortalitat provocada (no natural) i que ha comptat com a principal agent, pel que fa dur a terme l'estratègia actual, amb la figura del caçador.

Ha sigut el modus operandi a Catalunya i Collserola, en aquest sentit, no ha estat una excepció. 24 anys durant els quals la població, en termes generals, ha estat creixent. Es un fet.

La nostra proposta no té per finalitat controlar la població de senglars al parc de Collserola, té la finalitat de regular la població. Com? Explicarem el perquè i el com.

En definitiva, és un canvi de paradigma: tractar de regular la població, no mitjançant del que alguna veu científica anomena com erradicació total, sinó a través del que la mateixa veu anomena com l'erradicació funcional.

Per aconseguir dur a terme la regulació (incidint en la natalitat) i no el control (mitjançant la mortalitat), se'ns fa indispensable establir inicialment tres raons pel que fa a la necessitat de prohibició de la caça a Collserola.

Primera raó: perquè representa un 10% dels porcs senglars sacrificats els últims anys per temporada; per tant, l'impacte pel simple fet de deixar-la de practicar dintre del parc, en principi, no tindria gaire repercussió:

Any	Total de senglars capturats	Animals sacrificats per batuda	% que representa la mortalitat via batuda
2004	128	61	47,65
2005	129	26	20,15
2006	136	26	19,11
2007	173	77	44,50
2008	171	29	16,95
2009	168	50	29,76
2010	222	72	32,43
2011	269	84	31,22
2012	462	109	23,59
2013	448	114	25,44
2014	351	75	21,36
2015	692	123	17,77
2016	610	90	14,75
2017	489	83	16,97
2018	474	50	10,54
2019	746	75	10,05
2020	495	62	12,52
2021	853	87	10,19
2022	965	99	10,25

Taula 1: històric del tant per cent que representa la caça a Collserola

Segona raó, cal vetllar per la longevitat de la població: desestimant la mortalitat provocada, ja que evita que el porc senglar pugui allargar la seva vida, un aspecte clau per regular la població, perquè la presa més fàcil d'abatre, per un caçador, és la de major mida i que també acostuma a ser

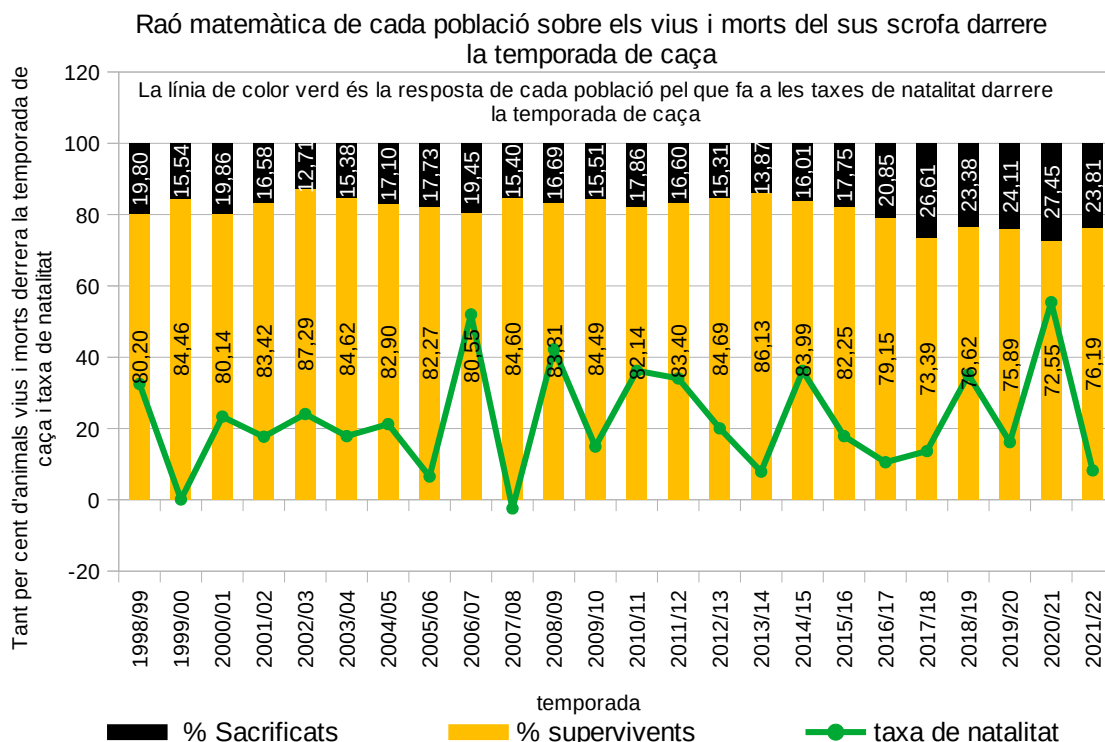
la que major longevitat té (acumulada). Hem observat, d'aquí que sigui un aspecte clau, que les poblacions que acumulen longevitat es reproduïxen menys (tenen taxes de natalitat més baixes).

Com les paraules sempre han d'anar acompanyades amb fets perquè siguin creïbles, la següent gràfica, ens mostrarà **els fets** que s'han donat en els últims anys a Catalunya.

El que s'ha fet, són raons matemàtiques per saber quin percentatge representen, de cada temporada, els individus capturats i/o sacrificats i quin percentatge representen els que han sobreviscut a la caça de la població estimada inicial a Catalunya.

La línia de color verd que es veurà a la gràfica, és la taxa de natalitat de cada població (no està expressada en tant per cent). Per evitar crítiques com, per exemple, que els resultats venen de poblacions estimades i que la correlació existent entre la natalitat i mortalitat podria estar afectada per la inexactitud de les dades publicades, que sempre tenen un +/- d'un valor x (essent x el nombre de senglers) i que en aquest cas no hem sabut trobar a la pàgina web www.gencat.cat, de la qual obtenim les dades de densitat de cada població. En aquesta ocasió, s'ha fet el càlcul de la taxa de natalitat bruta tenint en compte el total de la població estimada inicial.

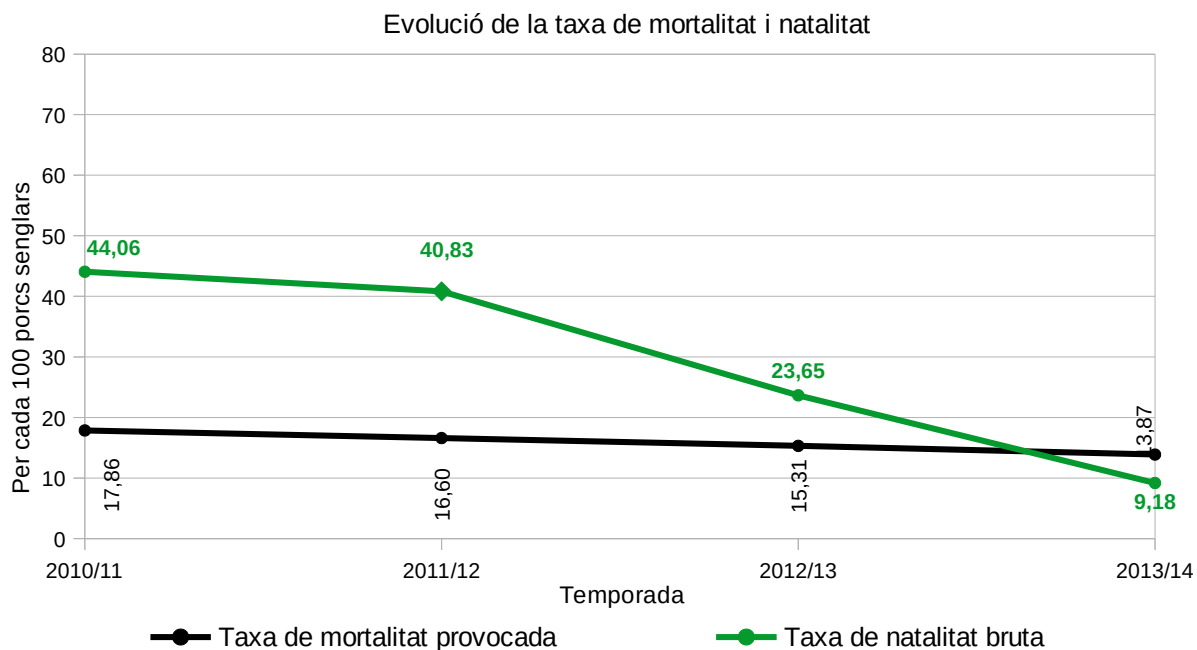
Això vol dir que la taxa de natalitat, s'ha calculat amb els animals sacrificats inclosos en el denominador (cosa que és molt improbable que afecti perquè els morts, almenys les femelles, i que són les que realment tenen un impacte directe sobre aquest marcador, essent animals sacrificats, la seva descendència és zero). D'aquesta manera, tenim la precaució d'aproximar-nos amb un possible error, sí, però que seria pràcticament inexistent i sempre dintre del valor aproximat des de la part baixa del marcador esmentat.



Gràfica 1: relació entre les poblacions supervivents i capturades/sacrificades amb la població estimada de la qual formaven part i evolució de les seves taxes de natalitat

En la majoria dels casos, de fet 20 de 24, hi ha una correlació entre la taxa de mortalitat provocada i la taxa de natalitat bruta si construïm el gràfic tenint en compte les relacions de la població sacrificada i supervivent en % conjuntament amb l'històric de les respectives taxes de natalitat. I que quan aquestes raons matemàtiques tenen resultats molt similars, el que vol dir que l'esperança de vida es manté sobre el senglar, hem observat, respon disminuint la taxa de natalitat; com són els casos fàcilment destacables de les temporades: 2004/05 i 2005/06 amb un 82% de població en ambdós casos; 2008/09 i 2009/10 amb un aproximat 84%; 2018/19 i 2019/20 amb un gairebé 76%. Però si es consulta el document titulat *EL PORC SENGLAR A CATALUNYA, OBSERVACIONS D'ESTUDIS CIENTÍFICS I ANÀLISI DE DADES*, elaborat per LIBERA! i lliurat a l'Administració, demostra de diferents maneres aquesta correlació, donant sentit, fins i tot, a la majoria dels pocs anys que no es compleix, explicant el més que possible per què. Amb altres explicacions que desestimen la caça i que si són d'interès figuren en la primera part del document.

És evident que una població que ha sobreviscut en major número, conté individus amb major longevitat. Com a exemple molt clar i exhaustiu ens agradaria mostrar el període 2010 – 2014 al qual la taxa de mortalitat provocada va anar disminuint ininterrompudament, fet que va vinculat directament a la longevitat dels individus de les poblacions que les componen, atès que la mort a mans d'escopetes és la causa principal de mortalitat actualment sobre el *Sus scrofa*:



Gràfica 2: evolució de la taxa de mortalitat i taxa de natalitat període 2010 – 2014

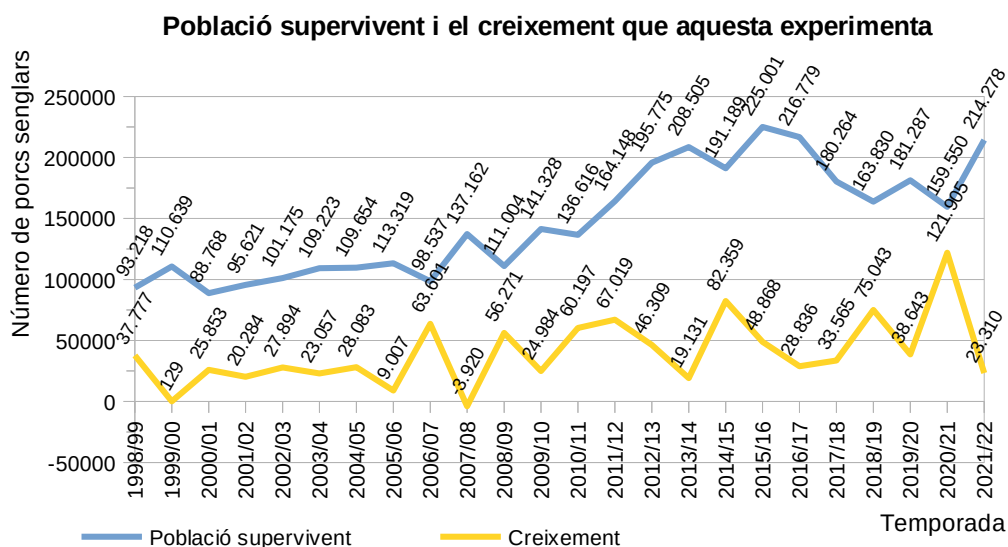
Temporada	2010/11	2011/12	2012/13	2013/14
Població estimada	166.612	196.813	231.168	242.084
Població supervivent	136.616	164.148	195.775	208.585
Descendència	60.197	67.019	46.309	19.131

taula 1: dades de les poblacions estimades inicialment, poblacions supervivents a la temporada de caça i la seva descendència.

Aquesta gràfica és un cas, i no l'únic, que fa evident la correlació entre mortalitat i natalitat (menor caça, menor reproducció). Per una altra banda, també es pot veure que poblacions més grans numèricament, tenen una descendència menor, tot i que potencialment tenen major capacitat (són més nombroses). La temporada 2011/12 té una descendència més nombrosa que l'anterior, però té un potencial molt major (és numèricament superior) i això fa que la seva taxa de natalitat, realment, sigui menor (quasi 4 punts de fet).

S'ha inclòs la gràfica 1, perquè es pugui observar que durant el període 2010/11 – 2013/14 el tant per cent dels vius cada vegada era més gran: 82, 83, 84 i 86% del total de les seves respectives poblacions; i que el tant per cent dels morts del total de la població estimada inicialment, en contrapartida, cada vegada era menor: 17, 16, 15 i 13% de la població. Un bon indicador de què la població estava envellint perquè estava augmentant numèricament, però les taxes de natalitat, any rere any, eren menors.

Perquè s'entengui millor la correlació compartirem un altre gràfic que mostra les poblacions supervivents a la caça (línia blava) i la seva descendència (línia groga):

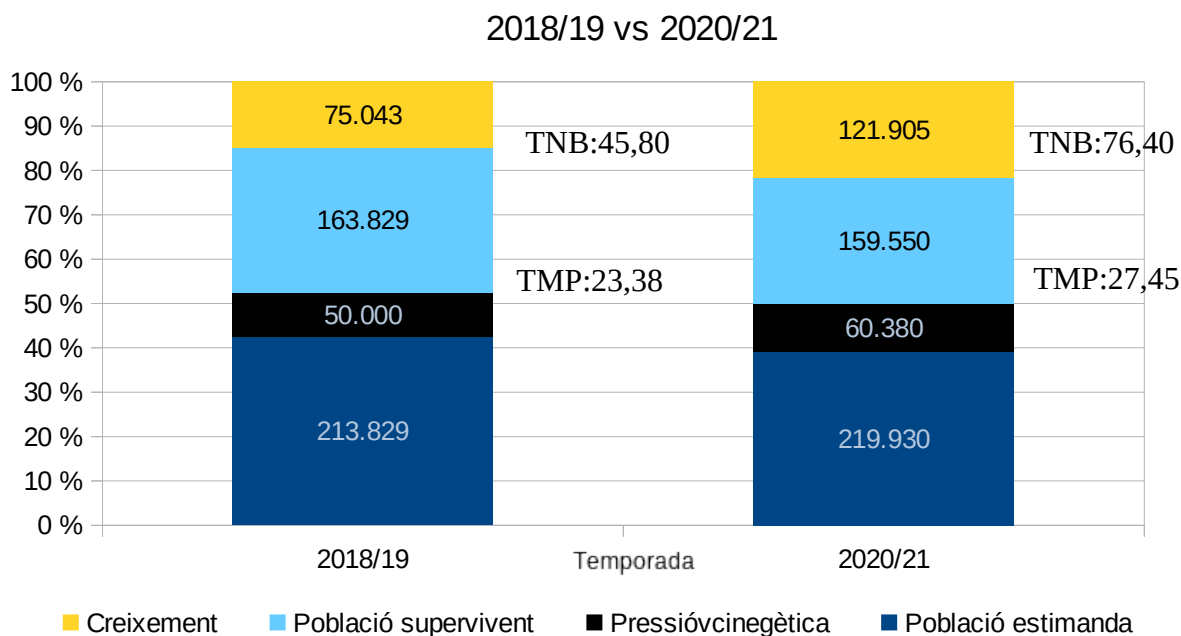


Gràfica 3: evolucions de les poblacions supervivents i creixement anual del total de la població supervivent que, conjuntament, formaran la temporada següent. Període 2016/17 -2019/20

A la gràfica 3 es veu com petites poblacions supervivents tenen major descendència que d'altres poblacions supervivents a la temporada de caça (línia blava), com són la temporada 2006/07,

2009/10 o 2014/15 tenen grans descendències (línia groga); i al contrari, poblacions més nombroses com les 2015/16, 2016/17 o 2017/18 tenint un gran potencial de reproducció es permeten tenir unes descendències molt menors que d'altres que són menys nombroses. Les temporades 2020/21 i 2021/22 són un bon exemple de les dues situacions clarament contraposades.

Ens agradaria exposar un cas de manera més il·lustrativa focalitzant la situació amb els casos de les temporades 2018/19 i 2020/21:



Gràfica 4: comparació de les temporades 2002/03 i 2008/09

Mapes de pluviometria¹ temporades 2018/19 i 2020/21:

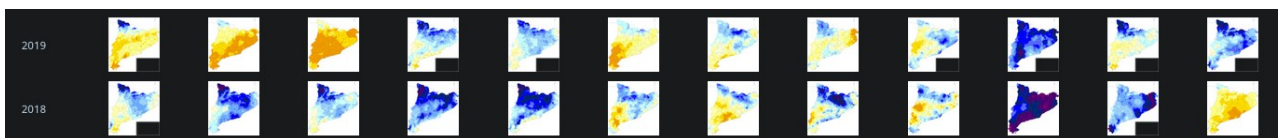


Figura 1: pluviometria temporada 2018/19



Figura 2: pluviometria temporada 2020/21

Cal dir que l'anomalia climàtica des de la temporada 2015/16 en endavant és pràcticament calcada per això no es considera d'interès i que de les dues temporades que es comparen, la que pitjor pluviometria té és la que presenta la taxa de natalitat més gran: la temporada 2020/21. És a dir, el porc senglar no vincula especialment les taxes de natalitat als condicionants climàtics.

¹ Font: [Meteocat](#), Generalitat de Catalunya. Consultada el 7/11/2023.

Amb poblacions supervivents molt similars i pitjors condicions pluviomètriques presentades la temporada 2020/21, té una natalitat superior, en 20 animals més per cada 100 individus amb la comparada.

La diferència radica en la diferent taxa de mortalitat provocada, que, com ja hem dit, actua sobre la població de senglar que és més voluminosa i que acostuma a ser la que major longevitat acumula. Així, la temporada 2020/21, amb una població supervivent similar a la 2018/19, és potencialment més jove perquè la de taxa de mortalitat provocada és més elevada (27 morts per cada 100 individus la temporada 20/21 i 23 la 18/19) i, en conseqüència, té una resposta molt superior pel que fa a la natalitat. De fet, si es comproven les dades de la gràfica 1 el tant per cent de la població viva de la temporada amb menor resposta, va ser la que va respondre amb una taxa de natalitat més baixa: 76% (20/21) i 72% (18/19) i taxes de natalitat de 76 (20/21) i 45 (18/19) nou-nascuts per cada 100 individus.

A la pàgina web de LIBERA!, es pot descarregar un document que analitza la situació àmpliament:

https://liberaong.org/files/El_porc_senglar_a_Catalunya.pdf

Hi ha més comparatives similars que, per no allargar més el document de proposta, es comparteixen amb el següent enllaç si són d'interès:

<https://liberaong.org/files/Lupa.pdf>

L'anàlisi dut a terme per LIBERA té com a principal motivació, la demostració per part de la Caroline Toïgo² i el seu equip, del que venim parlant durant aquesta anomenada segona raó. Vinculant, l'estudi científic, la longevitat a la natalitat: les femelles dediquen els recursos a viure més a canvi de reproduir-se menys. Assenyalen.

La clau és observar la Gràfica 1 i verificar que quan es dona el cas d'una gran taxa de natalitat, el tant per cent dels vius és coincident, molt majoritàriament, en una quantitat menor que l'anterior o posterior (és important el context i la temporada anterior o posterior, són una bona referència per contextualitzar). Fet que es vincula a una pèrdua de longevitat, perquè, tornem a repetir, els primers a ser abatuts són els de major mida i, per tant, edat. O com a mínim la matriarca del grup, el que ve a ser el mateix.

Per a més detalls consultar l'anàlisi al qual hem fet referència unes línies enrere i l'estudi et. al., Toïgo 2008.

Tercera raó: la caça provoca el desplaçament del senglar, el que eleva el risc de possible arribada fins a la perifèria d'espais urbans, buscant protecció fugint, precisament, de la mortalitat provocada per part de l'humà al bosc.

Un estudi, gens sospitós pel que fa a tenir cap afinitat o vinculació a les entitats que presentem la proposta present, ja que estudia quina és la millor estratègia per caçar al porc senglar, analitza el comportament de l'animal segons els diferents escenaris relatius als múltiples espais que habita. Però de retruc, demostra, científicament, que el senglar condiciona la seva mobilitat a la pressió cinegètica.

2 https://www.researchgate.net/publication/229519856_Disentangling_Natural_From_Hunting_Mortality_in_an_Intensively_Hunted_Wild_Boar_Population

Aquest estudi³ científic, conjuntament amb un segon dut a terme a Itàlia per un altre equip de científics els que, igualment, són independents entre si, demostren que la caça, novament, provoca el desplaçament del senglar. Al punt, que un dels dos recomana com la millor estratègia de caça implica fer-ho després de la recollida de la collita, perquè les femelles afectades per la pressió cinegètica passen a visitar més sovint aquests camps una vegada han sigut desplaçades per les caceres.

A continuació compartirem algunes figures d'aquests estudis que parlen per si soles. Per part del primer⁴ dels dos estudis, compartim unes figures (gràfics) que fa evident la demostració de què el senglar augmenta o disminueix la intensitat del seu moviment en funció de l'escenari de caça.

La Figura 3 relaciona els tres escenaris: abans, durant i després de la cacera amb el tipus d'àrea que habita l'animal en qüestió i com es mou o es comporta en funció de la mateixa:

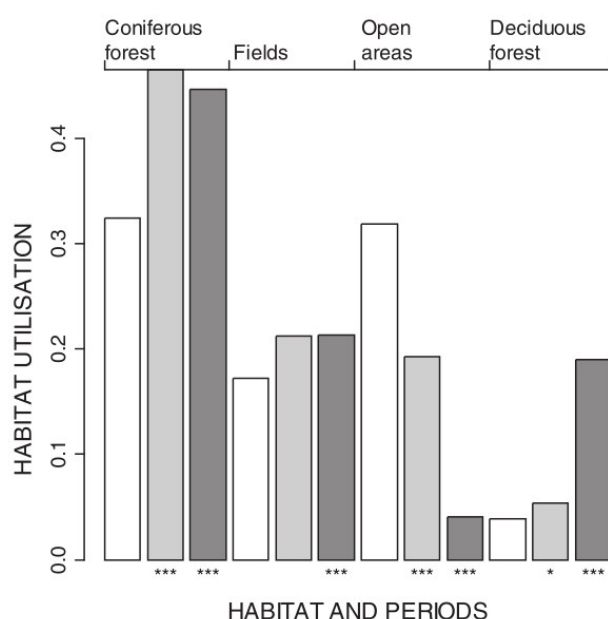


Figure 3⁵. Efectes dels 6 escenaris de caça sobre l'ús de l'habitat. Les barres mostren els efectes de la caça sobre cada model d'habitat triat (probabilitat), abans de la caça (barra en blanc), durant (barra rosa), i després (barra fosca). Els asteriscs indiquen si hi ha una diferència comparada amb el període abans de la cacera (*=P<0.05, **=P<0.01, ***=P<0.001 basat sobre contrastos d'identitat).

Els boscos de coníferes són els que major moviment registre. Cal destacar el comportament a les àrees obertes (alt risc de caça), que darrere de l'activitat cinegètica redueix significativament el seu moviment: alt risc de caça, menor moviment.

Però en àrees forestals, formades per coníferes o quercus, gairebé mantenen l'activitat o l'augmenten (se senten més segurs que no pas a les àrees obertes). Menor risc de caça, major moviment o activitat.

3 [\(PDF\) Do intensive drive hunts affect wild boar \(Sus scrofa\) spatial behaviour in Italy? Some evidences and management implications](https://www.researchgate.net/publication/328111111)

4 [Effects of hunting on wild boar Sus scrofa behaviour](https://www.researchgate.net/publication/328111111)

5 Font de la figura i text que la descriu: <https://bioone.org/accountAjax/Download?downloadType=Journal%20Article&urlId=10.2981%2F12-027&isResultClick=True>

Pel que fa als aguats nocturns l'estudi apunta:

La caça per mitjà d'aguats es duu a terme sovint després de la posta del sol, i com el senglar no percep als caçadors aguats com un risc immediat, reacciona als caçadors aguats reduint la seva activitat per a reduir el risc de detecció. Les nostres dades mostren clarament que els senglars es fixen en els caçadors quan continuen caçant, però com els animals no s'aixequen (no es mouen o no obertament), romanen amagats.

Aquest estudi titulat *Effects of hunting on wild boar Sus scrofa behaviour*, demostra que la caça té un impacte significatiu sobre el comportament del porc senglar fins al punt de què el senglar abandoni el territori que habita regularment.

I parlant del trasllat del senglar quan abandona l'espai que habita regularment, hem de parlar del segon estudi que presentem, que demostra, científicament, que a conseqüència de les caceres alguns grups familiars de porcs senglars s'havien trobat fins a 10 km dels punts de captura anteriors (per col·locar-los dispositius de seguiment per ràdio telemetria i, així, identificar-los). Les dades de ràdio telemetria dels autors, al contrari del que apuntaven altres investigacions, indiquen que la caça intensiva els feia abandonar el territori en el qual vivien habitualment, de forma definitiva.

Les següents figures, extretes del mateix estudi, ho escenifiquen i expliquen gràficament a peu de la imatge:

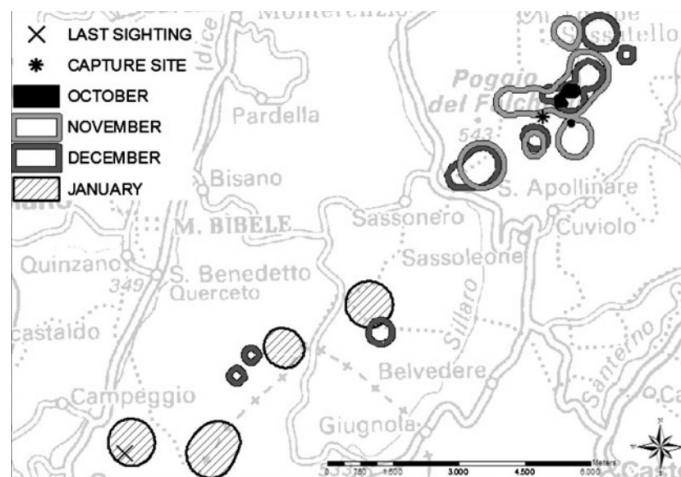


Figura 4⁶: Canvis mensuals en la grandària de l'àrea de descans i desplaçament geogràfic observats en un grup familiar (compost per tres femelles i almenys cinc garrins) que va estar subjecte a una intensa pressió cinegètica. L'asterisc indica el lloc de captura. En finalitzar la temporada de caça només van sobreviure una femella i un mascle juvenil, en la zona indicada amb la "X".

No cal afegir més pel que fa a la descripció de la figura. La mateixa descripció és prou explicativa.

6 Font de la figura i la seva descripció:

https://www.researchgate.net/publication/225749540_Do_intensive_drive_hunts_affect_wild_boar_Sus_scrofa_spatial_behaviour_in_Italy_Some_evidences_and_management_implications

La Figura 5, relaciona la diferència dels moviments del senglar abans, durant i després del període de caça pel que fa a l'espècie i que demostra plena consonància amb el primer dels dos estudis.

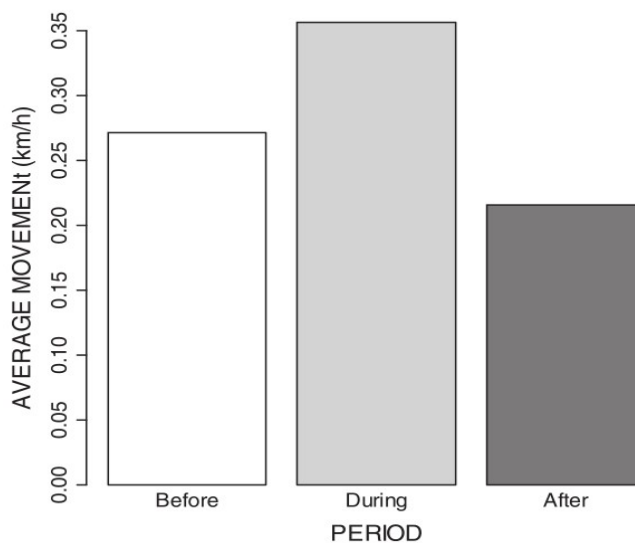


Figura 5'. Efecte de les caceres que van provocar que sis senglars abandonessin el seu territori. Durant el trasllat, el senglar es va moure més que abans de la caça, i a la zona de refugi el senglar es va moure menys ($P < 0,001$ segons els contrastos d'identitat).

Fins aquí hem demostrat el perquè de la primera premissa de la nostra proposta:

- La caça és una activitat desestimable pel que representa: el 10%
- La caça disminueix la longevitat de l'espècie i que quan aquesta es dona fa que l'espècie no necessiti ser més prolífica
- La caça contribueix al desplaçament de les zones a les quals s'estableix

Per tal d'evitar que el porc senglar deixi de considerar el cor del parc de Collserola com un entorn hostil, cal abandonar dins del mateix l'activitat que els hi provoca una mortalitat no natural: la caça. Però, en contrapartida, pel que fa als entorns urbans s'ha d'aconseguir que una fita important: limitar els recursos com el menjar i l'aigua.

7 Font de la figura i text que la descriu: <https://bioone.org/accountAjax/Download?downloadType=Journal%20Article&urlId=10.2981%2F12-027&isResultClick=True>

Amb les següents mesures:

- Els recursos de les colònies de gats, únicament les ubicades a les perifèries urbanes, han d'estar protegits en casetes, de manera que només fossin accessibles pels fèlids, instal·lant a l'interior dispensador d'aigua i pinso, amb una entrada i sortida i amb una mida feta de tal manera que només els fèlids puguin entrar:



Figura 6: casetes amb dispensador d'aigua i pinso per colònies felines



Figura 7: dispensador d'aigua i pinso per colònies felines

- Les rotondes i parcs, únicament les i els ubicats a les perifèries urbanes, siguin superfícies sense recs d'aigua excessius, ja que sota l'herba regada apareix tot un ecosistema de larves, que són font de proteïnes que el senglar, amb característiques que el converteixen en un hozador per naturalesa, sap trobar amb facilitat. Pel senglar són llaminadures.
- Contenedors i papereres de difícil accés per al senglar.
- Una campanya coordinada entre els ajuntaments i entitats públiques implicades, d'educació dirigida a les persones que donen menjar i veure als senglars.
- Conreus amb tanques adequades i amb un manteniment regular: ben esbrossades i amb un voltatge adequat.

I finalment, el més important i que fa possible que parlem de **regular** (per la via de la **natalitat**) en comptes de **controlar** (per via de la **mortalitat**): el projecte exitós per part de la UAB dirigit i coordinat pel degà **Manuel López Béjar**. Similar al sistema que regula les colònies felines

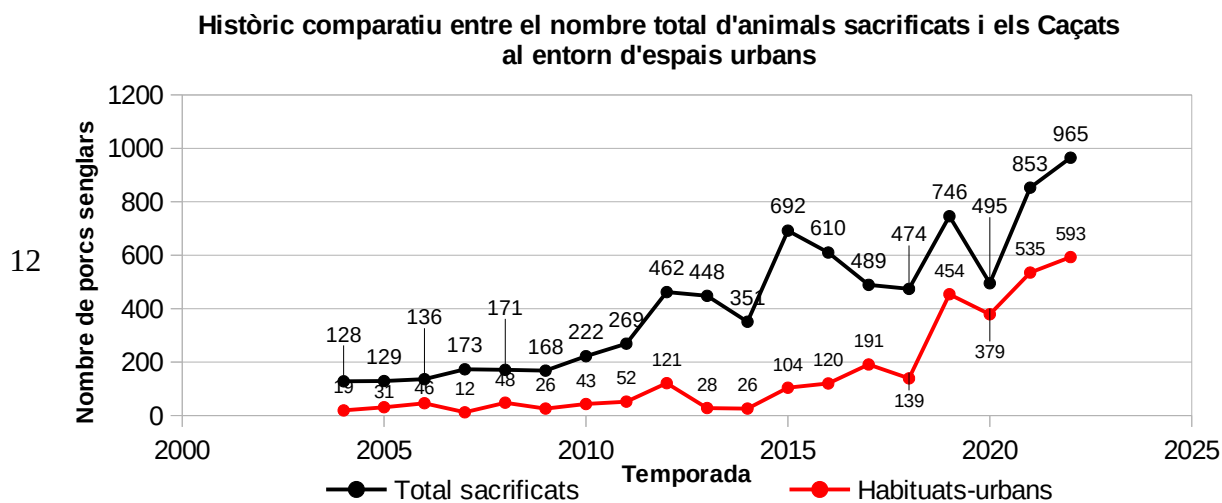
anomenat com a CER (Captura, Esterilització i Retorn). Substituint l'esterilització per [immunoconcepció](#)⁸. Que consisteix en una vacuna (Gonacon) injectable en el moment de captura i posterior alliberament i que esterilitza a l'animal, que com més jove sigui, millors resultats s'obté. D'eficàcia constatada!

És la millor manera que tenim, gràcies a la ciència i al coneixement, de regular artificialment les natalitats, tal com farien els depredadors⁹. Perquè, com ja s'ha apuntat, els animals volen obtenir l'energia necessària per subsistir, invertint, obligatòriament, una que sigui menor: el que descarta els senglars amb una mida i pes considerables (els més longeus).

D'aquesta manera s'aconsegueixen individus grans, sans i pacífics que es poden alliberar amb la seguretat de regular la població tenint la natalitat controlada.

De retruc, **dir baixes taxes de natalitat equival a menors atacs de senglars a humans**, ja que la majoria dels atacs són de mares acompanyades de cries. Tots els animals protegeixen la seva descendència, inclosos els ungulats, davant del que els hi sembla una amenaça, el senglar no és una excepció.

Per una altra banda, tot i que és la manera menys eficaç de caçar, no és el cas que ens ocupa per les característiques del parc de Collserola: atrapar als senglars amb gàbies o dards somnífers (el que també facilitaria la [immunoconcepció](#)). Amb el que no representaria cap canvi pel que fa a la captura principal:



Gràfica 6: evolució del total de sacrificats i sacrificats habituals-urbans

El caràcter regulador de l'estratègia de gestió proposada, que, al cap i a la fi, ara sí equival a substituir en gran part la funció biològica dels grans depredadors, que per les mateixes

8 <https://www.uab.cat/web/sala-de-premsa/detall-noticia/el-tractament-immunoconcepciu-en-senglars-urbans-i-periurbans-eficac-especialment-en-exemplars-joves-1345829508832.html?detid=1345852250380>

9 Diferents estudis vinculen la regulació dels ecosistemes a la **presència** dels grans depredadors, no a la mortalitat que duen a terme: depredar 70.000 senglars en una sola temporada representaria una quantitat de llops insostenible pel territori català.

característiques del parc, resulta inviable, permet, a mitjà termini, decidir el nombre d'individus que formaria la població de seglars adequada per al parc de Collserola, aplicant la vacuna Gonacon segons convingui: decidint aproximadament la taxa de natalitat convenient per un espai que no té corredors ecològics el que fa necessària la regulació per acció humana.

Finalment, la vacuna Gonacon, permet tenir una població longeva (i establerta a la perifèria de les ciutats) que formen un grup de contenció pel que fa a la població que viu al PN de la Serra de Collserola, ja que són territorials. I una vegada enclavats a un territori, els propis estudis que aportem, parlen de la dificultat en que marxin dels espais a on habiten

El primer estudi que relaciona la caça amb el desplaçament del sus scrofa, de fet, planteja dubtes pel que fa a les femelles desplaçades i el fet de que acabin voltant pels correus. Els autors de l'estudi, no saben del cert si es produeix perquè allà troben menjar o simplement entren en conflicte amb els seglars que regularment habiten el territori a on han anat a parar i acaben a terres de conreu (però al costat d'un depredador, que és l'home).

D'aquí la importància de tenir uns seglars amb poca descendència, es a dir, amb poca agressivitat perquè no l'han de defensar i amb una certa longevitat que els fa adequats per tenir una forta barrera de contenció al voltant del parc: una barrera natural entre les diferents poblacions humanes i el PN de la serra de Collserola.

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Disentangling Natural From Hunting Mortality in an Intensively Hunted Wild Boar Population

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ABSTRACT We assessed age-specific natural mortality (i.e., excluding hunting mortality) and hunting mortality of 1,175 male and 1,076 female wild boar (*Sus scrofa*) from Châteauvillain-Arc en Barrois (eastern France), using a 22-year dataset (1982–2004) and mark–recapture–recovery methods. Overall yearly mortality was >50% for all sex and age-classes. Low survival was mostly due to high hunting mortality; a wild boar had a >40% of chance of being harvested annually, and this risk was as high as 70% for adult males. Natural mortality rates of wild boar were similar for males and females (approx. 0.15). These rates were comparable to rates typical of male ungulates but high for female ungulates. Wild boar survival did not vary across sex and age-classes. Despite high hunting mortality, we did not detect evidence of compensatory mortality. Whereas natural mortality for males was constant over time, female mortality varied annually, independent of fluctuations in mast availability. Female wild boar survival patterns differed from those reported in other ungulates, with high and variable natural mortality. In other ungulates, natural mortality is typically low and stable across a wide range of environmental conditions. These differences may partly reflect high litter sizes for wild boar, which carries high energetic costs. High hunting mortality may induce a high investment of females in reproduction early in life, at the detriment to survival. Despite high hunting mortality, the study population increased. Effective population control of wild boar should target a high harvest rate of piglets and reproductive females. (JOURNAL OF WILDLIFE MANAGEMENT 72(7):1532–1539; 2008)

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KEY WORDS capture–mark–recapture and recovery, compensatory mortality, deciduous forest, France, hunting mortality, life-history tactic, natural mortality, *Sus scrofa*, wild boar.

Wild boar (*Sus scrofa*) are widespread in Western Europe and have been increasing in numbers for the last 3 decades, leading to increased damage to crops and forests (in Italy, Boitani et al. 1995; in Switzerland, Neet 1995; see Schley and Roper 2003 for a review in Western Europe; in France, Klein et al. 2004; in Austria, Bieber and Ruf 2005). In France the numbers of wild boar harvested annually increased 8-fold between 1974 and 2001, and wild boar currently occur throughout the country. Concurrently, damage caused to agriculture has increased, and costs of compensation to farmers have become very high (17,000,000 Euro in 2001, Klein et al. 2004).

Despite economic costs and other management problems caused by wild boar, the species remains poorly known compared to other temperate zone ungulates. Although reproductive traits such as age at primiparity, proportion of breeding females, and litter size have been well-documented (Gaillard et al. 1993, Neet 1995, Carranza 1996, Fernández-Llario and Carranza 2000, Nahlik and Sandor 2003), few studies have provided reliable estimates of age-specific survival for wild boar.

The dynamics of most European wild boar populations are strongly influenced by harvest. Disentangling natural from hunting mortality is important to understanding the dynamics of exploited populations. The functional relationship between hunting mortality and natural mortality may

range from additive to compensatory effects (Anderson and Burnham 1976, Burnham and Anderson 1984). Degrees of partial compensation can also occur. Lebreton (2005) suggested that compensation between hunting and natural mortality is expected to be very low in long-lived vertebrates such as wild boar.

In long-lived vertebrates, adult female survival consistently has the highest demographic elasticity (i.e., the highest potential effect for changing population growth rate). As a consequence, in large herbivores, annual adult survival of females is usually high (>90%) and robust to environmental variation, whereas juvenile survival is low (<70%) and highly variable over time and among populations (see Gaillard et al. 1998, 2000 for reviews). Wild boar are unusually productive for their body size, with a mean litter size as high as 5 (e.g., Boitani et al. 1995, Nahlik and Sandor 2003, Servanty et al. 2007). High productivity could lead to lower and more variable prime-age survival than usually reported in other ungulates, because of the high energetic costs of producing larger litters.

Our goal was to assess the relative contribution of age- and sex-specific hunting and natural mortality in an intensively monitored wild boar population in eastern France using capture–mark–recapture–recovery (CMRR) methods, which would allow us to combine live recaptures and hunting recoveries (see Schaub and Pradel 2004 for a similar approach) into a unified analysis. Because of the hunting

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regulations in our study area, we expected hunting mortality would be higher for males and young females than for adult females. Because of large litter sizes and current theory on life-history strategies of large vertebrates (Stearns 1992, Gaillard and Yoccoz 2003), we expected natural mortality of adult wild boar females to be high and more variable compared to females of other ungulates. Based on Lebreton (2005), we hypothesized little compensation between hunting and natural mortality.

STUDY AREA

We conducted our study in northeastern France, in the 11,000-ha forest of Châteauvillain-Arc-en-Barrois (48°02N, 4°56E). The territory was administratively divided into 2 parts: a core area that covered 8,500 ha of national forest and a surrounding area of 2,500 ha of private or communal forests. Dominant tree species were oak (*Quercus petraea*), beechnut (*Fagus sylvatica*), and hornbeam (*Carpinus betulus*). The climate was intermediate between continental (typical of eastern France's Alsace region), and oceanic (characteristic of the Parisian Basin). During the last 20 years (1983–2003), mean annual rainfall was 74.4 ± 8.6 mm, and average monthly temperatures ranged from $2.34 \pm 2.06^\circ\text{C}$ in January to $18.6 \pm 1.58^\circ\text{C}$ in August (Météo-France), which was within the norm for this climate.

Wild boar had no natural predators in the study area, except red fox (*Vulpes vulpes*) on newborns. Natural causes of mortality were mainly diseases, starvation, injuries and exhaustion linked to the rut for males, parturition complications for females, and boar–vehicle collisions.

METHODS

Since 1982, we monitored the study population by CMRR methods. Captures occurred during March to September each year in the national part of the forest using corral traps (Vassant and Brandt 1995, Sweitzer et al. 1997), box traps (Jullien et al. 1988, Choquenot et al. 1993), piglet traps (Jullien et al. 1988), and falling nets (Jullien et al. 1988); all methods were approved by the French Environment Ministry (articles L.424–11, R.411–14, and R.422–87 of the French code of environment). We marked each trapped animal with ear-tags allowing individual identification (combination of colors and no.). We determined the age of each individual captured on the basis of Matschke's (1967) procedure, validated and adjusted to our study area by Baubet et al. (1994). We distinguished 3 age-classes: piglets (aged 1–6 months at capture), yearlings (aged 13–18 months at capture) and adults (>18 months at capture). The youngest animals trapped were 1-month-olds, having survived the critical neonatal period.

Wild boar were harvested by ambush shooters each year between October and February. The number of wild boar harvested annually over the entire study area steadily increased from 200 in 1984 to 1,000 in 2004. Wild boar are sexually dimorphic; mean weights for adult sows were 72 kg (± 11 kg, $n = 379$) and for adult males were 102 kg (± 16 kg, $n = 176$) in our population (E. Baubet, Office National

de la Chasse et de la Faune Sauvage, unpublished data). Based on body size and social behavior (F live in matriarchal groups, whereas ad M are most often solitary; Kaminski et al. 2005), hunters can often target males. When harvesting larger groups hunters often avoided shooting individuals >60 kg to protect reproductive sows. Hunters randomly harvested marked and unmarked wild boar. Hunter bias relative to marked boar was unlikely because ear-tags were small, almost totally hidden by the deep autumn hair, and difficult to see on live animals.

In the National part of the forest, cooperation between hunters and the Office National de la Chasse et de la Faune Sauvage (ONCFS; the French Wildlife Agency) ensured that all wild boar harvested were checked by a government agent (from the ONCFS). We assumed that all marked animals harvested were recovered. Hunters in the surrounding areas received information about our study. However, wild boar harvested from these areas were not checked by a government agent, so there may have been some unreported harvest of marked animals. We assumed that the recovery rate was 0.9 based on field data and preliminary analysis of CMRR models.

The primary data were capture–recapture–recovery histories of marked animals. We analyzed these data using multistate models recently implemented in MSURGE 7 (Choquet et al. 2005b) to estimate overall mortality rate, mortality rate due to hunting, and natural mortality rate (i.e., excluding hunting mortality). To separate natural mortality from hunting mortality, we used a 3-state model: 1) the animal is alive, 2) the animal is harvested, and 3) the animal is dead from natural causes. The third state was not observable (see Gimenez et al. 2003 for a similar approach).

We were principally interested in capture (P) and transition (Ψ) probabilities. Survival probabilities were constrained to 1.0 for this analysis. Recapture probabilities depended on the arrival state, with $P(1)$ the probability of being captured in state 1 (i.e., alive in a trap), $P(2)$ the probability of being captured in state 2 (i.e., recovered when hunted, a probability we fixed at 0.9), and $P(3)$ the probability of being captured in the unobservable state 3 (i.e., naturally dead, a probability we fixed to 0.0).

Transition probabilities depended on departure and arrival states, with $\Psi_{1 \rightarrow 1} = P(\text{alive}) = \text{overall survival rate} = \text{OS}$; $\Psi_{1 \rightarrow 2} = P(\text{harvested}) = \text{hunting mortality rate} = \text{HM}$; and $\Psi_{1 \rightarrow 3} = P(\text{dead from natural causes}) = \text{natural mortality rate} = \text{NM}$. We defined the survival–mortality parameters as: $\text{HM} + \text{NM} = P(\text{dying}) = \text{overall mortality rate} = \text{OM}$. In addition, we invoked the following constraints: 1) The overall survival rate should be the complement of the overall mortality rate, so the models included the constraint $\text{OS} + \text{HM} + \text{NM} = 1$, and $\text{OS} = 1 - \text{OM}$. 2) Once a wild boar was dead, it could not transition to the live state, and once a wild boar had been shot, it was permanently in the dead state, so that the models implicitly included the constraints: $\Psi_{2 \rightarrow 1} = \Psi_{3 \rightarrow 1} = 0$ and $\Psi_{2 \rightarrow 3} = 1$. We conducted separate analyses for males and females.

We first tested the goodness-of-fit (GOF) of the

Arnason–Schwartz (AS) model, which is the multistate extension of the Cormack–Jolly–Seber model (Lebreton et al. 1992) with time-dependent survival and recapture probabilities (noted Ψ_t, P_t). We conducted the GOF test using U-CARE software (Choquet et al. 2005a). Starting from the AS model, we tested for time variation in recapture probability by comparing the AS model to a model with time-dependent survival and constant probability of recapture (Ψ_t, P). Then, from the best model, we tested for time and age variation in survival embodied in the following hypotheses: 1) wild boar survival is age-specific but varies annually and independently for the 3 age-classes (model $\Psi_{3a \times t}$ including interactive effects between age-class and time); 2) wild boar survival is age-specific but varies annually and similarly for the 3 age-classes (model Ψ_{3a+t} including additive effects of age-class and time); 3) wild boar survival is age-specific and is constant over time (model Ψ_{3a} including differences among the 3 age-classes); and 4) wild boar survival only differs between piglets and older animals (model Ψ_{2a} including differences between 2 age-classes).

To assess whether the total number of wild boar harvested in a given year was related to estimated annual hunting mortality, we used annual variation in harvest as a covariate (see Lebreton et al. 1992). To explore the possibility of compensatory mortality, we assessed the relationship between hunting mortality and natural mortality for each year, using the model including among-year variation in survival probabilities. If compensatory mortality occurred, natural mortality should have decreased when hunting rate increased.

Wild boar are opportunistic omnivores, but their diet is primarily composed of vegetation. When available, oak and beech mast is highly preferred to other foods, particularly compared to agricultural crops (Schley and Roper 2003 for a review). We indexed the availability of mast by analyzing the stomach contents of harvested animals since 1982 (see Bieber and Ruf 2005 for a similar approach). The index took 4 values and was related to stomach contents: 1) no mast production when maize was the preferred item, 15–55% of stomach contents, whereas acorn or beechnut represented <3%, 2) high beech-mast production when beechnut represented 65–85% of stomach contents, 3) medium oak-mast production when acorn represented 50–65% of stomach contents, and 4) high oak-mast production when acorn represented 75–90% of stomach contents. For models where natural mortality was assumed year-dependent, we tested whether mast conditions could account for observed variability over time, using an analysis of variance (because mast condition is a qualitative variable, we could not use it as an external covariate in survival models implemented in M-SURGE).

We based model selection on the corrected Akaike's Information Criterion (AIC_c ; Lebreton et al. 1992, Burnham and Anderson 2002). We calculated AIC_c weights and used these weights as evidence of statistical support among candidate models (Burnham and Anderson 2002), except for the first steps of the model selection when most models had

low AIC_c weights (<0.001), in which case we based selection on ΔAIC_c . We also compared age-specific survival probabilities using Wald tests.

RESULTS

Males

We estimated the survival rates from 1,175 males (1,065 piglets, 102 yearlings, and 8 ad; Table 1) captured and marked between 1982 and 2003. We could only test for transience effects (i.e., the difference in survival between newly marked and previously marked animals) in piglets, because the sample size of animals caught for the first time as yearlings or adults was small. We did not detect evidence of transience ($\chi^2 = 27.775$, $df = 29$, $P = 0.530$). We detected positive immediate trap-dependence (i.e., trap-happiness) in piglets ($\chi^2 = 100.215$, $df = 42$, $P < 0.001$) but not yearlings ($\chi^2 = 5.590$, $df = 9$, $P = 0.750$). Sample sizes were too small to test for immediate trap-dependence in adults. Thus recapture probability the year following the first capture of piglets was higher than recapture probability in subsequent years and recapture probability of individuals captured for the first time as yearlings or adults. To account for this, we invoked age-specific recapture probabilities.

Recapture probability was time-dependent (model Ψ_t, P_t with a lower AIC_c than model Ψ_t, P , respectively, 3,632.805 vs. 3,645.259). Recapture probability of piglets varied between 0.0 in 7 years and 0.618 (SE = 0.221) in 1999–2000. Recapture probabilities of yearlings and adults varied between 0.0 in 16 years and 0.161 (SE = 0.110) in 2000–2001.

The best model was one wherein hunting mortality was correlated with annual harvest, with a harvest \times age interaction and constant natural mortality. This model had an AIC_c weight of 0.88 and was better than the second-ranked model. We found little evidence of time-dependence in any components of survival (all models with time-dependent survival had AIC_c wt <0.001), but we did detect age-class differences among piglets, yearlings, and adults; models with all components of survival depending on 3 age-classes had lower AIC_c weights than constant models or 2 age-classes survival models (Table 1). We found evidence that probability of being harvested varied among the 3 age-classes, whereas natural mortality did not vary (i.e., the models including age-dependent hunting mortality and constant natural mortality all had lower model weights than models including age-dependence in both components).

We estimated natural mortality of wild boar males at 0.14 (corresponding to a survival rate excluding hunting mortality of 0.86) regardless of age-class (Table 2). Probability of being harvested was high and increased with age, from 0.41 for piglets to 0.70 for adults (Table 2). Accordingly, overall survival was low and decreased from piglets (0.44) to adults (0.23; Table 2).

Hunting mortality increased with total number of harvested males (i.e., models including a linear relationship between hunting mortality and the annual harvest best fit our data). For piglets and adults, the slope of the linear increase

Table 1. Number of parameters (N_p), Akaike's Information Criterion corrected for small sample size (AIC_c), difference in AIC_c between each tested model and the best model (ΔAIC_c), and Akaike weights (w_i) for effects of year (t), age-class (noted 3a for 3 age-classes: piglets, yearlings, and ad; noted 2a for 2 age-classes: piglets and ad), and annual harvest (AH) on survival probability (ψ , including overall survival [OS] hunting mortality [HM], and natural mortality [NM]) of male and female wild boar in the Châteauvillain-Arc en Barrois forest, France, 1983–2003. The selected model is identified with an asterisk. The probability of resighting is modeled as age- and year-dependent.

Model	Model biological meaning	N_p	ΔAIC_c	w_i
M				
$\Psi_{(HM)_{AH \times 3a}-(NM)^*}$	HM correlated to AH and 3a (interaction) – NM constant*	49	0	0.885
$\Psi_{(HM)_{AH \times 3a}-(NM)_{3a}}$	HM correlated to AH and 3a (interaction) – NM dependent on 3a	51	4.164	0.110
$\Psi_{(HM)_{3a}-(NM)}$	HM dependent on 3a – NM constant	46	10.925	0.004
Ψ_{3a}	OS, HM, and NM dependent on 3a	48	14.473	<0.001
Ψ_{2a}	OS, HM, and NM dependent on 2a	46	15.745	<0.001
Ψ_{3a+t}	OS, HM, and NM dependent on 3a and t (additivity)	68	17.294	<0.001
$\Psi_{(HM)_{AH \times 2a}-(NM)_{2a}}$	HM correlated to AH and 2a (interaction) – NM dependent on 2a	48	21.945	<0.001
$\Psi_{(HM)_{AH}-(NM)_{3a}}$	HM correlated to AH – NM dependent on 3a	47	31.921	<0.001
$\Psi_{2a \times t}$	OS, HM, and NM dependent on 2a and t (interaction)	126	46.049	<0.001
Ψ	OS, HM, and NM constant	44	63.715	<0.001
Ψ_t	OS, HM, and NM dependent on t	83	72.495	<0.001
$\Psi_{3a \times t}$	OS, HM, and NM dependent on 3a and t (interaction)	165	141.002	<0.001
F				
Ψ_{3a+t}^*	OS, HM, and NM dependent on 3a and t (additivity)*	68	0.000	0.681
Ψ_{2a+t}	OS, HM, and NM dependent on 2a and t (additivity)	66	3.929	0.096
$\Psi_{(HM)_{AH}-(NM)}$	HM correlated to AH – NM constant	45	4.132	0.086
$\Psi_{(HM)_{AH}-(NM)_{3a}}$	HM correlated to AH – NM dependent on 3a	47	4.290	0.080
$\Psi_{(HM)_{AH \times 3a}-(NM)_{3a}}$	HM correlated to AH and 3a (interaction) – NM dependent on 3a	51	5.133	0.052
$\Psi_{(HM)_{AH \times 3a}-(NM)}$	HM correlated to AH and 3a (interaction) – NM constant	49	10.048	0.004
Ψ_t	OS, HM, and NM dependent on t	83	17.413	<0.001
$\Psi_{2a \times t}$	OS, HM, and NM dependent on 2a and t (interaction)	126	18.433	<0.001
$\Psi_{(HM)_{AH}-(NM)_t}$	HM correlated to AH – NM dependent on t	65	23.833	<0.001
$\Psi_{(HM)_{3a}-(NM)_{3a}}$	HM constant – NM dependent on 3a	46	39.848	<0.001
$\Psi_{(HM)_{3a}-(NM)_{2a}}$	HM constant – NM dependent on 2a	45	40.638	<0.001
Ψ	OS, HM, and NM constant	44	40.812	<0.001
Ψ_{3a}	OS, HM, and NM dependent on 3a	48	41.086	<0.001
Ψ_{2a}	OS, HM, and NM dependent on 2a	46	42.247	<0.001
$\Psi_{(HM)_{2a}-(NM)}$	HM dependent on 2a – NM constant	45	42.908	<0.001
$\Psi_{(HM)_{3a}-(NM)}$	HM dependent on 3a – NM constant	46	45.044	<0.001
$\Psi_{(HM)_{AH}-(NM)_{3a \times t}}$	HM correlated to AH – NM dependent on 3a and t (interaction)	107	65.420	<0.001
$\Psi_{3a \times t}$	OS, HM, and NM dependent on 3a and t (interaction)	165	114.155	<0.001

in hunting mortality with increasing annual harvest was similar (0.0024 ± 0.0003 for piglets and 0.0029 ± 0.0008 for ad, on a logit scale), but the intercept was larger for adults (0.4640 ± 0.0007 vs. -0.5738 ± 0.0124), indicating that for a given annual harvest, more adults than piglets were shot (Fig. 1a). For yearlings, hunting mortality rate did not depend on total number of wild boar males shot in a given year (slope of -0.0001 ± 0.0004 on a logit scale; Fig. 1a).

Yearly natural mortality was not related to differences in mast availability for any age-class (piglets: $F = 1.463$, $df = 3, 16$, $P = 0.261$; yearlings: $F = 1.607$, $df = 3, 16$, $P = 0.227$; ad: $F = 1.655$, $df = 3, 16$, $P = 0.216$). Absence of an influence

of mast availability on age-specific survival and absence of detectable among-year variation in natural mortality both supported low variability over time ($CV = 10\%$ for ad) in natural mortality of wild boar males.

Because we did not detect any age-variability in natural mortality, we tested whether there was compensation between natural mortality and hunting mortality of all pooled age-classes. Natural mortality in a given year was not correlated to hunting mortality, in the same year ($t = 0.175$, $df = 19$, $P = 0.863$, $r^2 = 0.002$) or previous year ($t = 0.039$, $df = 18$, $P = 0.969$, $r^2 = 0$; Fig. 2a), suggesting no compensatory mortality occurred.

Table 2. Overall age-class specific survival, hunting mortality, and natural mortality (95% CI) for the wild boar population of Châteauvillain-Arc en Barrois, France, 1983–2003. We provide estimates from the selected model.

Age-class	Overall survival			Hunting mortality			Natural mortality			
	\bar{x}	Min.	Max.	\bar{x}	Min.	Max.	\bar{x}	Min.	Max.	
M	Young (1–12 months)	0.439	0.393	0.484	0.410	0.378	0.484	0.144	0.122	0.169
	Yearling (13–24 months)	0.351	0.244	0.475	0.590	0.542	0.475			
	Ad (≥ 2 yr)	0.228	0.169	0.299	0.696	0.608	0.299			
F	Young (1–12 months)	0.426	0.381	0.472	0.392	0.358	0.472	0.182	0.143	0.230
	Ad (≥ 13 months)	0.475	0.437	0.512	0.401	0.361	0.512	0.124	0.093	0.164

Females

We estimated survival rates from 1,076 females (927 piglets, 95 yearlings, and 54 ad; Table 1) captured between 1982 and 2003. We did not detect transience for any age-class ($\chi^2 = 33.045$, $df = 40$, $P = 0.774$ for piglets; $\chi^2 = 6.331$, $df = 14$, $P = 0.957$ for yearlings; and $\chi^2 = 0.936$, $df = 3$, $P = 0.817$ for ad). We did detect a positive immediate trap-dependence in piglets ($\chi^2 = 82.081$, $df = 57$, $P = 0.016$) but not yearlings ($\chi^2 = 13.359$, $df = 20$, $P = 0.861$) or adults ($\chi^2 = 14.848$, $df = 18$, $P = 0.672$). Recapture probability the year following the first capture of piglets was higher than recapture probability the following years and also higher than recapture probability of individuals captured for the first time as yearlings or adults. As in males, such patterns suggest real age-specific differences in recapture probabilities.

Recapture probabilities varied across years (model Ψ_t, P_t with a lower AIC_c than model Ψ_t, P , respectively 3,986.676 vs. 3,993.817). We started with the model including time-dependent recapture probabilities to test for effects of year and age on survival. Recapture probability of piglets varied between 0.0 in 4 years and 0.688 (SE = 0.140) in 2000–2001. Recapture probabilities of yearlings and adults varied between 0.0 in 3 years and 0.441 (SE = 0.219) in 1992–1993.

The best model included additive effects of time and 3 age-classes on survival probabilities, and had an AIC_c weight of 0.68, which was 7 times more weight than the second-best model. However, we could not estimate natural mortality of yearlings, so we selected the model with additive effects of time and 2 age-classes: piglets and adults (hereafter for F, from ≥ 13 months at capture).

Age-dependence of both natural and hunting mortality differed from the pattern exhibited by males. Models with constant hunting mortality and age-dependent natural mortality had higher model weights than models with age-dependent hunting mortality and constant natural mortality. Probability of being harvested did not differ between piglets and adults and averaged 0.38 (Table 2). However, piglet females had a higher natural mortality rate (0.18) than adults (0.12; Table 2). Females had an overall annual survival rate of 0.43 for piglets and 0.47 for adults.

In contrast with male survival, female natural mortality varied over time, with marked among-year variation (CV = 25% for ad). In addition, constraining hunting mortality as a function of total number of females harvested in a given year did not improve model fit. For any given year, probability of a female being harvested was independent of total number of females killed that year. However, the trend was the same as for males, with a tendency of increases in annual harvest corresponding with increased hunting mortality (slope of 0.0030 ± 0.0002 ; Fig. 1b).

We did not detect any relationship between observed fluctuations in mast availability and yearly natural mortality for any age-class (piglets: $F = 1.259$, $df = 3, 16$, $P = 0.322$; ad: $F = 1.248$, $df = 3, 16$, $P = 0.325$). The among-year variation of female natural mortality we reported was not

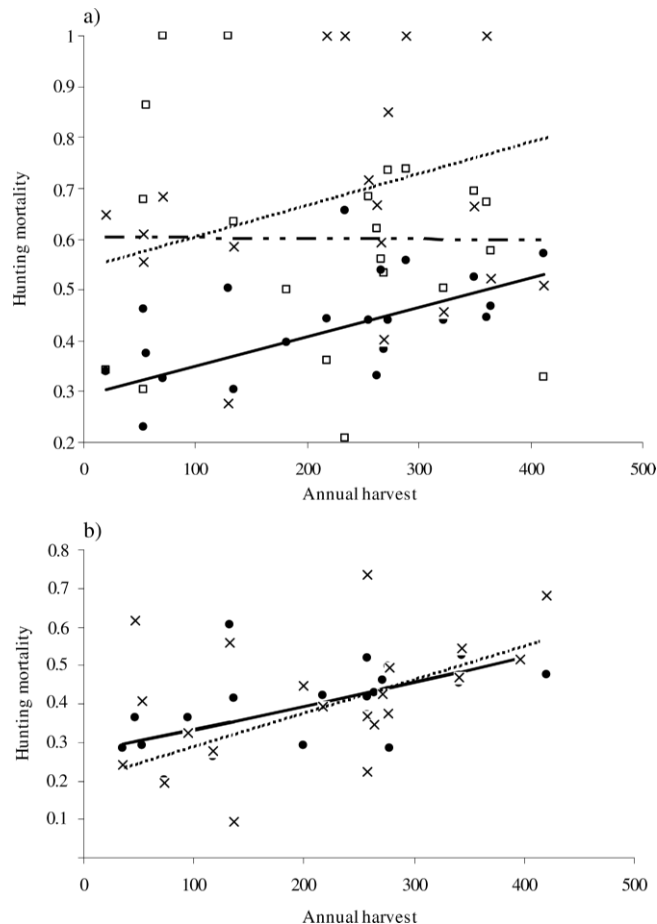


Figure 1. Relationship between the annual hunting mortality and total number of wild boar a) males and b) females hunted each year (annual harvest) in the population of Châteauvillain–Arc en Barrois, France, 1983–2003. Plain circles and plain line: piglets; open squares and dashed line: yearlings; crosses and dotted line: adults (pooled yearlings and ad for F).

accounted for by variations of oak- and beech-mast production.

We did not find any relationship between natural mortality of piglets and adults in a given year and the global hunting mortality rate for females the same year (piglets: $t = -0.660$, $df = 19$, $P = 0.517$, $r^2 = 0.022$; ad: $t = 1.475$, $df = 19$, $P = 0.157$, $r^2 = 0.103$) or previous year (piglets: $t = 0.395$, $df = 18$, $P = 0.697$, $r^2 = 0.009$; ad: $t = 1.562$, $P = 0.136$, $r^2 = 0.119$), suggesting little evidence of compensatory mortality for female wild boar, even though there was a slight positive tendency for adults (Fig. 2b).

DISCUSSION

Overall annual survival in our study population was low for both sexes, mainly due to high hunting pressure.

Natural mortality of adults was similar for males and females (approx. 0.15, $W = 0.924$, $P = 0.260$). In ungulates, annual adult survival of 0.85 is usual for males, with an average of 0.88 among 18 species in one review (Toigo and Gaillard 2003). This is low compared to average survival of females, which is commonly >0.95 in predator-free populations (Gaillard et al. 2000). After excluding hunting mortality, female wild boar survival varied substantially,

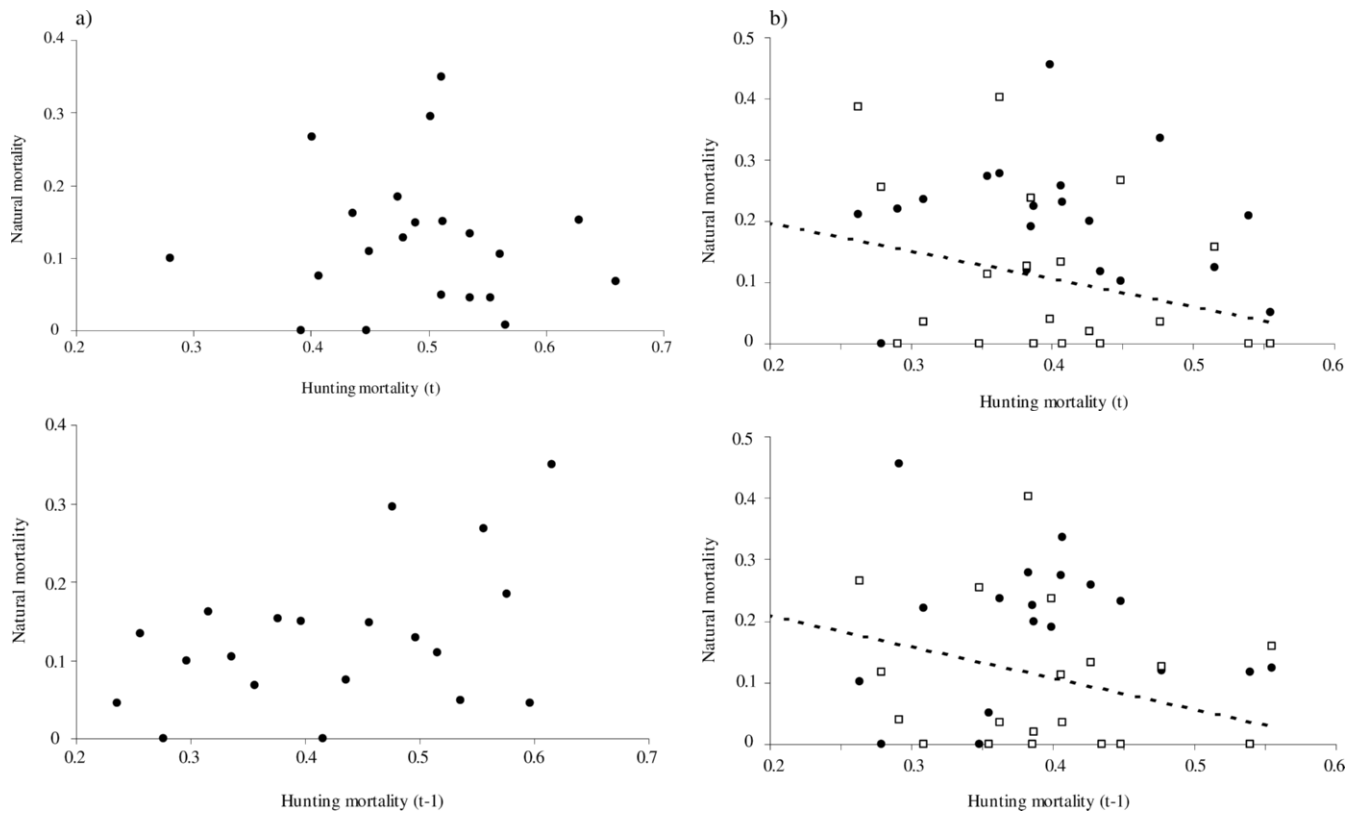


Figure 2. Relationship between wild boar natural mortality and hunting mortality the same year (t) and previous year ($t - 1$) for a) male and b) female wild boar in the population of Châteauvillain–Arc en Barrois, France, 1983–2003. For females, plain circles: piglets; open squares: yearlings and adults; all 3 age-classes pooled for males (see text).

whereas male survival did not. Such among-year variation of adult female survival ($CV = 0.25$) relative to male survival ($CV = 0.10$) is unusual for a dimorphic, polygynous ungulate. Male survival is typically more influenced by environmental variation because males expend considerable energy during mating, which can lead to exhaustion and starvation under harsh environmental conditions (see Coulson et al. 2001 for an example on Soay sheep [*Ovis aries*], Toïgo and Gaillard 2003 for a review, Toïgo et al. 2007 on Alpine ibex [*Capra ibex*]). Moreover, the observed amount of among-year variation in natural mortality of adult females ($CV = 25\%$) was almost 5 times higher than that commonly reported in other ungulates (median $CV = 5.5\%$ on 15 populations of 9 species, Gaillard and Yoccoz 2003). Energy allocated by wild boar females to reproduction early in their lifetime could account for their low and variable adult survival. In ungulate females, adult survival is generally high. When conditions are not optimal, female ungulates may sacrifice reproductive effort in a given year to enhance their own survival (Gaillard and Yoccoz 2003; see Festa-Bianchet et al. 1998 for empirical evidence on bighorn sheep [*Ovis canadensis*]). Wild boar females seem to have an unusual life-history strategy among ungulates, involving a high investment in reproduction by adult females. Wild boar females can reproduce as early as age 1 year and produce average litters as large as 5 (Taylor et al. 1998, Servanty et al. 2007). Compared to other ungulates, the population growth rate of wild boar may be less sensitive to adult survival and

more sensitive to reproductive parameters, such as breeding proportions or litter size (Bieber and Ruf 2005). Such a strategy might account for the low and variable adult survival of wild boar females.

The high natural mortality we reported in this intensively hunted population might have occurred through compensation (Schaub and Lebreton 2004, Lebreton 2005). Compensation may arise through density-dependent mortality and heterogeneity in survival across individuals (if the individuals more susceptible to hunting also have a higher risk of natural mortality). The latter mechanism may arise when hunting is selective and targets lower than average quality individuals within an age- and sex-class. Alternatively, hunting and natural mortality can be overcompensatory when hunters select higher than average quality individuals. Under this scenario, natural mortality should increase because the animals remaining in the population and, thus, subject to natural mortality have lower performance and are more susceptible to die from natural causes than animals that have been removed by hunting. Trophy hunting has been hypothesized to lead to overcompensatory mortality (Coltman et al. 2003, Garel et al. 2007). If hunters shoot individuals they encounter randomly, they should kill disproportionately the individuals easiest to harvest, presumably lower quality individuals. If so, natural mortality will be lower than in a nonhunted population because high-quality individuals will be less susceptible to die from natural causes. In our population, hunters appeared to indifferently

harvest boars, except that hunters avoided adult females, leading to little possibility of selection of individual quality within an age- and sex-class. However, even in the absence of selective harvesting, compensation between hunting and natural mortality can occur if hunting reduces population size and natural mortality decreases via release from density-dependence. We found little evidence of compensation between natural mortality and hunting mortality, despite high hunting pressure. These results support Lebreton's (2005) conclusions that compensation is expected to be rare in exploited populations of long-lived vertebrates, even under strong selectivity or high harvesting rates. Therefore, our estimates of natural mortality did not seem to have been influenced by hunting and could be expected to be close to wild boar survival in nonhunted populations with similar environmental conditions.

As expected, we found that, for a given year, hunting mortality for both sexes increased as reported harvests increased. These results would imply that hunters were able to control population increases in wild boar, whereas empirical evidence demonstrated that this did not occur. This paradox may be due to the numerical response of wild boar to hunting. According to our results (Fig. 2), a 6-fold increase in harvest led to less than a 2-fold increase of hunting mortality.

The absence of influence of mast availability on natural mortality was not surprising. The forest habitat of the study population was highly productive, and wild boar were likely on a high nutritional plane (Gaillard et al. 1993). Such a favorable environment for wild boar could also account for the absence of compensatory survival we reported here.

MANAGEMENT IMPLICATIONS

Despite high natural mortality at all ages, the hunted wild boar population we studied still increased, as evidenced by the 5-fold increase in number of wild boar harvested over the past 20 years. Efficient management of wild boar populations will likely depend on high harvest rates on all sex- and age-classes. We found that harvest focused on adult males, coincident with limited hunting pressure on adult females and piglets, reduced the effectiveness of hunting regulations designed to control growth of wild boar populations. We conclude that to achieve wild-boar management objectives across a broad agro-forested landscape highly sensitive to wild boar damage, wildlife managers should consider hunter willingness to harvest piglets and females when developing hunting regulations of wild boar.

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Effects of hunting on wild boar *Sus scrofa* behaviour

Henrik Thurffjell, Göran Spong & Göran Ericsson

Predation risk may affect space use and foraging patterns of prey animals, with strong down-stream effects on diet composition and ecological interactions. Wild boar *Sus scrofa* is a notorious crop raider but also a popular game species, yet little is known about how risk perception of human hunting affects wild boar space use. We studied the effects of human hunting on the movement of GPS-collared female wild boar. We found that the hunting method affected whether the wild boar fled or hid. After fleeing into refuge ranges, wild boar moved less and preferred habitats that provided cover and forage such as mast or crops. This suggests that the wild boar tried to reduce the risk of being detected, and possibly also that they avoided competition with resident wild boar in the refuge by using forage that could not be monopolised. The type of hunting thus strongly affected the type of avoidance behaviour displayed by wild boar, with implications for their movement and space use. This suggests that adjusting hunting method to season could be an important management tool for minimising crop losses.

Key words: escape, GPS, hunting, movement, *Sus scrofa*, wild boar

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Animals often change their behaviour in relation to predation risk (Lima & Dill 1990); for example by selecting areas with lower food quality or quantity in return for decreased predation risk (Sih 1980). Risk can also be reduced by increased vigilance, which reduces foraging efficiency (Lima & Dill 1990). Predator presence may hence lead to consistent and large-scale avoidance behaviours in herbivores (Creel et al. 2007). This may lead to heterogeneities in browsing pressure across the landscape, where plants in safer foraging patches may be highly utilised and plants in risky foraging areas less affected by herbivory (Brown et al. 1999). Such trophic cascades occur both in marine and terrestrial systems and typically have major effects on the ecosystem's function and form (Terborgh & Estes 2007).

Human hunting is likely to be perceived as a risk by many animals and has accordingly been shown to affect habitat use (e.g. Kilgo et al. 1998, Benhaïem et al. 2008, Sunde et al. 2009, Kamei et al. 2010). The

response to the perceived risk has also been shown to depend on hunting methods (Keuling et al. 2008b), where numerous factors play a role, e.g. the intensity of the hunt, detectability of hunters and the chance of animals learning from hunting experience. Reactions to hunting also depend on the prey's natural predators to which it has had evolutionary time to adapt. For example, dogs used for moose *Alces alces* hunting are behaviourally similar to wolves *Canis lupus*, and provoke similar reactions in the moose (Sand et al. 2005).

Farmers strive to minimise the loss of crops to wildlife. This may be accomplished by population control, fencing, dissuasive feeding (Geisser & Reyer 2004), deterring wildlife by scaring them (Berlinger et al. 2003), or by using repellents such as odour (Baker et al. 2008). While maintaining a small population size by intensive hunting is perhaps the most efficient way of reducing crop damage (Geisser & Reyer 2004), this strategy may be at odds with management

strategies aimed at improving hunting value or conservation of biodiversity. From a management perspective there is often a conflict of interest between stakeholders wanting to maintain a high population density of game species and stakeholders interested in minimising crop damage (Conover 1997, Brown et al. 2000, Riley et al. 2002, Gordon et al. 2004, Lischka et al. 2008). Thus the potential of inducing behavioural strategies that lead to avoidance of crop fields and preference of alternative habitats is an appealing management strategy as the use of crop fields could be assumed to be related to crop damages. However, we know relatively little about how hunting affects animal space use in agricultural regions, and in particular how hunting affects the behaviour of the wild boar *Sus scrofa*, which is now recolonising large areas of Europe (Thurfjell et al. 2009).

Wild boar can cause significant damage to crops (Genov 1981, Feichtner 1998, Bieber & Ruf 2005, Schley et al. 2008) and is also one of the more popular game species for recreational hunting (Geisser & Reyer 2004). Hunters commonly feed wild boar to facilitate hunting and sometimes also in an effort to reduce crop damage (Geisser & Reyer 2004). Wild boar hunting by humans has been studied previously (Feichtner 1998, Sodeikat & Pohlmeier 2003, Geisser & Reyer 2004, Keuling et al. 2008b, Tolon et al. 2009), but few studies on wild boar and hunting have provided data on the whereabouts of animals through radio telemetry (Sodeikat & Pohlmeier 2003, Keuling et al. 2008b, Tolon et al. 2009). Previous research has suggested that the wild boar has two main reactions to disturbance from hunting: hiding or running away (Sodeikat & Pohlmeier 2003). Escape distances of wild boar after drive hunts, where hunters and dogs flush and chase wild boar towards other hunters, can be up to 6 km (Sodeikat & Pohlmeier 2003). They usually show site fidelity (Graves 1984, Keuling et al. 2008a) and typically return to their home range a few weeks after being disturbed by a drive hunt (Sodeikat & Pohlmeier 2003, Keuling et al. 2008b).

In this paper, we study the effects of different types of hunting activities on movement of female wild boar equipped with Global Positioning System (GPS) collars in southern Sweden. We also quantify movement and habitat utilisation after wild boar had fled to a refuge home range.

We predict that running away and changing home range occur when hunting is perceived as intense and in close proximity, resulting in an increase in move-

ment. Conversely hiding should be the strategy to be used when hunting is not perceived as an immediate danger, i.e. less intense or further away, resulting in a reduction of movement. When leaving their home range, wild boar should move less and use habitats providing cover more than habitats providing forage compared to the period before the hunt in their home range, since the perceived risk should be higher after they have been chased.

Material and methods

Study area

Our 16,000 ha study area is located in southern Sweden, in the county of Scania (N 55°28'-55°43', E 13°44'-14°12'; WGS84) within the Nemoral vegetation zone (Ahti et al. 1968). The area comprises three large estates and several smaller land owners, and it is a mosaic of open and closed habitats. Agricultural land covers most of the area (65%) with wheat, rye and oats being the main crops. Open pastures and other open land cover 12%. The deciduous forest covers 7%, and is dominated by beech *Fagus sylvatica* and oak *Quercus robur*. About 12% of the area is classified as mixed deciduous and coniferous forest, mainly Norway spruce *Picea abies*. Other habitats such as water and urban areas make up the remaining 4% of the area.

Hunting

All hunting activities on the estates were recorded by professional game managers. The main types of hunts were drive hunts, pheasant *Phasianus colchicus* hunts, duck *Anas platyrhynchos* hunts, small-game hunts and still hunts, during which hunters try to remain unnoticed by game through hiding (Table 1).

The wild boar population

The density of wild boar in the area is high (> 2 wild boar/km²), partly due to supplementary feeding, mostly with sugar beet, but everything from maize to candy and bread were supplied at feeding stations surrounding the estates. The net supplementary feeding amounted to 100-200 kg/ha and year according to the game managers, which would be a large amount compared to amounts used in other countries in Europe (e.g. Keuling et al. 2008a). The hunting bag in the region was about 1 wild boar/km², but it was smaller on the estates (0.4 wild boar/km²; A. Jonsson, pers. comm.).

Wild boar capture and fitting of GPS/GSM collars

To fit radio-collars, wild boar were anaesthetised

Table 1. Intensity of hunting pressure.

Type of hunting	Intensity	Dogs	Time of day, season, hunts/year	Target	Habitat
Still	Low, hunters wait for game	No	Morning or evening, August-January, 3/year	Ungulates	All, usually where animals feed
Duck	High, ducks are shot by hiding hunters, > 100 shots fired/hunt	Yes, retrieving	Daytime, August-October, 5/year	Ducks	By water
Drive	High, game is chased towards a shooting line	Yes, chasing	Daytime, September-January, 11/year	Ungulates	Daytime resting areas
Pheasant	High, game is chased towards a shooting line, often > 100 shots fired.	Yes, retrieving	Daytime, October-December, 6/year	Pheasants	Open areas and brush
Small-game	Low-medium	Yes, searching	Daytime, August-January, 2/year	Small-game	Open areas and brush
Unknown	Not known, probably different, the category is added as a few times hunting was conducted and the method was not noted by the game keepers.				

using drugs administered via a tranquilliser gun. This was done either from a car or by still hunting close to feeding stations. We used a standard dose consisting of 10 mg Medetomidine, 20 mg Butorphanol and 500 mg Ketamine, as described in Kreeger & Arnemo (2007). Darted wild boar were usually anaesthetised within 2-3 minutes, or at a distance of about 200-300 m from where they were darted. To ensure that darted animals could be relocated, darts were fitted with a VHF transmitter. Each wild boar was equipped with a GPS/GSM Plus 2D collar from Vectronic Aerospace GmbH. A total of 15 females were collared. The collars obtained a position every half hour and transmitted accumulated positions to a computer using 'Short Message Service' (SMS) on the cell-phone network. Our study was approved by the Animal Care Committee for Northern Sweden, Umeå (Dnr A18-04).

Data collection

We only used positions with a dilution of precision (DOP) of < 5, and 3D positions calculated based on at least four satellites. Our study area was relatively flat with an altitudinal range of 100 m over 25 km; hence space use is unlikely to be affected by topological features of the landscape (Moen et al. 1996, Cain et al. 2005, DeCesare et al. 2005). On average, 81% of the attempts to localise a position were successful at night and 75% during the daytime for all collared wild boar, except for two individuals with malfunctioning collars. Because of the high success rate, we made no corrections for unsuccessful location attempts (Zweifel-Schielly & Suter 2007). In total, we retrieved > 100,000 successful locations from the 15 individuals. We analysed the data in

ArcGIS 9.1 with Hawth's Analysis Tools for ArcGIS extension and in R 2.10.

Analyses of the effect of hunting on movement of wild boar

We tested the effects on movement of all collared wild boar during the same day and the following night for the different types of hunts. We used a generalised linear mixed-effects model with movement as the response variable (Gamma distributed with an inverse link function; Venables & Ripley 2002). The explanatory variables chosen were sun up or down, month of year and type of hunt (drive hunt, small-game hunt, pheasant hunt, duck hunt, no hunting or hunting with an unknown method; see Table 1) and the interaction between sun up or down and type of hunt. The variables were chosen to explore the effects of hunting and to account for major factors affecting wild boar movement such as seasonality and daily activity patterns. We used identity contrasts to distinguish the effects of the different types of hunting from no hunting, day from night and the interaction between day and night and type of hunt.

Analyses of the effect of movement and habitat use by wild boar leaving their home range

To analyse effects on movement of drive hunts when female wild boar escaped, we used data from wild boar that escaped known drive hunts and left their previous home ranges. For wild boar that moved into refuge ranges for at least a week (seven nights), we calculated the distance between the centroid point of the initial home range and the first daily rest in the refuge range. We used a period before the drive hunt of the same duration as the time the wild boar stayed

in the refuge range as a basis for comparison. We constructed generalised linear mixed effects of models for different response variables; one with movement (Gamma distributed with an inverse link function) and four with habitat (Binomially distributed with a logit link function) as response variables. To correct for repeated measurements from the same individual, we fitted individual wild boar as a random variable. Hunting (before the hunt, during the hunt or after the hunt), month and sun up or down were fitted as fixed variables. Day or night and month were added to account for seasonal and daily differences in movement patterns.

Results

Type of hunt had an effect on movement of female collared wild boar. The effect of type of hunt was different during the day of the hunt compared to the night following the hunt (the interaction between sun up or down and hunting type), which means one type of hunting may increase movement of wild boar during the day of the hunt, but decrease movement during the following night. During the day of pheasant and drive hunting wild boar movement increased ($P < 0.001$), whereas duck hunting ($P < 0.05$), still hunting ($P < 0.01$) and unspecified hunting ($P < 0.001$) reduced their movement (Fig. 1). This suggests that unspecified hunting usually was a type of hunting that was noticed by wild boar, but was not targeting wild boar specifically. During the night after the hunt, pheasant hunting ($P < 0.001$) and still hunting ($P < 0.01$) reduced movement, whereas no effects were found from other the types of hunting. Factors other than hunting that were important for movement were month of the year and sun up or down (all $P_s < 0.001$). Identity contrasts applied to month of the year showed that all months except March and April differed from January (all $P_s < 0.001$).

Six wild boar left their home range as an effect of a drive hunt; they moved between two and 20 km and stayed in the refuge area between six and 29 days. Hunting events that resulted in flights showed that boar movement was affected by drive hunts (Fig. 2). Female wild boar moved more when moving between the home range and the refuge range than before drive hunts, and less in the refuge range (both $P_s < 0.001$). The drive hunts that resulted in flight ($N = 6$) had an effect on the use of all four tested habitats either during relocation or in the

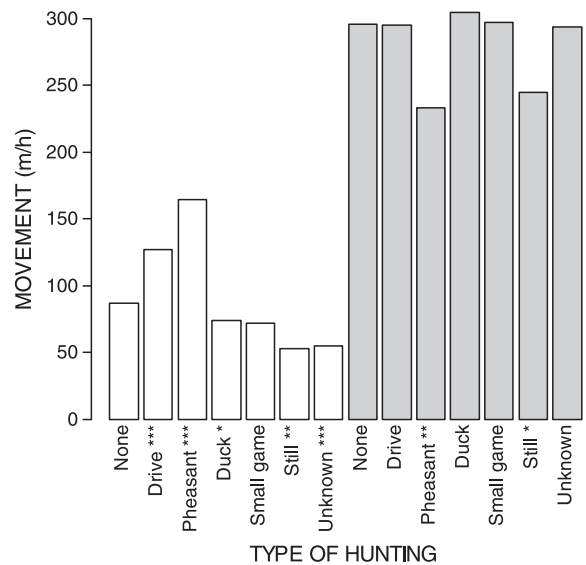


Figure 1. Effects of different types of hunting on the average movement speed of 15 female wild boar during November which is the month when most types of hunting commonly are performed. The white bars represent the day of the hunt and the grey bars represent the following night. Asterisks indicate significant differences compared to no hunting (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ based on identity contrasts).

refuge range (Fig. 3). Coniferous and deciduous forest was utilised more during relocation whereas open areas were less utilised. After relocation crop fields and forests were utilised more, whereas open areas were utilised less (all $P_s < 0.001$).

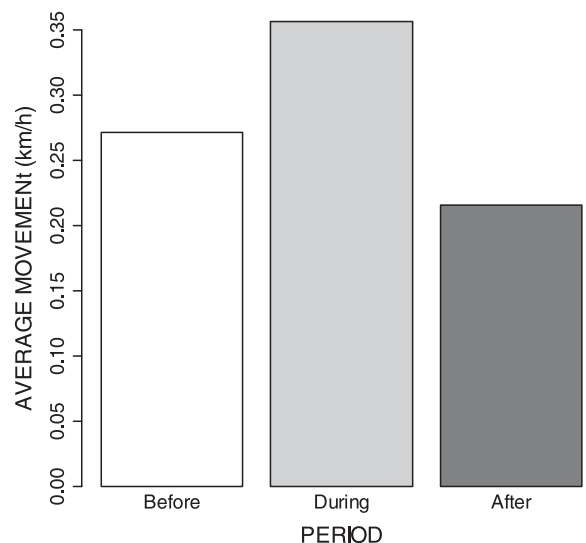


Figure 2. Effect of drive hunts that resulted in six wild boar leaving their home range. During the relocation wild boar moved more than before the hunt, and in the refuge range wild boar moved less ($P < 0.001$ based on identity contrasts).

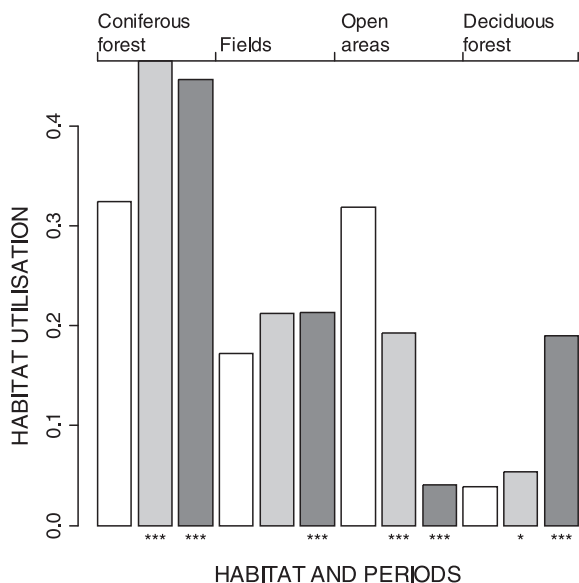


Figure 3. Effects of six drive hunts on habitat use. The bars show the effects of drive hunts on each model of habitat choice (probability), before drive hunts (□), during (◐) and after (◑). Asterisks indicate whether there is a difference compared to the period before the drive hunt (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$ based on identity contrasts).

Discussion

Our study suggests that wild boar react to hunting by either fleeing or hiding, depending on the intensity of the hunt and the distance to the hunting activity. After a flight reaction, wild boar reduced their movement and used habitats with good cover (to reduce visibility), but they also increased their use of habitats containing natural forage, possibly to avoid competition with resident wild boar using supplemental food.

Drive and pheasant hunts flushed wild boar out of their daily rest (see also Sodeikat & Pohlmeier 2003, Keuling et al. 2008b, Scillitani et al. 2010). Pheasant hunts also resulted in an overall reduction in movement during the night after the hunt. A possible explanation for the stronger reaction to pheasant hunting is that they may involve more people and that more shots are fired, thus creating a greater disturbance, leading to more cautious behaviour the night after the hunt. Duck and still hunting reduced boar movement during the same day, but only still hunting reduced their movement the following night. There may be different mechanisms behind these similar reactions. Duck hunting is probably perceived to be just as intense as pheasant hunting but limited to wetlands, which means that it is usually

further away, resulting in hiding rather than fleeing. Still hunting is often carried out after sun down, and as the wild boar does not perceive still hunters as an immediate risk, they react to still hunters by reducing their activity to reduce risk of detection. Our data clearly show that hunters are noticed by wild boar when still hunting, but as animals are not flushed, they stay in hiding.

Drive hunts resulted in escapes where wild boar left their home range and ran longer in our study than in previous studies performed in Germany (Sodeikat & Pohlmeier 2003, Keuling et al. 2008b). The reasons for these differences may be several. Difference in dog size used; terriers < 15 kg were used in Germany (O. Keuling, pers. comm.) and medium-sized dogs of 20–40 kg were used in our study. Harvest of wild boar is less intensive (1.1/km²) in our study area than in the study area of Keuling et al. (2008b; 2.8–5.1 animals/km²). The fragmentation and composition of the habitat seems to be similar on the European spatial pattern map (Vogt et al. 2007) although there are more forests in the German study areas than in ours (Sodeikat & Pohlmeier 2003, Keuling et al. 2008b). Thus, fragmentation does not seem to be a main reason for the difference in the results.

After fleeing to and relocating in a refuge range, wild boar reduced movement and changed their habitat use. Habitat with better cover, e.g. forest, was used more and open areas were used less. This suggests that the perception of an increased risk by wild boar makes them more cautious and increases the effect of fear on habitat use (Brown et al. 1999) as predicted. However, the increased use of crop fields after relocation is not in accordance with our prediction that foraging habitats should be used less. Instead, the increased use of crop fields and deciduous forest may be due to competition with resident wild boar groups. Crop fields and deciduous forests contain food that may not be monopolised in the same way as food at feeding stations. This may mean that part of the reason to why they return to their original home range may be competition with resident wild boar groups.

Further studies of hunting at a lower density of wild boar and at the edges of their current distribution might reveal if the effects of drive hunts on their behaviour are partially due to competition with other groups of wild boar or not. Such studies might also shed light on the recorded differences in flight distances, although controlled experiments changing one parameter at a time would be preferable. Spatial data on hunters' and dogs' location during hunts

would be preferable and would clarify the effects of distance and intensity of drive hunts on the reactions of wild boar. A spatial study including several areas with different hunting regimes (Keuling et al. 2008b) and with focus on damage to crops might be the most useful study from a management perspective.

Conclusions and management implications

Most types of hunting affect the behaviour of wild boar. But wild boar are not easily driven out of their home range by hunters and their dogs. However, when wild boar flee, pronounced changes in their movement and habitat use occur. These effects may arise from an increased perception of risk, but might also be due to increased competition with resident wild boar. The most important implication for crop damage is that female wild boar that have fled from drive hunts increase their use of crop fields. Thus, drive hunts should take place after the crops have been harvested.

Wild boar also show behavioural modifications during still hunting (even before any shot has been fired), suggesting that hunters have commonly been detected. Therefore, the strategies to stay unnoticed for hunters are to some extent inadequate and if improved, they might allow for an increased hunting success.

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Do intensive drive hunts affect wild boar (*Sus scrofa*) spatial behaviour in Italy? Some evidences and management implications

Laura Scillitani · Andrea Monaco · Silvano Toso

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Abstract Wild boar have been increasing in numbers all over Western Europe in the last 30 years. The species is a major pest for agriculture, but it has a high value as a game species, and in Italy, as in several other countries, it is traditionally hunted in drive hunts by hunting teams with several dogs. This hunting method can have disruptive effects on the demography and spatial behaviour of wild boar, especially family groups. We conducted a 2-year study (2003 and 2004) to determine the effects of drive hunt disturbance on the spatial behaviour of wild boar family groups in the Northern Apennines (central Italy). Twenty wild boar belonging to ten family groups were ear tagged with a radio device. We located resting sites daily and used intensive tracking sessions during drive hunts. Three seasons were determined: pre-hunting, hunting and post-hunting. A general pattern of increased spatial insta-

bility during the hunting season was shown. Resting ranges were larger, and resting sites were more interspersed. Distances between consecutive resting sites were greater during the hunting season and, especially, on hunting days. The displacement of family groups caused by drive hunts was generally short lived except for those groups that were repeatedly hunted and so abandoned their pre-hunt (native) range. During drive hunts, wild boar showed a moderate tolerance to hunting disturbance, and only family groups which were directly chased by dogs escaped or altered their behaviour. The response of wild boar to hunting disturbance seemed to be highly related to the degree of hunting pressure combined with individual variability. The impact on wild boar behaviour should be reduced, above all by avoiding repeated hunts in the same areas within a short period and by employing well-trained hounds.

Keywords Wild boar · Hunting · Human disturbance · Drive hunt

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Introduction

Over the last 50 years, wild boar have increased in number and range throughout western Europe (Saez-Royuela and Telleria 1986) including in Italy (Monaco et al. 2003; Carnevali et al. 2009). Wild boar are a polygynous species which have a very high fertility rate and a shorter generation time compared to similar sized temperate zone ungulates (Servanty et al. 2007), as well as an early age at first reproduction (Gaillard et al. 1993; Franzetti et al. 2002; Servanty 2007). The species has a matrilinear social organisation (Kaminski et al. 2005) centred on adult females and their offspring: kin-related females form family groups with dominance relationships (Teillaud 1986;

Kaminski et al. 2005). The size of family groups varies according to the season and the habitat composition, with the number of individuals within a group being up to 20 boar (Teillaud 1986; Dardaillon 1988). Family groups show high site fidelity (Keuling et al. 2008a), and usually, the direction and the length of displacements are determined by the dominant females (Briedermann 1986; Jezierski 2002). Wild boar are a major agricultural pest because of the crop damage they cause (Calenge et al. 2004; Klein et al. 2004; Monaco et al. 2003; Schley and Roper 2003) as well as being a problem for livestock farmers because of their role as a vector for several infectious diseases (Rossi et al. 2004; Sodeikat and Pohlmeier 2007) and because they may kill newborn lambs (Pavlov et al. 1981). However, wild boar also have a high economic value as one of the most important game species and are, as a result, subject to an intensive hunting pressure (Monaco et al. 2003; Toigo et al. 2008; Tsachalidis and Hadjisterkotis 2008). In Italy, the most commonly employed hunting method is the drive hunt (Massei and Toso 1993), which is carried out by a hunting team and involves several tracking dogs, usually in mixed packs of different breeds. The drive hunt is the preferred hunting method in Italy because it is thought to guarantee the highest hunting bag and because it is linked to rural traditions (Monaco et al. 2003). Nonetheless, the use of drive hunts is controversial since it may have a number of negative consequences.

First of all, this hunting method does not always allow to make an assessment and choose which animal to shoot (Martínez et al. 2005), especially in a Mediterranean habitat dominated by maquis and dense woods, which are characterised by poor visibility. When chased, wild boar run very fast away from their resting sites and pass through thick vegetation, and consequently hunters tend to shoot the biggest boar, irrespectively of their age or sex, because they are the most visible (Monaco et al. 2003).

The adoption of drive hunts in this environment therefore has consequences for the demography of the hunted populations (Monaco et al. 2003; Toigo et al. 2008) and can also affect the spatial behaviour of family groups as the loss of a dominant female can lead to increased spatial instability amongst the surviving individuals (Maillard 1996). In addition, wild boar drive hunts usually cover a large area, and in many cases, hunting dogs are not trained to selectively hunt wild boar. This can cause severe disturbance to other species occurring in the same area, such as the brown bear *Ursus arctos* (Boscagli 1987; Ciucci and Boitani 2008), the roe deer *Capreolus capreolus* (Cederlund and Kjellander 1991), the red deer *Cervus elaphus* (Bateson and Bradshaw 1997) and the wolf *Canis lupus* (Ciucci, personal communication).

Many studies highlight how hunting can seriously affect population structure (Ginsberg and Milner-Gulland 1994;

Milner et al. 2007), evolutionary traits (Festa-Bianchet 2003; Proaktor et al. 2007) and individual behaviour (Tuytten and McDonald 2000; Sutherland and Gill 2001) in large mammals. In particular, altered spatial behaviour in response to hunting pressure has been reported in several hunted mammalian species. Hunted wild ungulates can display increased movement (Root et al. 1988; Kilpatrick and Lima 1999), an enlarged resting range (Jeppesen 1987; Maillard and Fournier 1995) or changes in habitat selection (Swenson 1982; Kufeld et al. 1988; Kilgo et al. 1998). In some cases, animals remain within the established home range but shift their centre of activity (Vercauteren and Hyingstrom 1998, Kilpatrick and Lima 1999). In several cases, changes in spatial behaviour are transitory: hunted animals move to a refuge area outside of their home range during the hunting season, but in some cases they move back within a few days (Jullien et al. 1991; Jeppesen 1987; Vercauteren and Hyingstrom 1998), while in other cases they move back at the end of the hunting season (Millspaugh et al. 2000).

The effects of hunting pressure on spatial behaviour depend on several factors, including habitat characteristics (Vercauteren and Hyingstrom 1998; Conner et al. 2001; Millspaugh et al. 2000), the hunting method employed (Root et al. 1988; Millspaugh et al. 2000; Vieira et al. 2003) and the level of hunting pressure (Johnson et al. 2004). Social structure is also important for animals which live in a group: the loss of an individual may have different consequences depending on the hierarchical role it played within the group (Tuytten and McDonald 2000).

Few studies have monitored the effects of drive hunts on the choice of resting sites by wild boar family groups, and the results that exist are controversial. Hunted boar may enlarge their resting range, increase their length of movement or move to un-hunted areas outside their resting ranges in response to hunting pressure (Maillard 1996; Brandt et al. 1998; Calenge et al. 2002; Sodeikat and Pohlmeier 2003), though contrasting results (Jullien et al. 1991; Keuling et al. 2005, 2008b) have shown that boar remain within established resting ranges.

The aim of this study was to investigate the presence of short-lived changes in the spatial behaviour of wild boar family groups during the hunting season by detecting possible variation in the home range size and in its internal spatial structure during the hunting season. A knowledge of the response of wild boar family groups to hunting pressure may help improve management strategies. In fact the displacement of wild boar by drive hunts can reduce the effectiveness of management plans and worsen conflicts with farmers and landholders. For improved management of the species, it is therefore important to minimise the spatial instability induced by hunting.

Study area

The study area (about 20,000 ha) was located in the northern Apennines, Italy (44°16'49.32" N, 11°28' 37.49" E, Fig. 1). Elevation ranges were from 200 m a.s.l. to 1,200 m a.s.l.. The climate was temperate (the mean yearly temperature is 12°C, with variation according to the altitude). Precipitation is concentrated in spring and autumn, mean annual precipitation reaching about 1,000 mm and the mean snow cover length being 25–30 days per year. At lower altitudes (<600 m), the landscape was highly fragmented with fields and orchards (48% of the total area) interspersed with shrubland and woodland. The scrub layer was dominated by Spanish broom (*Spartium junceum*), dog rose (*Rosa canina*) and several bramble species (*Rubus* sp.). Tree species were few and mainly represented by downy oak (*Quercus pubescens*), white poplar (*Populus alba*) and false acacia (*Robinia pseudacacia*). At higher altitudes, woodland was more widespread, and the forest community was composed of downy oak, turkey oak (*Quercus cerris*), hop-hornbeam (*Ostrya carpinifolia*), manna ash (*Fraxinus ornus*), common beech (*Fagus sylvatica*) and European chestnut (*Castanea sativa*).

Forage for wild boar was abundant throughout the year, and supplemental feeding (corn and chestnuts) was provided by hunters, especially during autumn and winter.

There was an occasional wolf presence (*C. lupus*) but no other wild boar predators.

In the study area, wild boar hunting occurred twice a week from the first of November to the 31st of January.

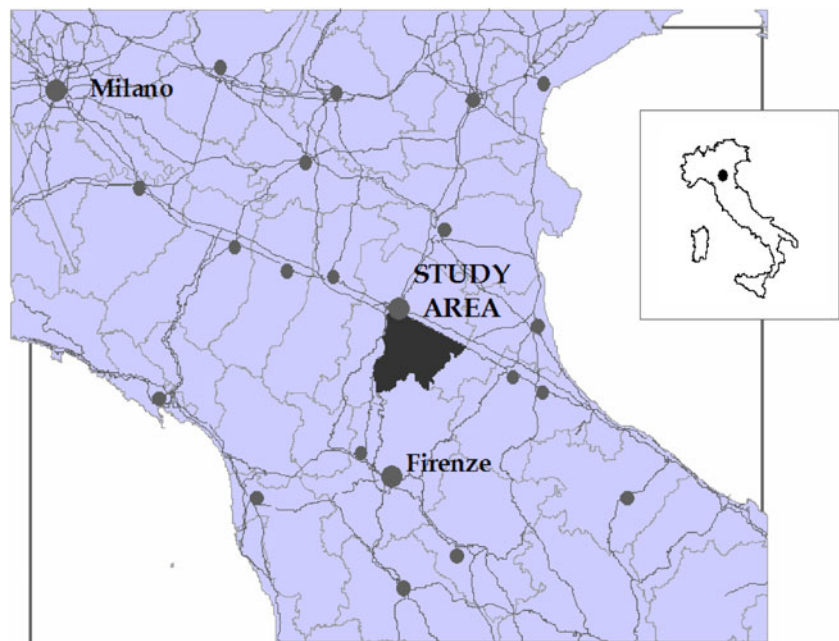
Hunting was carried out by several teams which had the exclusive right to hunt in a specific hunting area, with assigned minimum and maximum numbers of wild boar to harvest each year. The hunting teams, which operate mainly for recreational purposes and for the meat, aimed to maximise the number of animals shot in their area but at the same time preserve the reproductive segment of the population in order to have enough animals to hunt the following year. The hunting method used was the drive hunt, in which wild boar were chased by beaters with hounds and forced to run towards the hunters (hereafter called “shooters”) posted in strategic points around the hunted area (i.e. mountain ridges). Hunters communicated with each other using radio receivers in order to coordinate their actions, especially in relation to the dogs’ movements. The dog breeds employed were: ariege hound, griffon nivernaise, Istrian hound and Italian hound; all of which are typically capable of following the olfactory tracks of the boar (Monaco et al. 2003). If a dog leaves the drive hunt area while following the boar’ tracks, beaters use radio receivers to alert other hunters and to try to retrieve it as soon as possible.

Materials and methods

Data collection

Characteristics and effectiveness of drive hunts For each hunting intervention which occurred in the entire hunting

Fig. 1 Map of the study area (in dark grey) and its location in Italy



district during 2003–2004, we recorded data regarding the size and shape of the hunt area, the start and end times, the number of hunters and dogs, the composition of the pack, the numbers of shots, the barking of the dogs and the total number of wild boar shot. We also had a long-term data set detailing the characteristics of the wild boar which were shot: records were kept for each animal killed (sex, estimated age, eviscerated weight, females' reproductive status and the identifying numbers stamped on marks ear-tagged boar).

Wild boar capture and monitoring We captured wild boar using corral traps and mobile box traps baited with maize and chestnuts. We weighted, measured, aged by dentition (Monaco et al. 2003) and ear tagged all animals. Wild boar which were heavier than 30 kg were immobilised using a mix of tiletamine, zolazepam (Zoletil 100®) and Xylazine (Rompum®; Fenati et al. 2008). Sub-adult animals were fitted with an ear tag VHF radio device (Biotrack, UK), while a VHF radio collar (TXH3 Televilt, Sweden) was used for the adults (Monaco and Carnevali 2004). We captured a total of 279 wild boar (57% captured and 43% recaptured) and radio equipped 35 boar. Twenty of the radio-tagged wild boar (15 sows and five young males) belonged to ten family groups, as identified from sightings and capture–recapture data.

We collected data from October 2003 to April 2005, monitoring two hunting seasons. Several studies show how in hunted areas wild boar activity is strictly concentrated in nocturnal hours, while animals remain in resting sites during daylight (Mauget et al. 1984; Boitani et al. 1994; Maillard 1996, Monaco and Scillitani 2006). We therefore located resting sites once a day only for at least 20 days per month and twice a day (repeated localisations: one in the morning and one in the afternoon) on 10 days per month. During drive hunts, we performed intensive monitoring sessions (one localisation every 5 min) of radio-marked wild boar which were resting within (or near) the drive hunt area, in order to detect their reactions and follow their escape movements. Surviving wild boar were located every 15 min until the following day when they went to rest in a new resting site. Hunters were not informed about the position of radio-marked wild boar. During the hunting, we listened in constantly to the hunters with radio receivers so as to better understand how beaters with dogs were moving in the drive hunt area.

We performed triangulation with a portable receiver (R-100 Communication specialist, TRX-2000 Wildlife Materials Inc., USA) and a hand-held yagi antenna (Wildlife Materials Inc., USA); locations were computed using a minimum of three bearings obtained with LOCATE II (Nams, 1990).

Data analyses

Characteristics and effectiveness of drive hunts We investigated the effectiveness of drive hunting during the two hunting seasons. We computed a multiple regression analysis to analyse the number of boar harvested in the all hunting district from 2003–2005 in relation to the number of hunters (beaters and shooters) per square kilometre and the number of dogs per square kilometre. We also performed a linear regression between the number of boars harvested and the number of shots recorded during a hunt. The number of boar harvested was log-transformed to meet a normality assumption.

Wild boar spatial behaviour For each analysis, we used only resting site locations which allowed a good description of the disturbance caused by hunting. As hunting activity took place in daylight while some boar were in their resting sites, and as several studies (Dardaillon 1986; Meriggi and Sacchi 2000; Maillard 1996) point out that wild boar resting sites are located in shrubby or wooden habitat which guarantee shelter from predators, changes in resting site distribution may therefore be related to hunting activities. The use of resting site locations also facilitates a comparison with similar studies (Maillard and Fournier 1995; Calenge et al. 2002; Sodeikat and Pohlmeier 2007).

The analyses were computed at a monthly and seasonal level. We identified three seasons: pre-hunting (first of July to 31st of October), hunting (first of November to 31st of January) and post-hunting (first of February to 30th of June). Data from the 2-year study were pooled together after checking for differences in climate conditions (ANOVA: minimum temperature: $F_{1,347}=1.04$, $p=0.378$; maximum temperature: $F_{1,347}=1.04$, $p=0.378$; precipitation: $F_{1,347}=1.04$, $p=0.378$) and in hunting intensity (number of drive hunts: Mann–Whitney test, $U=121.50$, $p=0.131$; number of dogs used: Mann–Whitney test, $U=77989.00$, $p=0.762$).

Resting range We determined the seasonal resting range (the area including resting locations, Maillard and Fournier 1995) size using 100% Minimum Convex Polygon (MCP) and 95% kernel estimators and core areas with 50% kernel estimators. We expected to find an enlarged resting range size during the hunting season as a consequence of hunting disturbance.

Location of resting site Resting range size may provide little information about changes in resting site geographical position. We therefore measured:

- The straight-line distance between consecutive resting sites

- The interspersions of resting sites as an average of distances of resting sites from the arithmetic centre of their distribution
- The capture site fidelity: the distance between each resting site and the capture site location
- Human infrastructure avoidance: the distance between resting sites and human settlements (both single houses and villages) and roads (whether paved or gravel)

During the hunting season, we expected to find a higher variability in resting site location; thus, we predicted increased distances between resting sites and from the capture site, as well as a higher degree of interspersions. Wild boar should choose resting sites far from human infrastructure throughout the year, but during the hunting season we expected to find an increase in the avoidance of human infrastructure and especially of the gravel roads used by hunters.

Avoidance of hunted areas A more detailed analysis was performed to assess, on a small scale, the effect of hunting activity on resting site location. For each drive hunt, we compiled hunting maps which gave a measure of the relative shooting risk for the wild boar. Each map was composed of: (1) a high-risk area, the area involved in the drive hunt; (2) a low-risk area, the boundary area (a buffer zone of 500 m around the drive hunt area) in which wild boar could hear dogs and shots easily; and (3) a no-risk area, the external area not affected by the drive hunt. We superimposed buffered locations of the resting sites ($r=250$ m, which corresponds to the measured maximum telemetry error) occupied before and after the drive hunt onto these hunting maps in order to calculate the percentage use of areas with different impacts. Finally, we calculated the distance between the centroid of the high-risk area and the resting sites used by the wild boar on the hunting day and the following day. We expected an avoidance of high-risk areas after a drive hunt by animals initially resting within the high- and low-risk areas.

In each analysis, we tested differences between months or seasons using a Kruskal–Wallis H test (hereafter KWt). For pair comparison between seasons, we used the Mann–Whitney U test (MWt). To test differences between hunting days and days free from hunts, we used the Wilcoxon (Wt) test for paired data. Differences among frequency distributions were tested by means of the chi-squared (χ^2) test.

We used the statistical software SPSS 13® (SPSS Inc.) and SAS 9.1® (SAS 1989) in all analyses. Data handling and spatial analyses were conducted using ArcView GIS 3.2® (ESRI) with Spatial Analyst (Environmental Systems Research Institute 1992) and Animal Movement 2.0 (Hooge and Eichenlaub 2001) extensions.

Results

Characteristics and effectiveness of drive hunts The hunting teams were composed of an average of 23 hunters (range, 7–67) and eight dogs (range, 4–18). The mean duration of a drive hunt was 3 h and 40 min. During the hunts, we recorded an average of 24 shots (range 2–103), in many cases the beaters using shots to increase the rate of disturbance in the area and to try to force wild boar to move towards shooters. The area involved in a drive hunt was from 34.4 to 649.0 ha wide (mean value=165.3 ha SD=104.7 ha). The same area was hunted from one to eight times during a hunting season (mean value=2.6 times SD=1.5). The mean number of hunters per square kilometre was 25.31 (SD=19.01), divided into 4.49 beaters per square kilometre (SD=3.81) and 20.85 shooters (19.01 SD) per square kilometre. Although several other species were hunted in the study area between June and March, the largest number of hunters and dogs present in the study area (64.3% of the total number of hunters who hunt in the area) was observed during the wild boar hunting season. A mean number of 2.49 wild boar were shot per square kilometre (SD=4.50), and an average of 2.74 boar were harvested in a single drive hunt (SD=3.24). We found a significant level of regression ($F_{3,628}=5.28$, $p=0.001$) between the hunting bag achieved and the variables investigated, but the R^2 obtained was very low ($R^2=0.025$) indicating that the model used does not consistently explain the variation in the hunting bag size. The estimated regression coefficients are reported in Table 1. Neither the number of dogs per square kilometre nor the number of beaters per square kilometre affected the number of boar killed. The number of shooters per square kilometre was the only factor that was significantly related to the hunting bag achieved ($p=0.003$); however, the regression coefficient is almost null ($b=0.003$), indicating a weak linear relationship.

The total number of shots was not related to the hunting bag obtained ($F=0.46$, $p=0.503$).

Resting range and movements Resting range size calculated with 100% MCP varied significantly from season to season (KWt, $H=6.40$, $df=2$, $p=0.041$), while no significant variation was found either for 95% kernel size (KWt, $H=3.62$ $df=2$, $p=0.164$) nor for 50% kernel (KWt, $H=5.19$, $df=2$, $p=0.074$). We observed an enlarged resting range size during the hunting season (Table 2). During the hunting season, three family groups abandoned their pre-hunt resting range and established a new one outside of the familiar territory. In all of these cases, the group had been repeatedly hunted within a short time (two or more times per month) or had lost adult females which were the leading

Table 1 Relationship between the number of wild boar shot in drive hunts and the number of hunters and dogs per Km²

	DF	Estimated <i>b</i>	SE	<i>t</i> value	<i>p</i>
Intercept	1	1.118	0.04409	25.36	<0.001
Beaters/km ²	1	0.004	0.01211	0.3	0.764
Shooters/km ²	1	0.008	0.00268	3.01	0.003
Dogs/km ²	1	-0.007	0.00565	-1.32	0.188

components of the group. We defined these groups “heavily hunted” in contrast to groups which were chased less often (one drive hunt per month). The mean resting range size for heavily hunted family groups during the hunting season (1,775 ha) was larger than the value observed in groups subjected to a lighter hunting pressure (255 ha; MWt: $U=2.00$, $p=0.083$). Figure 2 reports the case of a family group which was hunted five times during a month and progressively moved away from the area occupied during the pre-hunting season. At the end of the hunting season, the remaining individuals from the group (a sow and a juvenile male) remained in an area 15 km far from the capture site.

The distance between consecutive resting sites followed the same seasonal pattern observed for resting range size: the greatest distances occurred during hunting and post-hunting seasons (KWt: $H=28.38$, $df=2$, $p=0.000$; Table 3). We observed the same pattern on a monthly basis (MWt: November, $U=1119$, $p=0.053$; December, $U=646$, $p=0.03$), except in January (MWt: $U=336$, $p=0.812$). However, this may be due to the reduction in the sample size during the first 2 months of hunting. More in detail, mean distances were greater on hunting days, compared to those for non-hunting days (MWt: $U=5235$, $p=0.001$).

The higher spatial instability during hunting season was confirmed by the analysis of the interspersion of resting sites. During the hunting season, resting sites were more interspersed within the resting range area than during pre-hunting and post-hunting seasons. Observed seasonal values differed significantly (Fig. 3; KWt: $H=138.23$, $df=2$, $p=0.000$) and paired comparison between seasons confirmed this pattern (MWt: pre-hunting vs hunting seasons $U=18013.5$, $p<0.001$; hunting vs post-hunting,

$U=68785.5$, $p<0.001$; pre-hunting vs post-hunting, $U=12938.0$, $p<0.001$). The tendency of family groups to occupy different geographic areas for resting was also indicated by the frequency distribution of kilometre classes of distances from the capture site, which differed significantly between seasons (χ^2 test, $\chi^2=115.23$, $df=10$, $p<0.001$, Fig. 4). Distances greater than 4 km were observed only during the hunting and post-hunting seasons, and distances above 10 km occurred only in the hunting season; however, once we had isolated data from heavily hunted groups from that for other groups, it was clear that the less hunted animals remained within the 4 km value all year long, while the higher distance values occurred only for the heavily hunted groups. In fact, during the hunting season, we observed a progressive monthly increase in the average distance from the capture site in all heavily hunted groups in contrast to animals which experienced lighter hunting pressure (Fig. 5; MWt: $U=18290.00$, $p=0.000$).

We observed a high significant difference in the avoidance of different kinds of human infrastructure (KWt: $H=102.542$, $df=3$, $p=0.000$): wild boar resting sites were located further from paved roads and villages than from gravel roads and single settlements. We found no seasonal pattern of avoidance for any of the human settlements and roads (KWt: single settlements, $H=5.73$, $df=2$, $p=0.057$; villages, $H=3.46$, $df=2$, $p=0.208$; paved roads, $H=3.46$, $df=2$, $p=0.178$; gravel roads, $H=0.340$, $df=2$, $p=0.844$).

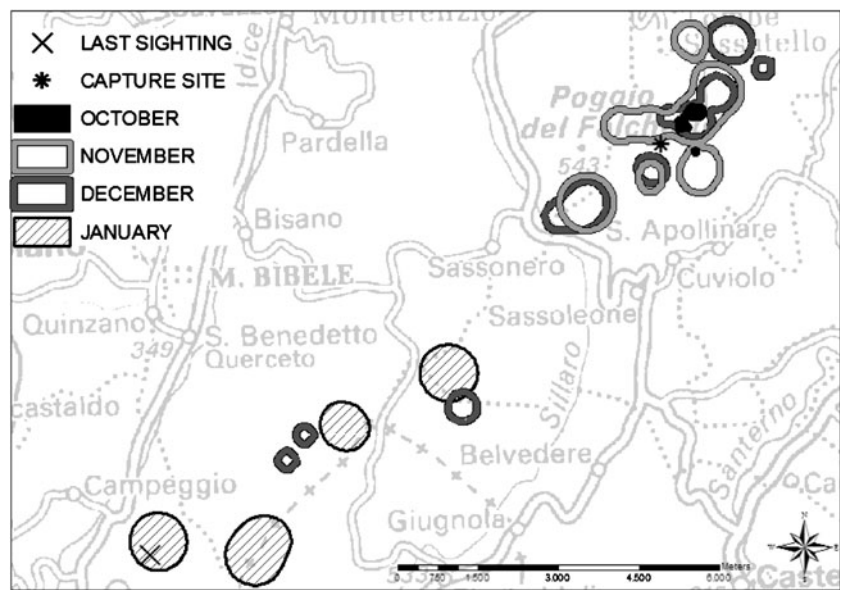
Avoidance of hunted areas Only wild boar resting in high-risk areas avoided hunted areas. A paired comparison of habitats used before and after the hunting day (Fig. 6) showed a significant change in the use of high-risk areas (Wt, $Z=-2.24$, $p=0.025$) and no-risk areas (Wt, $Z=-2.23$, $p=0.026$), while no changes were detected for the use of low-risk areas (Wt, $Z=-0.14$, $p=0.89$). Likewise, the distance between resting sites and the centroid of high-risk area on the day after the hunt only increased significantly (Wt, $Z=-2.66$, $p<0.008$) for family groups which had been resting in high-risk areas (Fig. 7).

These results were confirmed by the data obtained from the intensive radio-tracking sessions performed during

Table 2 Median values, interquartile distances and arithmetic mean with standard error of seasonal resting range size for wild boar family groups, calculated by means of 100% MCP, 95% and 50% kernel

Season	100% MCP				95% kernel				50% kernel			
	Median	Q ₃ -Q ₁	Mean	SE	Median	Q ₃ -Q ₁	Mean	SE	Median	Q ₃ -Q ₁	Mean	SE
Pre-hunting	80	104	88	25	66	156	98	39	4	14	10	3
Hunting	428	1360	825	358	221	696	457	192	23	68	45	16
Post-hunting	195	544	358	151	189	488	284	99	20	88	45	20

Fig. 2 Monthly changes in resting range size and geographical displacement observed in a family group (composed of three females and at least five piglets) which was subject to intensive hunting pressure. The asterisk indicates the capture site. At the end of the hunting season, only one female and one juvenile male survived, in the area indicated by the “X”



drive hunts on wild boar family groups resting inside high-risk areas: 76% of family groups moved when the dogs found them and started chasing them, while the remaining 24% of wild boar remained at the resting site for the whole duration of the drive hunt because the dogs did not directly chase them. In contrast, none of the family groups resting in low-risk areas moved for the entire duration of the drive hunt, except in one case in which a dog moved out of the high-risk area into the low-risk area and chased the group.

Discussion

The results of this study suggest that intensive hunting activity may affect the spatial behaviour of wild boar family groups. Most of the studies on wild boar spatial behaviour have focused on factors affecting the home range size. Wild boar home range size is mainly affected by sex, the availability of food and population density (Wood and Brenneman 1980; Singer et al. 1981; Boitani et al. 1994; Maillard 1996; Massei et al. 1997). Few studies have detected a marked seasonal variation due to environmental

factors (Singer et al. 1981; Gabor et al. 1999; Lemel et al. 2003; Keuling et al. 2008a), but they do refer to study areas with harsh climatic conditions in which the weather can affect the availability of forage. In this study, we considered only family groups, and we used resting sites which are mainly influenced by the shelter provided rather than by the abundance of food resources or by weather conditions (Dardaillon 1986). In addition, in our study area, the climate was mild all year long, the snow depth was not a limiting factor, hunters provided artificial feeding whenever a shortage of natural forage occurred, and there were no

Table 3 Median values (with relative interquartile distances) and arithmetic mean (with standard error) of seasonal distances between consecutive resting sites

Season	Median (ha)	Q ₃ -Q ₁	Mean (ha)	SE
Pre-hunting	186	381	286	24
Hunting	383	864	891	87
Post-hunting	401	757	733	74

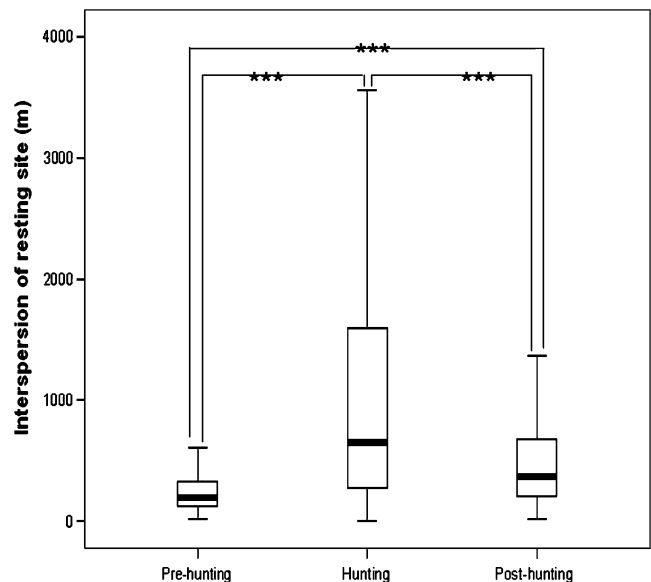


Fig. 3 Box and whisker graph for the seasonal interspersion pattern of wild boar resting sites within the resting range area. ****p*<0.001

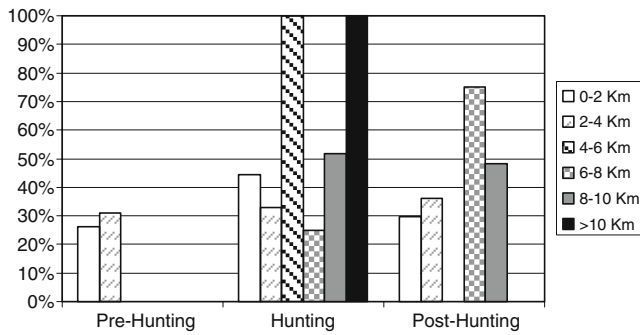


Fig. 4 Frequency distribution of distances between resting sites and capture sites

established populations of predators. Human activity peaked during the 3 months of wild boar hunting, while for the rest of the year human presence and activity was low (Scillitani 2006). Therefore, the modifications in spatial behaviour occurring during the hunting season were most likely due to hunting activity.

In this study, we observed changes in the seasonal distribution of resting sites of wild boar family groups and therefore an altered spatial behaviour. During the hunting season, we observed an enlarged resting range size and a significant raise in spatial instability. Moreover, during the hunting season we observed an increased distance between consecutive resting sites, which were also more interspersed, meaning that wild boar not only chose resting sites further from each other but also tended towards considerably reduced site fidelity. According to some studies (Mauget 1980; Kowalski 1985), wild boar alternate “nomadic phases”, in which they change resting site location every day, with “sedentary phases”, in which they use always the same place. We did not find such a clear pattern but, in line with other studies (Maillard 1996), we recorded a high individual variability amplified by the occurrence of hunting activity, as indicated by the greater distances between resting sites recorded on days following

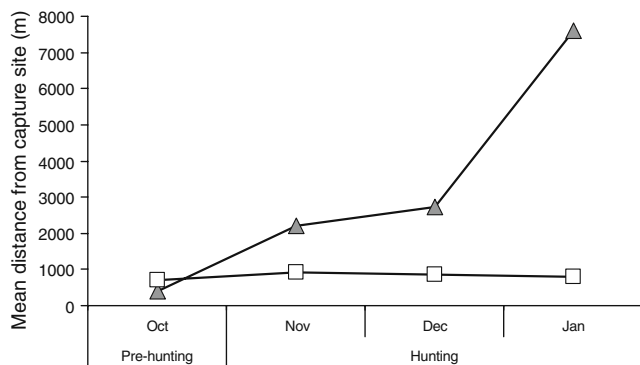


Fig. 5 Mean distances from capture site observed in heavily hunted family groups (grey triangles) and in wild boars subjected to a lighter hunting pressure (white squares)

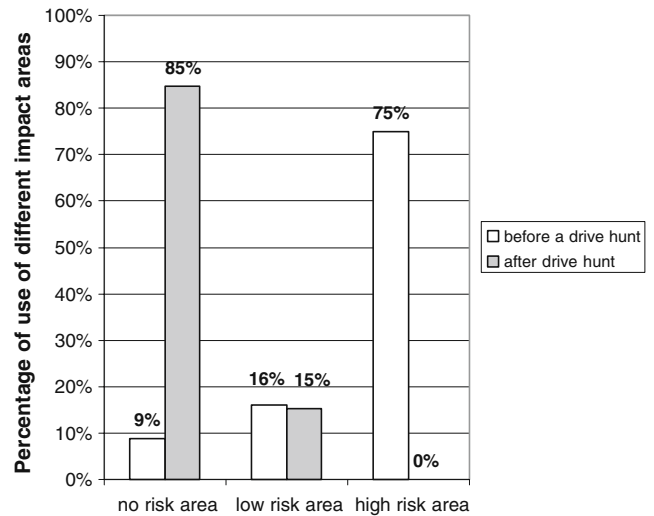


Fig. 6 Percentage of use of no-risk, low-risk and high-risk areas before a drive hunt (in white) and after it (in grey) by animals involved in a drive hunt

a drive hunt. During the hunting season, we also observed an increased tendency to change resting site in daylight (Scillitani 2006), though this was rare. In fact, in our study area, wild boar were active during the night, and the start of the active phase strongly correlated with the hour of sunset (Monaco and Scillitani 2006), as has also been observed for other populations subject to hunting pressure (Briedermann 1986).

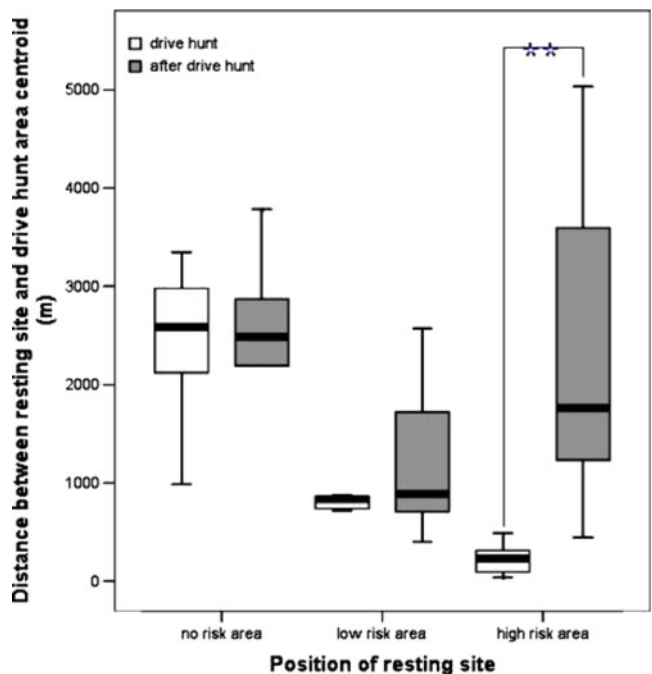


Fig. 7 Box and whisker graphs of the distance of resting sites from the centroid of a drive hunt area, as observed before (in white) and after a drive hunt (in grey). ** $p < 0.01$

As a consequence of drive hunts, some family groups left their familiar territory and moved considerable distances away, sometimes over 10 km from the area where they had been captured. According to other studies (Maillard 1996; Brandt et al. 1998; Sodeikat and Pohlmeier 2003), these displacements of family groups are usually short lived since they return to their familiar areas at the end of hunting season. In contrast, our data, which were obtained from the recovery of ear tags of shot animals and from radio telemetry, seem to indicate that intensively hunted family groups left their familiar areas definitively (Monaco and Scillitani, unpublished data).

Conversely, the response of wild boar to hunting disturbance seemed to be highly related to the degree of hunting pressure combined with individual variability. The groups exposed to intensive hunting disturbance (both in terms of the frequency of drive hunts and the loss of components) were the ones which showed a significantly increased spatial instability and moved away to other areas. On the contrary, groups exposed to lighter hunting disturbance showed a stronger site fidelity and increased their movements within their habitual range or slightly enlarged their resting range area.

A similar behavioural pattern is also reported by other authors (Maillard and Fournier 1995; Brandt et al. 1998; Baubet et al. 1998; Sodeikat and Pohlmeier 2007), though some found only a slight modification of spatial behaviour and attributed seasonal variability in wild boar movements to factors other than hunting (Keuling et al. 2005, 2008b). However, the frequency of drive hunts in the areas concerned was much lower than that observed in this study: one of our marked family groups was directly involved in a drive hunt on four occasions in the space of a week.

Wild boar are often described as a sedentary species (Vassant et al. 1992). Our results confirm a tendency towards spatial stability in family groups: wild boar showed a high tolerance of human activities other than hunting, and we found no increased avoidance of human infrastructure during the hunting season, though we expected a negative selection of areas near gravel roads used by hunters. Moreover, only wild boar directly involved in drive hunts escaped or altered their activity patterns, while animals resting in low-risk areas, where shots and dog barking were clearly audible, remained in their resting sites and used the hunted area the following day. Even during drive hunts, family groups did not move until the dogs actively harassed them. This hiding behaviour is probably an anti-predator strategy, and it is interesting to notice that in the cases in which wild boar were resting inside the hunted area but were not found by the dogs, no displacement was found. This may indicate that wild boar tolerate hunting disturbance and react only when directly persecuted. Consistent with this hypothesis are the results of a comparison of

different hunting methods in Switzerland and France (Tolon et al. 2008), which showed how boar involved in drive hunts moved more than animals stalked by a single hunter. In contrast, a study in Northern Germany (Keuling et al. 2008b) found no significant differences between hunting methods, though it also found that hunting had a slight impact on wild boar spatial behaviour.

In conclusion, family groups reacted to drive hunts if directly chased by dogs and beaters but moved to areas far from their native range only when frequently disturbed. In lightly hunted areas, the behavioural modification exhibited were less pronounced and short lived.

Management implications

The results of this study may have some useful implications for the improvement of the management of wild boar, especially in Italy. As previously stated, wild boar may be considered a pest species, and the major increase in numbers is a great concern for wildlife managers. A management priority is to encourage the culling of wild boar to reduce overall numbers. However, hunters are interested in maintaining a high density of wild boar so as to maintain a constantly high number of animals to hunt.

Our results showed that drive hunts can alter the spatial behaviour of wild boar family groups. Nevertheless, the magnitude of this altered behaviour is highly variable: in most cases, the response of wild boar is moderate, though it increases steadily with hunting pressure and can culminate in the permanent abandonment of the home range area. The displacements exhibited by wild boar family groups are an indication of the hunting disturbance suffered by the animals but are also a major problem for management policies. First, most of the areas frequented by the species are interspersed with cultivated land, and the increased range of wild boar due to hunting activities can result in an increase in crop damage which may exacerbate the conflict between boar and farmers and between hunters and farmers. Furthermore, wild boar can play a role as a reservoir and vector of diseases which affect domestic animals (Aubert et al. 1994; Fritzeimer et al. 2000; Rossi et al. 2004), so increased displacement of family groups should also be avoided in the interests of effective sanitary management.

Finally, most Italian territory is made up of a fine mosaic of different management units (each with their own hunting quota to achieve during the hunting season); even a short range displacement of wild boar can significantly affect the local density of the species and consequently the hunting bags. As previously described, in fact, a family group is often made by up to 20 individuals.

On the basis of our results we propose to reduce hunting pressure in order to minimise the human-induced displacements of wild boar. Since wild boar family groups move away from hunted areas only if heavily disturbed, we strongly recommend the avoidance of repeated hunts in the same area at short time intervals in order to reduce the stress level of family groups and prevent the abandonment of their native areas. Moreover, as this study and similar ones (Maillard 1996) have shown, an important loss of the components of a group increases the spatial instability of the group and should therefore also be avoided.

The reduction of hunting disturbance should also be achieved by decreasing the number of dogs and the number of beaters. In fact, as our analysis of drive hunt effectiveness shows, hunting efficiency is related neither to the number of dogs used nor to the number of beaters, but there is only a weak relationship with the number of shooters per square kilometre. However, since the level of correlation was really low, an increase in the number of shooters would not reliably improve the hunting effectiveness. Therefore, rather than employing a big pack, hunters should rely use of few and well-trained hunting dogs which will selectively search for wild boar only, will actively stalk the animal but will give up the chase in case of a charge and will immediately come back to its owner when called, even if following a track (Monaco et al. 2003). Data on wild boar hunts with a single well-trained dog show that the harvest can be even more successful than using drive hunts. The number of harvested boar per dog and per participant was higher and, as a consequence, the quantity of meat per hunter was greater (Monaco, unpublished data). Adopting this method, the hunt would be more productive, the management of the species would improve, and the impact on the spatial behaviour should be reduced at the same time.

Furthermore, cutting back on the number of beaters and dogs also reduces the disturbance of other species, in particular in areas where species of high conservation concern, such as the brown bear, are present.

In conclusion, we believe that adopting the proposed actions (reducing the size of dogs' pack and avoiding repeated hunting intervention in the same area in a short time) would significantly improve the management of the species. In fact, the negative consequences of human-induced displacements of family groups would be minimised, but at the same time, hunting bag would not decrease.

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