



HAL
open science

Does mast seeding shape mating time in wild boar? A comparative study

Jessica Cachelou, Christine Saint-Andrieux, Eric Baubet, Éveline Nivois, Emmanuelle Richard, Jean-Michel Gaillard, Marlène Gamelon

► To cite this version:

Jessica Cachelou, Christine Saint-Andrieux, Eric Baubet, Éveline Nivois, Emmanuelle Richard, et al.. Does mast seeding shape mating time in wild boar? A comparative study. *Biology Letters*, 2022, 18 (7), 10.1098/rsbl.2022.0213 . hal-03736665

HAL Id: hal-03736665

<https://cnrs.hal.science/hal-03736665v1>

Submitted on 10 Oct 2022

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Research



Cite this article: Cachelou J, Saint-Andrieux C, Baubet E, Nivois E, Richard E, Gaillard J-M, Gamelon M. 2022 Does mast seeding shape mating time in wild boar? A comparative study. *Biol. Lett.* **18**: 20220213. <https://doi.org/10.1098/rsbl.2022.0213>

Received: 2 May 2022
Accepted: 27 June 2022

Subject Areas:
ecology

Keywords:
breeding time, oak seeding, pulse resources, seed consumers, phenology, comparative analysis

Author for correspondence:
Jessica Cachelou
e-mail: jessica.cachelou@gmail.com

Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.6080789>.

Population ecology

Does mast seeding shape mating time in wild boar? A comparative study

Jessica Cachelou^{1,2,3}, Christine Saint-Andrieux⁴, Eric Baubet², Eveline Nivois⁵, Emmanuelle Richard³, Jean-Michel Gaillard¹ and Marlène Gamelon^{1,6}

¹Laboratoire de Biométrie et Biologie Evolutive, UMR 5558, CNRS, Université Lyon 1, Villeurbanne, France

²Office Français de la Biodiversité, DRAS-Service conservation et gestion des espèces à enjeux, Montfort, Birieux 01330, France

³Fondation François Sommer, Pôle Nature, 3e arrondissement de Paris, 75003 Paris, France

⁴Office Français de la Biodiversité, DRAS-Service anthropisation et fonctionnement des écosystèmes terrestres, 8 Chemin de la Sablière, ZA SUD 67560 Rosheim, France

⁵Office Français de la Biodiversité, DRAS-Service conservation et gestion des espèces à enjeux, Chemin du Longeau, Rozérieulles 57160, France

⁶Department of Biology, Centre for Biodiversity Dynamics, Norwegian University of Science and Technology, Trondheim, Norway

JC, 0000-0002-2969-390X

In seasonal environments, the timing of reproduction often matches with the peak of food resources. One well-known effect of global warming is an earlier phenology of resources, leading to a possible mismatch between the timing of reproduction for consumers and food peak. However, global warming may also change the dynamics of food resources, such as the intensity and frequency of pulsed mast seeding. How quantitative changes in mast seeding influence the timing of reproduction of seed consumers remains unexplored. Here, we assess how yearly variation in mast seeding influences mating time in wild boar (*Sus scrofa*), a widespread seed consumer species. We took advantage of the intensive monitoring of both female reproduction (1636 females) and acorn production over 6 consecutive years across 15 populations of wild boar in the wild. We found that mating time occurs earlier when acorn production increases in most but not all populations. In two out of 15 populations, heavy females mated earlier than light ones. Our findings demonstrate that mast seeding advances the mating time in some populations, which could perhaps impact how boars respond to climate change.

1. Introduction

In seasonal environments, the timing of energy-demanding reproduction should match the resource peak [1,2]. There is increasing evidence in the literature for an earlier peak of resources in many ecosystems due to global warming, potentially leading to a mismatch between reproductive timing and resource peak when females cannot breed earlier [2–4]. This phenological mismatch can have negative demographic consequences through increased offspring mortality (e.g. in roe deer (*Capreolus capreolus*) [5] or muskoxen (*Ovibos moschatus*) [6]). However, earlier spring and increased food availability may also benefit females through improved reproductive success (e.g. reindeer (*Rangifer tarandus*) in Fennoscandia [7]).

In pulsed-resource environments, global warming is expected to change the dynamics of food resources. For instance, both the intensity and frequency of mast seeding, a well-known example of pulsed-resources, are influenced by warmer environmental conditions (see [8] for review). Higher frequencies of seed production for European beech (*Fagus sylvatica* L.) [9,10] and oak (*Quercus* sp.) [11–14] and lower frequency for Norway spruce (*Picea abies*) [15] are expected under warmer conditions in some places. However, heterogeneity in the response

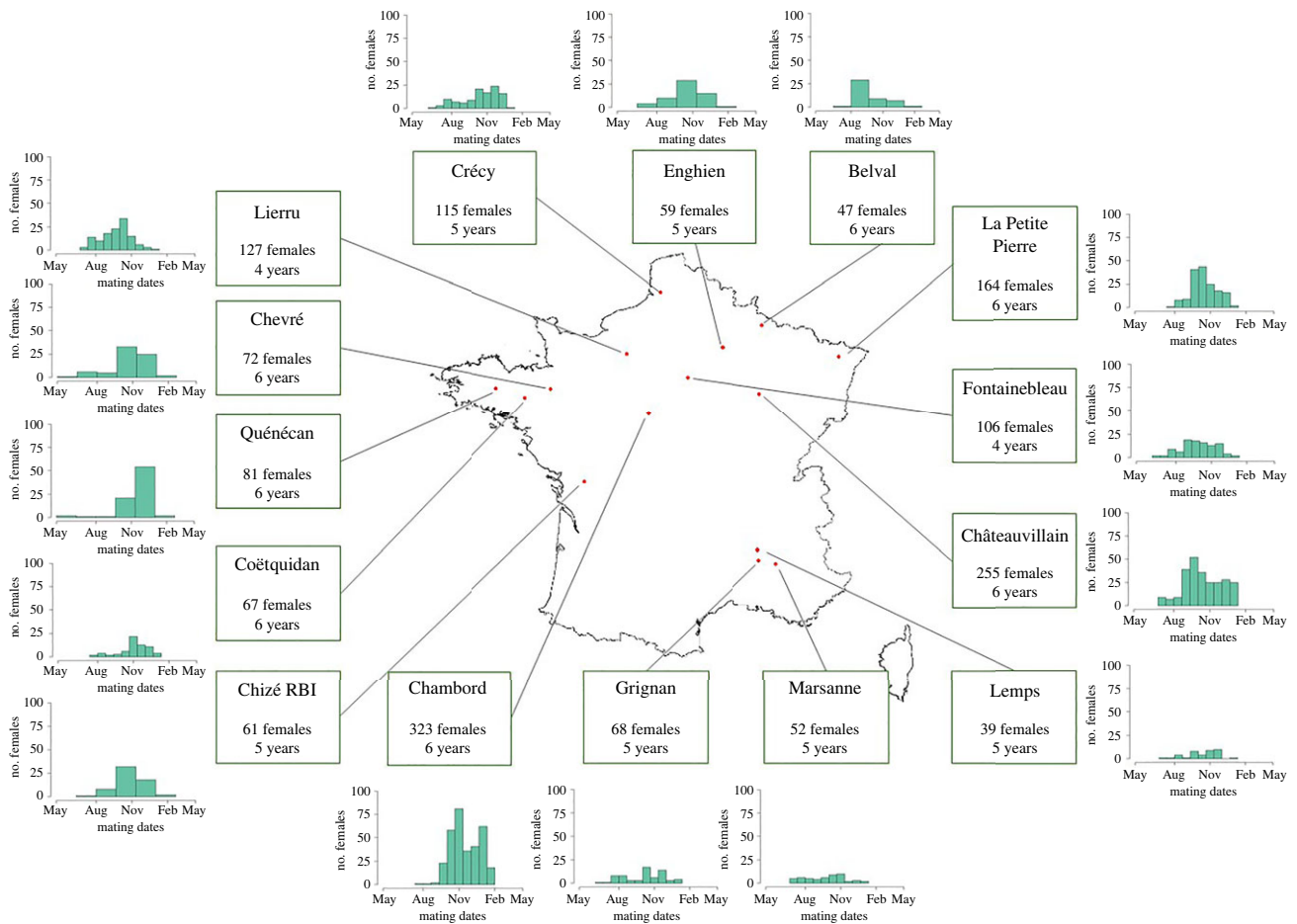


Figure 1. Location of the study sites in France. Displayed are the number of culled pregnant females, the study period and the distribution of mating dates during the study period for each site.

of trees to warmer conditions does exist across the globe [16]. In turn, these changes in resources may influence the reproductive output of consumer species. Brown bears (*Ursus arctos*) rely on berries, a pulsed-resource, during the summer and autumn [17] to build fat reserves, which are then allocated to reproduction [18,19]. Any changes in the amount of berries available may thus impact bears' reproduction. Likewise, high seed production positively influences the reproductive output of seed consumer species such as eastern chipmunk (*Tamias striatus*) [20] or wild boar (*Sus scrofa*) [11,21]. For the latter, improved reproductive performance following high acorn availability positively influences population growth rate [11,21–23], with potentially important implications for management and conservation [24]. Understanding how quantitative changes in mast seeding influence the timing of reproduction of seed consumers, not only their reproductive output, is crucial in the current context of global warming and remains to be investigated.

Here, we fill this knowledge gap using a widespread seed consumer species, the wild boar as a case study. This widespread species [25–28] is of high concern to biodiversity [29]. The species is omnivorous, but mainly feeds on pulsed-resources such as acorns when this resource is available [30–35]. Therefore, the level of acorn production in a given year at a given place reliably reflects wild boar consumption. From the analyses of reproductive tracts in 15 populations widespread across France, with detailed information on annual seed production [36], we assess the influence of acorn production on mating time. We predict earlier mating dates with increasing acorn production in all the studied populations.

2. Material and methods

(a) Study areas and data collection

Fifteen sites have been monitored in France from 2015 to 2021 (figure 1). Oak (*Quercus* sp., which included different oak species like *Quercus ilex* or *Quercus petraea*) was consistently present. Acorns fall between August and mid-November [37,38], and their production was measured annually on each site. From 1 August to 30 September, the canopy of 30 to 100 trees were sampled with binoculars by the same observers during 3 min. A seed production index was given to each tree [39], ranging between 0 (no seed) and 4 (high seed production, when hundreds of fruits were counted—see [38] for the whole protocol). The annual acorn production index was calculated for each site as the average of the tree-specific acorn production index in a given year.

We collected, in all sites, reproductive tracts of female wild boar shot during the hunting season (August–March). Shooting date and live body mass (in kg) were recorded for each female. Two age-classes (subadults (greater than 1 year and less than or equal to 2 years) versus adults (greater than 2 years of age) [40]) were distinguished using tooth eruption patterns [41]. Fetuses were measured (in mm) and the mating date was back-calculated thanks to the Mauget model [42], which links gestation stage (in days) to mean fetus length (in cm): [gestation stage = ((6.18 + mean fetus length)/1.85) × 7]. Mating date thus corresponded to the difference between shooting date and gestation stage. A total of 1636 pregnant females were analysed.

(b) Data analyses

To identify how the amount of mast seeding influences mating time, we fitted a linear model with mating time (in days) as the

Table 1. Model selection for the effects of acorn production index (I), population (P), age (A) and body mass (BM) on the mating time of female wild boar ($N = 1636$). N_p is the number of parameters, and $\Delta AICc$ is the difference in AICc between each tested model and the best one (in italics).

model	N_p	AICc	$\Delta AICc$
A + I + BM + P + I × P	33	16406.3	0.00
<i>I + BM + P + I × P</i>	32	<i>16406.7</i>	<i>0.37</i>
A + I + BM + P + I × A + I × P	34	16408.3	2.03
A + I + BM + P + A × BM + I × P	34	16408.4	2.07
A + I + BM + P + I × BM + I × P	34	16408.4	2.07

response variable. For each female, mating time was calculated as the difference between the estimated mating date and the first day of hunting (i.e. 18 August). The annual average acorn production in the population was included as an explanatory continuous variable (I). We accounted for possible population differences in mating time (site effect as a categorical variable, P), for a potential effect of age (categorical variable with two classes, A) and for the expected allometric effect of female body mass (continuous, BM) [35]. Interactions between acorn production and population, and between body mass and population were included to test for a different effect of acorn production and body mass on mating time according to the studied population. In the same way, interaction between acorn production and body mass was included to test for a different effect of acorn production on mating time according to female mass. Age class was added in interaction with all variables to test for age class differences.

We used the Akaike information criterion corrected for small sample size (AICc) for model selection and retained the model with the lowest AICc [43]. When the AICc difference between competing models was less than 2, we retained the model including the lowest number of parameters according to parsimony rules. Analyses were performed with R (v. 4.1.1) using the `lm()` function of the 'stats' package for linear model and function `dredge()` of the 'MuMIn' package [44] for model selection.

3. Results

The overall average mating time was around 79 days after 18 August, i.e. 6 November, but mating occurred during a wide period of time, in all sites (figure 1). Noticeably, as mating times were back-estimated from females shot during the hunting season, females mating too late (after the hunting season) could not be included in the analysis.

We found little evidence for an effect of the age (i.e. subadult versus adult) of the female on mating time, but strong evidence for among-population differences and complex interactions (table 1). The global model indicated that higher body mass and acorn production both led to earlier mating time (see electronic supplementary material, appendix S1). The same analysis conducted in each population separately, without age effect, thus allowed a simpler interpretation of these effects.

The best models retained for each population indicated that acorn production negatively influenced mating time in 12 out of 15 populations (table 2): the higher the acorn production, the earlier the mating time (figure 2). For instance, a change in the acorn production index from 1 to 3 at La Petite Pierre leads to a 59-day advance in mean mating time.

We also found evidence for an effect of body mass on mating time in three out of 15 populations (table 2). The

Table 2. Effects of acorn production index (I) and body mass (BM) on the mating time of female wild boar at each site. Predicted mating times (in days after 18 August) were calculated for a female of 65 kg and with an acorn production index of 1.4.

site	no. females	model	predicted mating time
Belval	47	I + BM + I × BM	93.86 ± 7.23
Chambord	323	I	121.42 ± 1.81
Châteauvillain	255	I	41.35 ± 3.19
Chevré	72	1	82.19 ± 5.61
Chizé RBI	61	I	61.07 ± 5.69
Coëtquidan	67	I + BM	95.98 ± 4.84
Crécy	115	I + BM	60.90 ± 6.93
Enghien	59	I	93.1 ± 8.76
Fontainebleau	106	I	65.80 ± 4.80
Grignan	68	1	65.21 ± 6.17
La Petite Pierre	164	I	65.97 ± 2.10
Lemps	39	1	71.44 ± 6.14
Lierru	127	I	49.78 ± 3.35
Marsanne	52	I	-11.14 ± 19.90
Quénécan	81	I	94.60 ± 5.87

heavier the females, the earlier the mating time for two out of three populations (figure 2). Thus, a 10 kg increase for a female of 65 kg in Crécy led to an advance of 5 days in mating time for a given year.

Predicted mating times were calculated from the best model retained in each population, for a female of 65 kg and with an acorn production index of 1.4 (table 2). We found wide variation in predicted mating times across populations. For instance, from 11.14 days before 18 August (i.e. 7 August) in Marsanne to 121.42 days after 18 August (i.e. 17 December) in Chambord. Noticeably, mating happened after the acorn crop in most populations.

4. Discussion

We found clear evidence for earlier mating times with increasing acorn production, and earlier mating times for heavier females in some but not all populations, which revealed high heterogeneity across populations and females. Variation in environmental conditions may influence both the timing and the amount of food resources. Some consumer species can track these changes by shifting mating time. For instance, topi (*Damaliscus korrigum*) and warthog (*Phacochoerus aethiopicus*) females were in better condition and gave birth earlier [45] during years with high food availability, and red squirrel (*Tamiasciurus hudsonicus*) females gave birth earlier following a year with high cone abundance [46]. There are some advantages of earlier breeding, such as offspring can take advantage of resource abundance, grow faster and increase their survival [47] through, for instance, reduced mortality by predation [48]. Likewise, our findings show that wild boar females can mate earlier when facing high resource availability, in some, but not all, populations. For instance, in Chevré, Grignan and Lemps, food availability had virtually no influence on

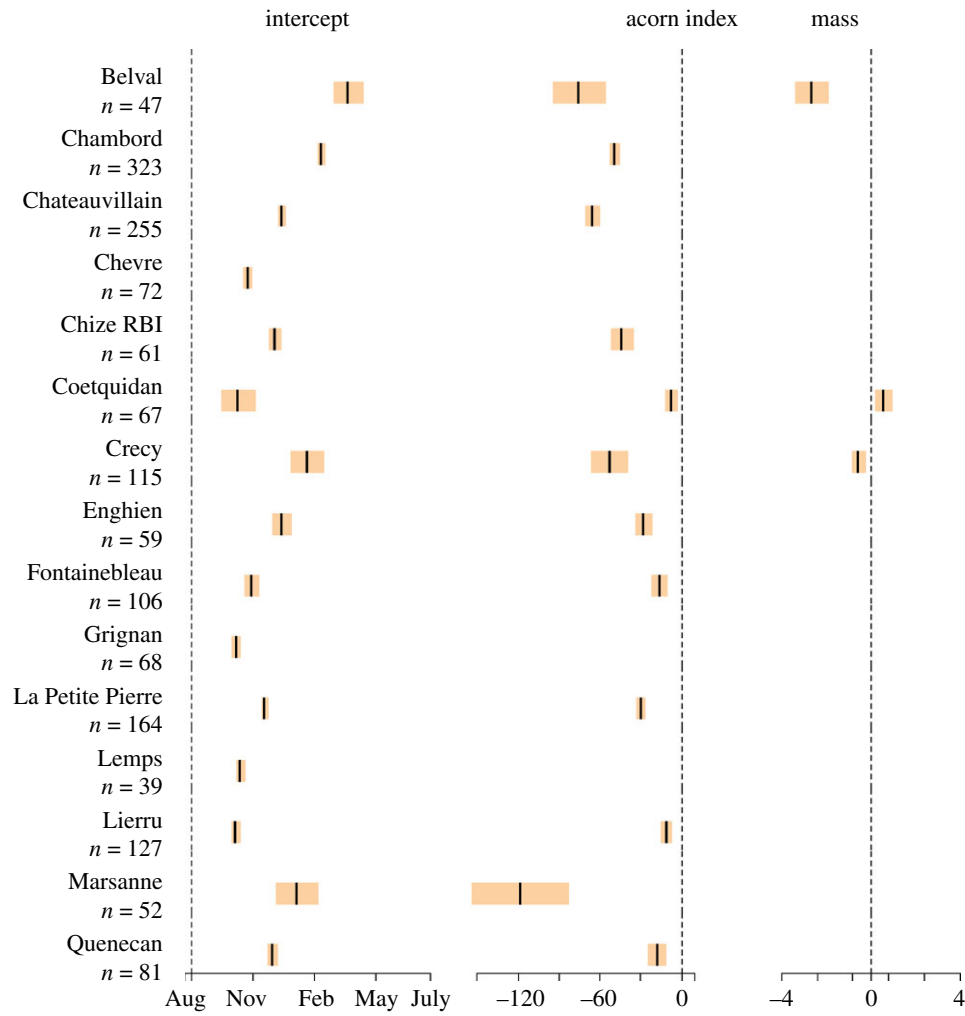


Figure 2. In columns, coefficients of the best models are retained (table 2) assessing the effects of acorn production index (I) and body mass (BM) on the mating time in all sites (in rows). Number of wild boar females at each site is represented. Displayed are the mean estimates (black) together with s.e. (orange). Zero values are indicated with dotted lines. For intercept, the dotted line corresponds to the first day of the hunting season (i.e. 18 August). For Belval, where the interactive effect of body mass and index was retained (table 2), intercept was displayed for a body mass of 65 kg and an acorn index of 1.4.

mating time. The heterogeneity of mating time response to changes in food availability we revealed across different wild boar populations questions the generality of previous conclusions based on a single wild boar population that both ovulation and pregnancy times take place earlier under good environmental conditions [49]. More generally, our findings demonstrate the importance of comparative studies.

Several studies have investigated the effect of resource availability on mating times on one single population [50–52]. For instance, the painted honeyeater (*Grantiella picta*) initiates clutches earlier when the fruit-abundance index increases [51]. For red squirrels, in the year following a high food availability, females reproduce earlier [50,52], up to 17 days [50]. Other studies have compared mating time responses to changes in food availability across species, i.e. at the interspecific level [53,54], but to the best of our knowledge, very few comparative studies among populations within a given species have been conducted (but see [55] for an example in house mouse (*Mus musculus*)). Notable exceptions include experiments, where the influence of supplemental feeding on breeding times in birds [56,57] and rodents [58–60] has been assessed. *In natura*, however, comparative studies on the effect of pulsed-resources on mating times remain very scarce (but see [50] for a study on Siberian flying squirrels (*Pteromys volans*)). Our comparative study is thus quite unique and provides novel insights into the effect of

acorn production—a pulsed-resource—on mating times, demonstrating high heterogeneity in mating time response to changes in food availability across populations. The high among-population heterogeneity we report from our comparative analysis of 15 populations with contrasting environmental conditions indicates that variation in population density [61], age structure [40], hunting pressure [35,40], weather conditions ([35,62,63,64] for instance), oak species, other food resources (e.g. beechnuts [35,65]), or interspecific competition [66] are all potentially fine-tuning mating time in a given population.

Wild boar females can thus adjust the timing of their oestrus, allowing earlier or delayed mating times, so that gestation starts at different times according to environmental conditions [35]. Although female wild boars reproduce each year [35], the timing of mating also depends on female body reserves [35]. Accordingly, we found that heavier females have earlier mating dates than lighter ones in some populations. Contrary to previous findings [67,68] (but see [40,69]), this result indicates that all females are not necessarily synchronized in their reproduction within a year [70]. This contrasts with all other ungulates living in seasonal environments, such as roe deer [71] or red deer [72], or mountain ungulates that all display high mating synchrony leading to high birth synchrony (with 80% of births in less than 30 days and 13 days, respectively).

5. Conclusion

In the current context of climate change, the potential of a species to adjust the timing of reproductive events is extremely beneficial because it can minimize the mismatch between reproductive timing and food resources. Wild boar illustrates the case of a species with highly plastic mating times, which might explain its success as a strongly widespread species nowadays [25–28]. Our research highlights the importance of comparative studies to better understand how ongoing climate change is likely to influence populations in the wild.

Ethics. All applicable institutional and/or national guidelines for the care and use of animals were followed.

Data accessibility. Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.zs7h44jck> [36].

Authors' contributions. J.C.: formal analysis, writing—original draft and writing—review and editing; C.S.-A.: data curation, project

administration and writing—review and editing; E.B.: funding acquisition and writing—review and editing; E.N.: data curation, project administration and writing—review and editing; E.R.: funding acquisition and writing—review and editing; J.-M.G.: supervision and writing—review and editing; M.G.: supervision and writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. This work was supported by the Research Council of Norway through its Centre of Excellence funding scheme, project number 223257.

Acknowledgements. We thank Thomas Abrial for preliminary analyses. This study is part of the programme 'Observatoire national du sanglier'. We are grateful to all the people involved in data collection, and all sites, hunters and owners with the Fédération des chasseurs of 51, 26, 56, 35, 27, 80, the Office National des Forêts of 77, Chambord, Belval, military's territory of Coëtquidan, Domaine of Lierru, Quénécan, La Petite Pierre, Chizé and Châteauvillain. We warmly thank the Editor, Ian Pearse and one anonymous referee for constructive comments on the previous draft.

References

1. Thomas DW, Blondel J, Perret P, Lambrechts MM, Speakman JR. 2001 Energetic and fitness costs of mismatching resource supply and demand in seasonally breeding birds. *Science* **291**, 2598–2600. (doi:10.1126/science.1057487)
2. Stenseth NC, Mysterud A. 2002 Climate, changing phenology, and other life history traits: nonlinearity and match–mismatch to the environment. *Proc. Natl Acad. Sci. USA* **99**, 13 379–13 381. (doi:10.1073/pnas.212519399)
3. Durant JM, Hjernmann DØ, Ottersen G, Stenseth NC. 2007 Climate and the match or mismatch between predator requirements and resource availability. *Clim. Res.* **33**, 271–283. (doi:10.3354/cr033271)
4. Parmesan C, Yohe G. 2003 A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42. (doi:10.1038/nature01286)
5. Plard F, Gaillard JM, Coulson T, Hewison AJM, Delorme D, Warnant C, Nilsen EB, Bonenfant C. 2014 Long-lived and heavier females give birth earlier in roe deer. *Ecography* **37**, 241–249. (doi:10.1111/j.1600-0587.2013.00414.x)
6. Kerby J, Post E. 2013 Capital and income breeding traits differentiate trophic match–mismatch dynamics in large herbivores. *Phil. Trans. R. Soc. B* **368**, 20120484. (doi:10.1098/rstb.2012.0484)
7. Tveraa T, Stien A, Bårdsen BJ, Fauchald P. 2013 Population densities, vegetation green-up, and plant productivity: impacts on reproductive success and juvenile body mass in reindeer. *PLoS ONE* **8**, e56450. (doi:10.1371/journal.pone.0056450)
8. Hacket-Pain A, Bogdziewicz M. 2021 Climate change and plant reproduction: trends and drivers of mast seeding change. *Phil. Trans. R. Soc. B* **376**, 20200379. (doi:10.1098/rstb.2020.0379)
9. Nussbaumer A *et al.* 2016 Patterns of mast fruiting of common beech, sessile and common oak, Norway spruce and Scots pine in Central and Northern Europe. *For. Ecol. Manag.* **363**, 237–251. (doi:10.1016/j.foreco.2015.12.033)
10. Övergaard R, Gemmel P, Karlsson M. 2007 Effects of weather conditions on mast year frequency in beech (*Fagus sylvatica* L.) in Sweden. *Forestry* **80**, 555–565. (doi:10.1093/forestry/cpm020)
11. Touzot L, Schermer É, Venner S, Delzon S, Rousset C, Baubet É, Gaillard JM, Gamelon M. 2020 How does increasing mast seeding frequency affect population dynamics of seed consumers? Wild boar as a case study. *Ecol. Appl.* **30**, e02134. (doi:10.1002/eap.2134)
12. Schermer É *et al.* 2019 Pollen limitation as a main driver of fruiting dynamics in oak populations. *Ecol. Lett.* **22**, 98–107. (doi:10.1111/ele.13171)
13. Caignard T, Kremer A, Firmat C, Nicolas M, Venner S, Delzon S. 2017 Increasing spring temperatures favor oak seed production in temperate areas. *Sci. Rep.* **7**, 8555. (doi:10.1038/s41598-017-09172-7)
14. Shibata M, Masaki T, Yagihashi T, Shimada T, Saitoh T. 2020 Decadal changes in masting behaviour of oak trees with rising temperature. *J. Ecol.* **108**, 1088–1100. (doi:10.1111/1365-2745.13337)
15. Hacket-Pain A, Ascoli D, Berretti R, Mencuccini M, Motta R, Nola P, Piussi P, Ruffinatto F, Vacchiano G. 2019 Temperature and masting control Norway spruce growth, but with high individual tree variability. *For. Ecol. Manag.* **438**, 142–150. (doi:10.1016/j.foreco.2019.02.014)
16. Pearse IS, LaMontagne JM, Koenig WD. 2017 Inter-annual variation in seed production has increased over time (1900–2014). *Proc. R. Soc. B* **284**, 20171666. (doi:10.1098/rspb.2017.1666)
17. Bojarska K, Selva N. 2012 Spatial patterns in brown bear *Ursus arctos* diet: the role of geographical and environmental factors. *Mamm. Rev.* **42**, 120–143. (doi:10.1111/j.1365-2907.2011.00192.x)
18. Robbins CT, Ben-David M, Fortin JK, Nelson OL. 2012 Maternal condition determines birth date and growth of newborn bear cubs. *J. Mammal.* **93**, 540–546. (doi:10.1644/11-MAMM-A-155.1)
19. McLellan BN. 2015 Some mechanisms underlying variation in vital rates of grizzly bears on a multiple use landscape. *J. Wildl. Manage.* **79**, 749–765. (doi:10.1002/jwmg.896)
20. Bergeron P, Réale D, Humphries MM, Garant D. 2011 Anticipation and tracking of pulsed resources drive population dynamics in eastern chipmunks. *Ecology* **92**, 2027–2034. (doi:10.1890/11-0766.1)
21. Gamelon M, Touzot L, Baubet É, Cachelou J, Focardi S, Franzetti B, Nivois É, Veylit L, Sæther BE. 2021 Effects of pulsed resources on the dynamics of seed consumer populations: a comparative demographic study in wild boar. *Ecosphere* **12**, e03395. (doi:10.1002/ecs2.3395)
22. Bieber C, Ruf T. 2005 Population dynamics in wild boar *Sus scrofa*: ecology, elasticity of growth rate and implications for the management of pulsed resource consumers. *J. Appl. Ecol.* **42**, 1203–1213. (doi:10.1111/j.1365-2664.2005.01094.x)
23. Cutini A, Chianucci F, Chirichella R, Donaggio E, Mattioli L, Apollonio M. 2013 Mast seeding in deciduous forests of the northern Apennines (Italy) and its influence on wild boar population dynamics. *Ann. Forest Sci.* **70**, 493–502. (doi:10.1007/s13595-013-0282-z)
24. Pearse IS, Wion AP, Gonzalez AD, Pesendorfer MB. 2021 Understanding mast seeding for conservation and land management. *Phil. Trans. R. Soc. B* **376**, 20200383. (doi:10.1098/rstb.2020.0383)
25. Cuthbert RN, Diagne C, Haubrock PJ, Turbelin AJ, Courchamp F. 2021 Are the “100 of the world's worst” invasive species also the costliest? *Biol. Invasions* **29**, 1–10. (doi:10.1007/s10530-021-02568-7)
26. Massei G *et al.* 2015 Wild boar populations up, numbers of hunters down? A review of trends and

- implications for Europe. *Pest. Manag. Sci.* **71**, 492–500. (doi:10.1002/ps.3965)
27. Apollonio M, Andersen R, Putman R. 2010 *European ungulates and their management in the 21st century*. Cambridge, UK: Cambridge University Press.
 28. Stillfried M, Fickel J, Börner K, Wittstatt U, Heddergott M, Ortmann S, Kramer-Schadt S, Frantz AC. 2017 Do cities represent sources, sinks or isolated islands for urban wild boar population structure? *J. Appl. Ecol.* **54**, 272–281. (doi:10.1111/1365-2664.12756)
 29. Vallée M, Lebourgeois F, Baubet E, Saïd S, Klein F. 2017 Le sanglier en Europe: une menace pour la biodiversité? *Rev. For. Fr. LXVIII* **6**, 505–518. (doi:10.4267/2042/62398)
 30. Bruinderink Groot GWTA, Hazebroek E, Van Der Voot H. 1994 Diet and condition of wild boar, *Sus scrofa scrofa*, without supplementary feeding. *J. Zool.* **233**, 631–648. (doi:10.1111/j.1469-7998.1994.tb05370.x)
 31. Vassant J. 1997 *Agrainage et gestion des populations de sangliers. Fiche technique N° 92*. Supplément Bull. Mens. ONC, 227.
 32. Baubet ERIC, Bonenfant C, Brandt SERGE. 2004 Diet of the wild boar in the French Alps. *Galemys* **16**, 101–113.
 33. Brandt S, Baubet E, Vassant J, Servanty S. 2006 Régime alimentaire du sanglier (*Sus scrofa* L.) en milieu forestier de plaine agricole. *Faune Sauvage* **273**, 20–27.
 34. Schley L, Roper TJ. 2003 Diet of wild boar *Sus scrofa* in Western Europe, with particular reference to consumption of agricultural crops. *Mamm. Rev.* **33**, 43–56. (doi:10.1046/j.1365-2907.2003.00010.x)
 35. Servanty S, Gaillard JM, Toigo C, Brandt S, Baubet E. 2009 Pulsed resources and climate-induced variation in the reproductive traits of wild boar under high hunting pressure. *J. Anim. Ecol.* **78**, 1278–1290. (doi:10.1111/j.1365-2656.2009.01579.x)
 36. Cachelou J, Saint-Andrieux C, Baubet E, Nivois E, Richard E, Gaillard JM, Gamelon M. 2022 Data from: Does mast seeding shape mating time in wild boar? A comparative study. Dryad Digital Repository. (doi:10.5061/dryad.zs7h44jck)
 37. Touzot L *et al.* 2018 The ground plot counting method: a valid and reliable assessment tool for quantifying seed production in temperate oak forests? *Forest Ecol. Manag.* **430**, 143–149. (doi:10.1016/j.foreco.2018.07.061)
 38. Vajas P, Saïd S, Rousset C, Holveck H, Baubet E. 2018 Quand, comment et pourquoi mesurer une glandée? Quelles méthodes disponibles? *Faune Sauvage* **319**, 35–42.
 39. Koenig WD, Mumme RL, Carmen WJ, Stanback MT. 1994 Acorn production by Oaks in central coastal California: variation within and among years. *Ecology* **75**, 99–109. (doi:10.2307/1939386)
 40. Gamelon M, Besnard A, Gaillard JM, Servanty S, Baubet E, Brandt S, Gimenez O. 2011 High hunting pressure selects for earlier birth date: wild boar as a case study. *Evolution* **65**, 3100–3112. (doi:10.1111/j.1558-5646.2011.01366.x)
 41. Matschke GH. 1967 Aging European wild hogs by dentition. *J. Wildl. Manage.* **31**, 109–113. (doi:10.2307/3798365)
 42. Mauget R. 1980 Régulations écologiques, comportementales et physiologiques (fonction de reproduction) de l'adaptation du sanglier, *Sus scrofa* L., au milieu. PhD thesis, University of Tours, Tours, France.
 43. Burnham KP, Anderson DR. 2002 *Model selection and inference: a practical information theoretic approach*. New York, NY: Springer Science & Business Media.
 44. Barton K. 2016 MuMIn: multi-model inference. R package version 1.15.6. See <https://CRAN.R-project.org/package=MuMIn>.
 45. Ogutu JO, Piepho HP, Dublin HT, Bhola N, Reid RS. 2010 Rainfall extremes explain interannual shifts in timing and synchrony of calving in topi and warthog. *Popul. Ecol.* **52**, 89–102. (doi:10.1007/s10144-009-0163-3)
 46. Williams CT, Lane JE, Humphries MM, McAdam AG, Boutin S. 2014 Reproductive phenology of a food-hoarding mast-seed consumer: resource- and density-dependent benefits of early breeding in red squirrels. *Oecologia* **174**, 777–788. (doi:10.1007/s00442-013-2826-1)
 47. Côté SD, Festa-Bianchet M. 2001 Birthdate, mass and survival in mountain goat kids: effects of maternal characteristics and forage quality. *Oecologia* **127**, 230–238. (doi:10.1007/s004420000584)
 48. Cavallini P, Santini S. 1995 Timing of reproduction in the red fox *Vulpes vulpes*. *Zeitschr Saugetier* **60**, 337–342.
 49. Brogi R, Merli E, Grignolio S, Chirichella R, Bottero E, Apollonio M. 2021 It is time to mate: population-level plasticity of wild boar reproductive timing and synchrony in a changing environment. *Cur. Zool. zoab077*. (doi:10.1093/cz/zoab077)
 50. Selonen V, Wistbacka R, Korpimäki E. 2016 Food abundance and weather modify reproduction of two arboreal squirrel species. *J. Mammal.* **97**, 1376–1384. (doi:10.1093/jmammal/gyw096)
 51. Barea LP, Watson DM. 2007 Temporal variation in food resources determines onset of breeding in an Australian mistletoe specialist. *Emu-Austral. Ornithol.* **107**, 203–209. (doi:10.1071/MU07003)
 52. Boutin S, Wauters LA, McAdam AG, Humphries MM, Tosi G, Dhondt AA. 2006 Anticipatory reproduction and population growth in seed predators. *Science* **314**, 1928–1930. (doi:10.1126/science.1135520)
 53. Eeva T, Veistola S, Lehikoinen E. 2000 Timing of breeding in subarctic passerines in relation to food availability. *Can. J. Zool.* **78**, 67–78. (doi:10.1139/z99-182)
 54. Wesołowski T, Hebda G, Rowiński P. 2021 Variation in timing of breeding of five woodpeckers in a primeval forest over 45 years: role of food, weather, and climate. *J. Ornithol.* **162**, 89–108. (doi:10.1007/s10336-020-01817-1)
 55. Bomford M. 1987 Food and reproduction of wild house mice. 1. Diet and breeding seasons in various habitats on irrigated cereal farms in New South Wales. *Wildl. Res.* **14**, 183–196. (doi:10.1071/WR9870183)
 56. Whelan S, Hatch SA, Benowitz-Fredericks ZM, Parenteau C, Chastel O, Elliott KH. 2021 The effects of food supply on reproductive hormones and timing of reproduction in an income-breeding seabird. *Horm. Behav.* **127**, 104874. (doi:10.1016/j.yhbeh.2020.104874)
 57. Rollinson DJ. 2002 Food caching behaviour in the Australian magpie *Gymnorhina tibicen*. *Sunbird* **32**, 20–22.
 58. Lobo N, Millar JS. 2013 Indirect and mitigated effects of pulsed resources on the population dynamics of a northern rodent. *J. Anim. Ecol.* **82**, 814–825. (doi:10.1111/1365-2656.12062)
 59. Eccard JA, Ylönen H. 2001 Initiation of breeding after winter in bank voles: effects of food and population density. *Can. J. Zool.* **79**, 1743–1753. (doi:10.1139/z01-133)
 60. Haapakoski M, Sundell J, Ylönen H. 2012 Predation risk and food: opposite effects on overwintering survival and onset of breeding in a boreal rodent. *J. Anim. Ecol.* **81**, 1183–1192. (doi:10.1111/j.1365-2656.2012.02005.x)
 61. Gamelon M, Tufto J, Nilsson ALK, Jerstad K, Røstad OW, Stenseth NC, Sæther BE. 2018 Environmental drivers of varying selective optima in a small passerine: a multivariate, multiepisodic approach. *Evolution* **72**, 2325–2342. (doi:10.1111/evo.13610)
 62. Przybylo R, Sheldon BC, Merilä J. 2000 Climatic effects on breeding and morphology: evidence for phenotypic plasticity. *J. Anim. Ecol.* **69**, 395–403. (doi:10.1046/j.1365-2656.2000.00401.x)
 63. Gienapp P, Väisänen RA, Brommer JE. 2010 Latitudinal variation in breeding time reaction norms in a passerine bird. *J. Anim. Ecol.* **79**, 836–842. (doi:10.1111/j.1365-2656.2010.01693.x)
 64. Coulson T, Kruuk LEB, Tavecchia G, Pemberton JM, Clutton-Brock TH. 2003 Estimating selection on neonatal traits in red deer using elasticity path analysis. *Evolution* **57**, 2879–2892. (doi:10.1111/j.0014-3820.2003.tb01528.x)
 65. Gamelon M, Focardi S, Baubet E, Brandt S, Franzetti B, Ronchi F, Venner S, Sæther BE, Gaillard JM. 2017 Reproductive allocation in pulsed-resource environments: a comparative study in two populations of wild boar. *Oecologia* **183**, 1065–1076. (doi:10.1007/s00442-017-3821-8)
 66. Forsman JT, Seppänen JT, Mönkkönen M. 2002 Positive fitness consequences of interspecific interaction with a potential competitor. *Proc. R. Soc. Lond. B* **26**, 91 619–91 623. (doi:10.1098/rspb.2002.2065)
 67. Maillard D, Fournier P. 2004 Timing and synchrony of births in the wild boar (*Sus scrofa* Linnaeus, 1758) in a Mediterranean habitat: the effect of food availability. *Galemys* **16**, 67–74.
 68. Delcroix I, Mauget R, Signoret JP. 1990 Existence of synchronization of reproduction at the level of the social group of the European wild boar (*Sus scrofa*). *Reproduction* **89**, 613–617. (doi:10.1530/jrf.0.0890613)
 69. Veylit L, Sæther BE, Gaillard JM, Baubet E, Gamelon M. 2020 How do conditions at

- birth influence early-life growth rates in wild boar? *Ecosphere* **11**, e03167. (doi:10.1002/ecs2.3167)
70. Baubet E, Servanty S, Brandt S. 2009 Tagging piglets at the farrowing nest in the wild: some preliminary guidelines. *Acta Silvatica. Lignaria Hungarica* **5**, 159–166.
71. Gaillard JM, Delorme D, Jullien JM, Tatin D. 1993 Timing and synchrony of births in roe deer. *J. Mammal.* **74**, 738–744. (doi:10.2307/1382296)
72. Loe LE *et al.* 2005 Climate predictability and breeding phenology in red deer: timing and synchrony of rutting and calving in Norway and France. *J. Anim. Ecol.* **74**, 579–588. (doi:10.1111/j.1365-2656.2005.00987.x)