Neonatal antipredator tactics shape female movement patterns in large herbivores

Kamal Atmeh[1,2], Christophe Bonenfant[1], Jean-Michel Gaillard[1], Mathieu Garel[3], A. J. Mark Hewison[4], Pascal Marchand[5], Nicolas Morellet[4,6], Pia Anderwald[7], Bayarbaatar Buuveibaatar[8], Jeffrey L. Beck[9], Matthew S. Becker[10], Floris M. van Beest[11], Jodi Berg[12], Ulrika A. Bergvall[13], Randall B. Boone[14], Mark S. Boyce[15], Simon Chamaillé-Jammes[16,17,18], Yannick Chaval[4,6], Chimeddorj Buyanaa[19], David Christianson[9], Simone Ciuti[20], Steeve D. Côté[21], Duane R. Diefenbach[22], Egil Droge[23], Johan T. du Toit[24,25,18], Samantha Dwinnell[26], Julian Fennessy[27,20], Flurin Filli[7], Daniel Fortin[28], Emma E. Hart[29], Matthew Hayes[26], Mark Hebblewhite[30], Morten Heim[31], Ivar Herfindal[32], Marco Heurich[33,34,35], Christian von Hoermann[36], Katey Huggler[26], Craig Jackson[31], Andrew F. Jakes[37], Paul F. Jones[38], Petra Kaczensky[39,35], Matthew Kauffman[40], Petter Kjellander[13], Tayler LaSharr[26], Leif Egil Loe[41], Roel May[31], Philip McLoughlin[42], Erling L. Meisingset[43], Evelyn Merrill[44], Kevin L. Monteith[26], Thomas Mueller[45], Atle Mysterud[46], Dejid Nandintsetseg[45], Kirk Olson[47], John Payne[39,48], Scott Pearson[49], Åshild Ønvik Pedersen[50], Dustin Ranglack[51,52], Adele K. Reinking[53,9], Thomas Rempfler[7], Clifford G. Rice[49], Eivin Røskaft[55], Bernt-Erik Sæther[56], Sonia Saïd[57], Hugo Santacreu[4], Niels Martin Schmidt[11], Daan Smit[58], Jared A. Stabach[47], Martin-Hugues St-Laurent[59], Joëlle Taillon[60], W. David Walter[61], Kevin White[62], Guillaume Péron[1], Anne Loison[2*]

[1]Laboratoire "Biométrie et Biologie Évolutive" – UMR CNRS 5558,
Université Claude Bernard Lyon 1, 43 Boulevard du 11 novembre 1918,
Villeurbanne, 69622, France.

[2*]Laboratoire d'Écologie Alpine – UMR UGA-USMB-CNRS 5553, Université de Savoie Mont-Blanc, Savoie Technolac, Le Bourget-du-Lac, 38058, France.
[3]Direction de la Recherche et de l'Appui Scientifique, Service Anthropisation et Fonctionnement des Écosystèmes Terrestres, Office Français de la Biodiversité, 5 rue Bethléem, Gières, 38610, France.
[4]Université de Toulouse, INRAE, CEFS, Castanet-Tolosan, 31326, France.
[5]Direction de la Recherche et de l'Appui Scientifique, Service Anthropisation et Fonctionnement des Écosystèmes Terrestres, Office Français de la Biodiversité, 147 avenue de Lodève, Juvignac, 34990, France.
[6]LTSER ZA PYRénées GARonne, Auzeville-Tolosane, 31320, France.
[7]Swiss National Park, Runatsch 124, Zernez, 7530, Switzerland.
[8]Mongolia Program, Wildlife Conservation Society, Amar Street 29, Ulaanbaatar, 14200, Mongolia.
[9]Department of Ecosystem Science and Management, University of Wyoming, 1000 East University Avenue, Laramie, 82071, Wyoming, USA.
[10]Department of Ecology, Montana State University, 1156-1174 South 11th Avenue, Bozeman, 59735, Montana, USA.
[11]Department of Ecoscience, Aarhus University, Frederiksborgvej 399, Roskilde, DK-4000, Denmark.
[12]Department of Biological Sciences, University of Alberta, Biological Sciences Building, Edmonton, T6G 2E9, Alberta, Canada.
[13]Department of Ecology, Grimsö Wildlife Research Station, Swedish University of Agricultural Sciences, Riddarhyttan, Sweden.
[14]Department of Ecosystem Science and Sustainability, Colorado State University, 1476 Campus Delivery, Fort Collins, 80523, Colorado, USA.
[15]Department of Biological Sciences, University of Alberta, Biological Sciences Building, Edmonton, T6G 2E9, Alberta, Canada.
[16]CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France.
[17]LTSER France, Zone Atelier Hwange, CNRS, Hwange National Park, Bag 62, Dete, Zimbabwe.
[18]Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Lynnwood Road, Pretoria, Gauteng, South Africa.
[19]Mongolia Program Office, World Wide Fund for Nature, Amar Street 4, Ulaanbaatar, 210620A, Mongolia.

[20]Laboratory of Wildlife Ecology and Behaviour, School of Biology and Environmental Science, University College Dublin, Belfield Campus, Dublin, D4, Ireland.
[21]Department of Biology, Centre d'Études Nordiques, Université Laval, 1045 avenue de la Médecine, Québec, G1V 0A6, Québec, Canada.
[22]U.S. Geological Survey, Pennsylvania Cooperative Fish and Wildlife Research Unit, The Pennsylvania State University, 419 Forest Resources Building, University Park, 16802, Pennsylvania, USA.
[23]WildCRU, Department of Biology, University of Oxford, Abingdon Road, Tubney, OX13 5QL, Oxfordshire, United Kingdom.
[24]Institute of Zoology, Zoological Society of London, Regent's Park, London, NW1 4RY, England, United Kingdom.
[25]Department of Wildland Resources, Utah State University, 5230 Old Main Hill, Logan, 84322-5230, Utah, USA.
[26]Haub School of Environment and Natural Resources, University of Wyoming, 804 East Fremont Street, Laramie, 82072, Wyoming, USA.
[27]Giraffe Conservation Foundation, PO Box 86099, Windhoek, 9000, Khomas, Namibia.
[28]Department of Biology, Center for Forest Research, Université Laval, 1045 avenue de la Médecine, Québec, G1V 0A6, Québec, Canada.
[29]Habitats Research Centre, Oysterhaven Biodiversity Reserve, Oysterhaven, Co. Cork, Ireland.
[30]Wildlife Biology Program, Department of Ecosystem and Conservation Sciences, Franke College of Forestry and Conservation, University of Montana, 32 Campus Drive, Missoula, 59812, Montana, USA.
[31]Department of Terrestrial Ecology, Norwegian Institute for Nature Research (NINA), 5685 Torgarden, Trondheim, NO-7485, Norway.
[32]Gjærevoll Centre for Biodiversity Foresight Analyses, Norwegian University of Science and Technology (NTNU), Høgskoleringen 1, Trondheim, NO-7491, Norway.
[33]Department of National Park Monitoring and Animal Management, Bavarian Forest National Park, Freyunger Straße 2, Grafenau, 94481, Germany.
[34]Faculty of Environment and Natural Resources, University of Freiburg, Tennenbacher Straße 4, Freiburg, 79106, Germany.
[35]Department of Forestry and Wildlife Management, Inland Norway University of Applied Sciences, Anne Evenstad vei 80, Koppang, NO-2480, Norway.

[36]Field Station Fabrikschleichach, Department of Animal Ecology and Tropical Biology, University of Würzburg, Glashüttenstraße 5, Rauhenebrach, 96181, Bavaria, Germany.
[37]Wyoming Migration Initiative, Wyoming Cooperative Fish and Wildlife Research Unit, University of Wyoming, 1000 East University Avenue, Laramie, 82071, Wyoming, USA.
[38]Alberta Conservation Association, 817-4th Avenue South, Lethbridge, T1J 0P3, Alberta, Canada.
[39]Research Institute of Wildlife Ecology, University of Veterinary Medicine Vienna, Savoyenstraße 1, Vienna, A-1160, Austria.
[40]U.S. Geological Survey, Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, 1000 East University Avenue, Laramie, 82071, Wyoming, USA.
[41]Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, Høgskoleveien 12, Ås, 1432, Norway.
[42]Department of Biology, University of Saskatchewan, 112 Science Place, Saskatoon, S7N 5E2, Saskatchewan, Canada.
[43]Department of Forestry and Forestry Resources, Norwegian Institute of Bioeconomy Research, Tingvoll gard, Tingvoll, NO-6630, Norway.
[44]Department of Biological Sciences, University of Alberta, 116 Street and 85 Avenue, Edmonton, T6G 2R3, Alberta, Canada.
[45]Senckenberg Biodiversity and Climate Research Centre, Senckenberg Gesellschaft für Naturforschung, Georg-Voigt-Straße 14, Frankfurt am Main, 60325, Germany.
[46]Centre for Ecological and Evolutionary Synthesis, Department of Biosciences, University of Oslo, 1066 Blindern, Oslo, NO-0316, Norway.
[47]Conservation Ecology Center, Smithsonian National Zoo & Conservation Biology Institute, 1500 Remount Road, Front Royal, 22630, Virginia, USA.
[48]Blue Dot Research, LLC, PO Box 2690, Vashon, 98070, Washington, USA.
[49]Wildlife Research Division, Washington Department of Fish Wildlife, 1111 Washington St SE, Olympia, 98501, Washington, USA.
[50]Norwegian Polar Institute, Hjalmar Johansens gate 14, Tromsø, 9296, Norway.
[51]Department of Biology, University of Nebraska at Kearney, 2504 9th Avenue, Kearney, 68849, Nebraska, USA.

[52]Utah Field Station, USDA APHIS WS National Wildlife Research Center, 4200 S 600 E Cache County Road, Millville, 84326, Utah, USA.
[53]Cooperative Institute for Research in the Atmosphere, Colorado State University, 3925a Laporte Avenue, Fort Collins, 80523, Colorado, USA.
[54]Washington Department of Fish Wildlife, 1111 Washington St SE, Olympia, 98501, Washington, USA.
[55]Department of Biology, NTNU, Norway, Norwegian University of Science and Technology (NTNU), Høgskoleringen 1, Trondheim, NO-7491, Norway.
[56]Department of Biology, Centre for Biodiversity Dynamics, Norwegian University of Science and Technology (NTNU), Høgskoleringen 1, Trondheim, NO-7491, Norway.
[57]Direction de la Recherche et de l'Appui Scientifique, Service Conservation et Gestion des Espèces à Enjeux, Office Français de la Biodiversité, "Montfort", Birieux, 01330, France.
[58]Zambian Carnivore Programme, PO Box 80, Mfuwe, Zambia.
[59]Centre for Forest Research, Centre for Northern Studies, Université du Québec à Rimouski, 300, Allée des Ursulines, Rimouski, G5L 3A1, Québec, Canada.
[60]Ministère de l'Environnement, de la Lutte contre les Changements Climatiques, de la Faune et des Parcs, Gouvernement du Québec, 880, chemin Sainte-Foy, Québec, G1S 4X4, Québec, Canada.
[61]U.S. Geological Survey, Pennsylvania Cooperative Fish and Wildlife Research Unit, The Pennsylvania State University, 403 Forest Resources Building, University Park, 16802, Pennsylvania, USA.
[62]Division of Wildlife Conservation, Alaska Department of Fish and Game, Juneau, 99811, Alaska, USA.

*Corresponding author(s). E-mail(s): anne.Loison@univ-smb.fr; Contributing authors: kam.atmeh@gmail.com; christophe.bonenfant@cnrs.fr; jean-michel.gaillard@univ-lyon1.fr; Mathieu.Garel@ofb.gouv.fr; Mark.Hewison@inrae.fr; pascal.marchand@ofb.gouv.fr; Nicolas.Morellet@inrae.fr; pia.anderwald@nationalpark.ch; buuveibaatar@wcs.org; jlbeck@uwyo.edu; matt@zambiacarnivores.org; flbe@ecos.au.dk; jberg@ualberta.ca; Ulrika.Alm.Bergvall@slu.se; Randall.Boone@colostate.edu; boyce@ualberta.ca; simon.chamaille@cefe.cnrs.fr; yannick.chaval@inrae.fr;; chimeddorj@wwf.mn; david.christianson@uwyo.edu; simone.ciuti@ucd.ie; Steeve.Cote@bio.ulaval.ca; drd11@psu.edu;

egil.droge@biology.ox.ac.uk; johan.dutoit@usu.edu; sdwinnel@uwyo.edu;
julian@giraffeconservation.org; flurin.filli@nationalpark.ch;
Daniel.Fortin@bio.ulaval.ca; emma@habitats.ie;
matt@lonepineanalytics.com; mark.hebblewhite@umontana.edu ;
Morten.Heim@nina.no; ivar.herfindal@ntnu.no; marco.heurich@npv-bw.bayern.de; Christian.vonHoermann@npv-bw.bayern.de;
katey.huggler@gmx.com; Craig.Jackson@nina.no; ajakes@uwyo.edu;
Paul.Jones@ab-conservation.com; petra.kaczensky@inn.no;
mkauffm1@uwyo.edu; Petter.Kjellander@slu.se; tlasharr@uwyo.edu;
leif.egil.loe@nmbu.no; Roel.May@nina.no; philip.mcloughlin@usask.ca;
erling.meisingset@nibio.no; emerrill@ualberta.ca;
Kevin.Monteith@uwyo.edu; thomas.mueller@senckenberg.de;
atle.mysterud@ibv.uio.no; nandintsetseg.dejid@senckenberg.de;
kolson.kao@gmail.com; drjohnpayne@gmail.com;
Scott.Pearson@dfw.wa.gov; ashild.pedersen@npolar.no;
dustin.ranglack@usda.gov; Adele.Reinking@colostate.edu;
thomas.rempfler@nationalpark.ch; ricecgr@comcast.net;
eivin.roskaft@ntnu.no; bernt-erik.sather@ntnu.no;
sonia.said@ofb.gouv.fr; santacreuhugo@gmail.com; nms@ecos.au.dk;
daan@zambiacarnivores.org; StabachJ@si.edu; Martin-hugues_St-laurent@uqar.ca; Joelle.Taillon@mffp.gouv.qc.ca; wdw12@psu.edu;
kevinwhite0714@gmail.com; guillaume.peron@univ-lyon1.fr;

Abstract

Caring for newborn offspring hampers resource acquisition of mammalian females, curbing their ability to meet the high energy expenditure of early lactation. Newborns are particularly vulnerable, and large herbivores have evolved a continuum of neonatal anti-predator tactics, ranging from immobile hider to highly mobile follower offspring. How these tactics constrain female movements around parturition is unknown, particularly within the current context of increasing habitat fragmentation and earlier plant phenology caused by global warming. Using a comparative analysis across 54 populations of 23 species of large herbivores, we show that mothers adjust their movements to variation in resource productivity and heterogeneity according to their offspring's neonatal tactic. Mothers with hider offspring are unable to exploit environments where the variability of resources occurs at a broad scale, which might alter resource allocation compared to mothers with follower offspring. Our findings reveal that the overlooked neonatal tactic plays a key role for predicting how species are coping with environmental variation.

Keywords: reproductive tactic, resource productivity, resource variation, diffusion, follower, hider, home range size, ungulates

1 Introduction

Mammalian females that provide extensive maternal care need access to high-quality or abundant food resources to meet the marked increase in energetic demands of late gestation and early lactation [11, 38]. Many species synchronize births with the seasonal flush of resources [13, 63]. At that time, reproductive females often move to track the best food resources [15, 45, 51, 72]. Following parturition, the movement of mothers should, however, be restricted by the limited mobility of their newborn, even when precocial. In absence of any protection provided by a nest or burrow, such as observed in large herbivores, predation threatens offspring survival. Parturient females should hence trade resource acquisition against resource provision (lactation) and protection of their offspring [53]. Evolved behavioral adaptations to this trade-off include neonatal anti-predator tactics, which range along a continuum from immobile and concealed offspring ("hider" tactic *sensu* [37]) to mobile offspring that follow their mother ("follower" tactic *sensu* [37]). Having hider or follower offspring imposes different constraints on mothers' movements (Fig. 1). The bed sites of immobile hider offspring correspond to central places to which the mother has to return at regular intervals to provide care [51, 53, 74]. On the other hand, mothers of follower offspring have to adjust their daily ranging behavior to the movement capacity of their offspring to keep in contact with them [14, 28]. Surprisingly, we currently lack a comprehensive understanding of how offspring's anti-predator tactics interplay with environmental conditions to shape fine- and large-scale movements of reproductive females in a dynamic landscape.

We aim to fill this knowledge gap by investigating how neonatal tactics affect female movement patterns of large herbivores around parturition, across gradients of resource productivity and spatial scales of resource variation (*sensu* [72]). We performed a comparative analysis across 54 populations of 23 species distributed worldwide, which displayed contrasting neonatal anti-predator tactics (Fig. 2). Using continuous-time stochastic movement models [7, 18], we overcame the methodological hurdles of heterogeneous sets of GPS locations, and propose insightful ecological interpretations of three main statistical properties of individual trajectories, namely the stationarity, the diffusion, and the return rate to a central place (glossary in Tab. 1). This led us to delve into the interplay of resources and neonatal tactics on residency and movement components. Where resource productivity is high and resource variation occurs at a fine scale, females should manage to fulfill their energetic requirements both before and after parturition in the same area, without having any incentive to leave [6]. Hence, in such environments, we expected high levels of residency, irrespective of the neonatal tactic (Fig. 1). In contrast, where resource productivity is low and spatial scale of resource variation occurs at broad scale, neonatal tactics should influence the level of female residency after parturition [17]: mothers with hider offspring that need to be fed regularly should be more resident than mothers with follower offspring. Likewise, after parturition, we expected differences between neonatal tactics in movement metrics (Fig. 1 – 2nd step): Only mothers of hider offspring should increase their return rate to places in their home range where offspring hide, while mothers of follower species may only reduce diffusion to cope with the limited movements of their offspring. This influence of neonatal tactics on movement metrics after parturition should be more acute where resource productivity is low and spatial scale of resource variation is broad, i.e. in environments that require females to explore a larger range to allow their resource intake [66]. Overall, female movements should be more constrained by resource dynamics in time and across spatial scales, when they have a hider than a follower offspring, leading neonatal tactics to play a key role on female movement.

2 Results

2.1 Neonatal tactics and residency in relation to parturition

The two neonatal tactics were equally represented among the 23 species we studied (11 followers and 12 hiders, Fig. 2). Across species, most females were resident (79±11% and 83±11% before and following parturition, respectively) but, as expected, females with hider offspring were more often resident (81% before and 88% after parturition) than females with follower offspring (76% before and 77% after parturition, Supplementary Fig. C1).

Contrary to our expectation, irrespective of the neonatal tactic, there was no relationship between resource productivity and residency, either prior to or following parturition (Fig. C2). On the other hand, in support of our expectation, when the spatial scale of resource variation increased, the propensity to be resident decreased, and more strongly so in females with hider than with follower offspring (Fig. 3a–b). However, this difference among neonatal tactics occurred only prior to parturition (estimated slope with 95 percent credibility intervals as subscripts; hiders: $_{-2.786}\,-2.530\,_{-2.272}$; followers: $_{-1.540}\,-1.276\,_{-1.037}$), and declined after (hiders: $_{-1.149}\,-0.926\,_{-0.696}$; followers: $_{-1.030}\,-0.771\,_{-0.524}$) (Fig. C2). When resource variation varied at a broad spatial scale ($SS_{NDVI} > 56$km), females with hider offspring were almost four times more likely to be resident following parturition than before it, whereas the magnitude of this change was less than two in followers (Fig. 3a–b). When resource variation occurred at this broad spatial scale, a substantial proportion of females was not resident after parturition, even with hider offspring (*e.g.* up to 20% of pronghorn in the Northern Sagebrush Steppe and of mule deer in Wyoming's Red Desert USA and western Washington USA).

2.2 Neonatal tactic and shift in female movements

Prior to parturition, the diffusion was similar for females with hider and follower offspring, irrespective of resource productivity (difference between tactics: $_{-0.102}\,-0.018\,_{0.068}$, Fig. 4a–b, Fig. D5, model output in Figs. D3–D4). Following parturition, as expected, the diffusion decreased more in females with hider than follower offspring (difference between tactics: $_{-0.517}\,-0.426\,_{-0.325}$, Fig. 4a–b). This impact of parturition on the mother's diffusion varied with resource productivity, but there was no difference between neonatal tactics (Fig. 4a-b) in how diffusion decreased with increasing resource productivity ($_{-0.277}\,-0.194\,_{-0.106}$; Figs. D3–D4–D5). Overall, the change in diffusion post-parturition was lower when productivity was low (4% increase in followers, 26% decrease in hiders) than when productivity was high (38% decrease in followers, 56% in hiders) (Fig. 4a). The spatial scale of resource variation influenced the diffusion more than the resource productivity (Fig. D5, model output in Figs. D3–D4). Prior to parturition, the diffusion increased more strongly with spatial scale of resource variation for females with hider ($_{0.938}\,0.996\,_{1.054}$) than with follower ($_{0.731}\,0.807\,_{0.889}$, Fig. D5) offspring. However, the same relationship did not differ between neonatal tactics following parturition ($_{0.273}\,0.330\,_{0.385}$ and $_{0.291}\,0.369\,_{0.448}$ for females with hider and follower offspring, respectively). When the spatial scale of resource variation was low, the diffusion actually increased following parturition in both hiders (by 41%) and followers (by 30%). In contrast, when the spatial scale of resource variation was intermediate or high, the diffusion decreased after parturition, especially in hiders (Fig. 4b).

As expected, females with hider offspring had a consistently higher return rate than females with follower offspring (Fig. 4c–d, Figs. D3 – D4). The return rate increased with resource productivity irrespective of the neonatal tactic (difference between tactics: $_{-0.027}\,0.022\,_{0.060}$) prior to parturition, and only in females with follower offspring after parturition (Fig. D5). Indeed, following parturition, the return rate of females with follower offspring increased by 12% regardless of resource productivity. In contrast, the return rate of females with hider offspring markedly increased after parturition, at values that remained similar across the whole range of resource productivity (slope: $_{-0.089}\,0.005\,_{0.085}$, Fig. D3). To reach this high return rate following parturition, the return rate of females with hider offspring increased by 61% in an environment with poor resource productivity but only by 1% when in an environment with high resource productivity (Fig. 4c).

Spatial scale of resource variation also had a strong impact on return rate. Return rate peaked when spatial scale of resource variation was low, especially for females with hider offspring (Fig. 4). Overall, return rate decreased with increasing spatial scale of resource variation, with a steeper slope for females with hider than follower offspring (prior to parturition: $_{-0.791}\,-0.724\,_{-0.659}$ *vs.* $_{-0.680}\,-0.588\,_{-0.494}$; after parturition: $_{-0.646}\,-0.584\,_{-0.521}$ *vs.* $_{-0.543}\,-0.458\,_{0.358}$ respectively; Fig. D5). Noticeably, the impact of the spatial scale of resource variation on return rate was attenuated following parturition irrespective of the neonatal tactics (see slope estimates above). Hence, when the spatial scale of resource variation was high, the difference in return rates between neonatal tactics dampened (Fig. 4). To sum up, the consequences of parturition on return rates differed between neonatal tactics and depended on the spatial scale of resource variation: it increased by 11%, 31%, and 53% for low, intermediate, and high values of spatial scale of resource variation for females with hider offspring, and it decreased by 5% for low values, and then increased by 12% and 31% for intermediate and high values of spatial scale of resource variation, for females with follower offspring (Fig. 4d).

Irrespective of the neonatal tactic, resource productivity impacted home range sizes mostly through its effect on return rate, while the spatial scale of resource variation influenced the size of home ranges both through diffusion and return rates (Fig. 5). Regardless of the resource variable considered (resource productivity Fig. 5a, or spatial scale of resource variation, Fig. 5b), females with hider offspring altered their movement after parturition, which explains marked changes in resulting home ranges (decrease by 54%, 55% and 58% following parturition in low, medium, and high productivity areas, and increase by 20%, and decreased by 55% and 82% in areas with low, medium and high spatial scale of resource variation, Fig. 5a). The presence of an offspring at heel also impacted females of follower offspring and thereafter, the size of their home ranges, but to a lesser extent, and mostly when resource productivity was high and spatially variable at a broad scale (decrease by 20%, 36% and 45% following parturition in low, medium, and high productivity areas, and increase by 49%, and then decrease by 36% and 61% in areas with low, medium, and high spatial scale of resource variation, Fig. 5).

3 Discussion

Life history variation across species is highly structured by differences in body size [44], phylogenetic relatedness [59], habitat features [23], and lifestyle [32] along a slow-fast continuum [24, 70]. However, most studies have been performed on traits that directly describe the life cycle [8], which limits the focus on resource allocation. Up to now, very few comparative studies across species have investigated the consequences of life history on the movement ecology of animals, besides the well-established allometry of home range size [36] and of large-scale movements such as dispersal or migration [*e.g.* 71]. One main limitation for conducting comparative analyses of movement was the highly variable sampling designs to collect data locations, which affects the estimation of movement parameters [see 62, for an example on speed]. The continuous-time stochastic movement models framework accommodates this limitation and decomposes home range size into two movement components, namely the frequency of return to a central place (called return rate here) and the diffusion [7]. We propose here a first behavioral interpretation of these statistical parameters, and highlight the contrasting responses of the movement components to ecological and evolutionary drivers. For instance, the well-documented home range size decrease with increasing plant productivity [20, 66] mostly results from a decrease in diffusion, while the return rate remains largely unchanged. Indeed, the comparison of return rate and diffusion across populations of 23 species of large herbivores (Fig. 2) that lived in highly diverse ecosystems reveals the complex interaction between a life history trait (here the tactics of maternal care) and the dynamics of food resource distribution on the different facets of the spatial behavior of mothers during the critical period of maternal care [11].

The anti-predator neonatal tactics are crucial life history traits for the reproductive success of female large herbivores [37]. Our findings demonstrate that these tactics deeply shape movement and habitat use by females around parturition (Fig. 5). Across-species differences and similarities we report from our comparative analysis [*sensu* 16] inform about the past selective pressures on the movement behavior of females in response to the limited mobility (follower) and spatial constraints (hider) imposed by the presence of their newborns. Females with hider offspring such as in roe deer, pronghorns, or giraffes are resident to a larger extent, display higher return rate, and have a lower diffusion than females with follower offspring such as reindeer, chamois, or ibex (Figs. 2–4). This pattern is consistent before and after parturition (Fig. 3), making the requirement of regular visits to immobile hider offspring only a partial explanation. Presumably, the combination of a high propensity for residency, a high return rate, and a low diffusion of mothers with hider offspring has been selected to improve their overall reproductive success. However, it might also constrain female movements both within and outside the breeding season, leading them to occupy small home ranges (Figs. 1 & 5). To compensate for the potential loss of food resources induced by restricted movement and foraging areas, females with hider offspring should be more selective in terms of habitat quality [73] or have a more specialized diet [34] to improve energy acquisition and raise their hider offspring successfully, without compromising their own survival. These constraints can explain the tight association between habitat quality and reproductive success in females with hider offspring [see 43, in roe deer]. On the other hand, females with follower offspring are less limited in their movement by their young at heel, and can adopt different tactics to secure enough energy to raise offspring successfully, such as surfing the green wave [26, 27].

While both return rate and diffusion are under differential selection depending on the anti-predator tactics displayed by offspring, these movement metrics exhibit a substantial amount of variation within species among large herbivores (Fig. 4e). Movement is the quickest and most efficient behavior for most animals to cope with environmental variation and unpredictability in food resources [49]. At the same time, moving is energetically costly [29, 67], and mothers seem to trade return rate with diffusion (Fig. 5) to increase home range size in the landscapes with the broadest scale of resource variation. Accordingly, the probability of being resident and the two movement components all change depending on the spatial and temporal distribution of resources at the time of parturition, though differently before and after parturition and according to whether offspring are hider or follower (Fig. 3). As the size of a home range should be as small as possible to avoid movement costs [31], it should decrease with increasing plant productivity around the time of parturition (Fig. 5), as previously reported in other mammals [*e.g.* 40]. Yet, the magnitude of the influence of the spatial distribution of food resources on movement during the most critical time for female fitness has remained underappreciated up to now, and the fact that it could be tactic-dependent has not been envisioned so far. Accordingly, the return rate displayed as much as a three-fold decrease between an environment with a fine grain variation in food resources and an environment where food is fragmented into larger, distant vegetation patches (Fig. 4).

Including an influential life history tactic, the neonatal anti-predator tactic, into studies of movement, improves the understanding of the spatial distribution of species and their response to future changes in resource variation in space and time [33]. For species with hider offspring, the drop in return rate after parturition increases with scale of resource variation, while the change is negligible for species with follower offspring (Figs. 4-5). Hence, raising a hider offspring emerges as a great constraint for the movement of females in less productive and very patchy environments. In some extreme situations, females with hider offspring may entail too high energetic costs of movement for breeding, making the environment unsuitable for the long-term viability of local populations. This framework opens new avenues of research to delve into other structuring life history traits on movement such as diet [76], the degree of gregarity [42], or the level of sociality [35].

4 Methods

4.1 Study sites and GPS data

We collected data sets either through the Movebank animal tracking database and repository available online (https://www.movebank.org), or by direct contact with the co-authors and data providers (see Table A1). Because we were focusing on movement prior to and following parturition, we only included adult females that reproduced and removed individuals with no monitoring covering the entire reproductive period as well as individuals known to be non-reproductive. Survival of newborn over that period was unknown because only the mothers were monitored. We therefore assumed that the initial status of a female – with or without a young a heel – remained unchanged over time.

We excluded GPS location outliers using the method proposed by Bjørneraas et al [1]. Following this selection procedure, our data set contained 3 907 880 GPS locations (when considering only the 2 months centered around parturition) in 54 populations of 23 large herbivore species (11 classified as followers and 12 as hiders) worldwide distributed along longitudinal and latitudinal gradients (Fig. 2), including 2 386 individuals monitored from 1997 to 2019, thus representing a total of 3 942 individual-years.

4.2 Defining reproductive periods

Because we investigated changes in movement prior to and following parturition, we defined time frames that best capture the pre- and post-parturition periods, while accounting for methodological constraints of having a long-enough period of monitoring for fitting continuous time movement models (see next section). We choose a one-month window pre- and post-parturition that allowed us to cover the last third of the gestation and the first part of the lactation, which are the most demanding periods in terms of energetic intake for females [64]. Gestation length ranges from 140 to 450 days, so the last month is within the last third of the gestation for all species (it represents between 20 and 60 percent of the last third of the gestation for the largest to the smallest species respectively, see Table G3). In addition, one month after parturition allows for a time frame which ensures that offspring, even from the smallest species, are still fed almost exclusively by their mother. Hence, we position ourselves in the period where changes in movement, whatever the species, are most likely to be influence by the need for female to frequently care for her offspring, even though the duration of these interactions varies across species.

When precise information on reproduction was available (12 populations), we used individual parturition dates to divide the data into a one-month pre-parturition (parturition date −30 days) and one-month post-parturition periods (parturition date +30 days). This was the case for 27% of the follower species and 26% of the hider species. In the remaining 42 populations (half of which follower species and half of which hider species), individual parturition dates were unavailable. However, most large herbivores exhibit markedly pulsed breeding [13, 63, 69], yielding a normal or log-normal distribution of birth dates. We therefore defined a population-based cut-off date, corresponding to 5% of birth events (Fig. E8), using both data previously published or a best-informed guesstimate provided by data owners (Supplementary Table E2). With a 5% cut-off date, we made sure that most females did not give birth preceding that date but would eventually do so afterward, thus leaving a small margin of error with the presumably 5% of females who had already given birth. This method was applied to females with unknown parturition dates (representing 2 906 or 73.72% of individual-year). In populations where individual parturition dates were only available for a proportion of females (10 out of 12 populations), we used the on-hand available individual parturition dates to compute the 5% cut-off. We repeated our analyses including a factor indicating whether the date of parturition was known at the individual or population level and it led to qualitatively similar results to the ones presented in details in the results, though with an enlarged effect size for the neonatal tactics, meaning that our results based on the whole data set were conservative.

4.3 Continuous-time stochastic movement models and model fitting

In modern telemetry data, continuous-time stochastic movement models (CTSMM) offer more robust statistical approaches than discrete-time models by accounting for temporal autocorrelation [7, 18, 19]. They describe movement as continuous through time, with a relatively stable process-mean accompanied by random deviations from the expected path (*i.e.* stochasticity). While being the simplest of CTSMM classes, the Brownian Motion model, fails to account for the emergence of home ranges given its assumption of an infinite diffusion process ([2], Table 1), other classes of CTSMM do actually lead to bounded home ranges, such as Ornstein-Uhlenbeck (OU) models [12]. This class of models is especially attractive because the movement variance (usually denoted σ^2) can be decomposed into the contribution of diffusion (D) and position autocorrelation time ([7], *i.e.* time in autocorrelation of positions) (τ_p), two parameters of interest (Table 1). The diffusion coefficient determines how an animal move away from its expected path while being constantly attracted back to it at a rate defined by the position autocorrelation time, thus leading to a range-defined movement process. As a consequence, the net squared displacement ([3, 22], *i.e.* squared Euclidean distance between start and end point of a trajectory) and the semivariogram of the location time series reaches an asymptote which scales to the home range size ([18], Fig. F9). In fact, the asymptotic value of the Gaussian distribution of the movement process represents σ^2 which is a proxy of home range size, and the rate of increase of the semivariance with time before it reaches σ^2 represents τ_p which its inverse represents the return rate to a central point.

Given that the low number of parameters of OU models do not reconcile complex animal movement patterns at fine time scales, further classes of models have been introduced (*e.g.* Ornstein-Uhlenbeck Foraging model [18]), and incorporate temporal autocorrelation in position (τ_p) and velocity (τ_v). τ_v Quantifies the intensity of persistence in the direction and speed of movement. Using these models and parameters, we tested biological hypotheses about stationarity (stationary OU vs non-stationary BM), diffusion, and return rate (inverse of τ_p).

For each period (*i.e.* before/after parturition), we first determined whether the individual was stationary or not using empirical semivariograms (Fig. F9). The semivariance is a measure of the similarity in distance between two recorded locations, as a function of the time lag between them [18]. The semivariogram is a useful diagnosis tool to categorize movement types. If the semivariance increases monotonically with the time lag, the movement is endlessly diffusive, like a Brownian Motion (BM). By contrast, if the semivariance exhibits an inflexion and reaches an asymptote for large time lags, the animal is stationary or home-range-bounded, like an Ornstein-Uhlenbeck process [7, 12, 18].

Given the heterogeneity in frequency of location records and the duration of the monitoring among individuals and species, we applied a decision rule about the inclusion of an individual in the analyzed data set. We selected only tracks with a median sampling interval not higher than 6 hours, with at least 14 days of data and a minimum of 60 locations per period. This rule offered the best compromise between the number of different individuals retained and the minimum number of locations to fit statistical models (using the rule of thumb of at least 30 observations per estimated parameters). We followed Bunnefeld et al [6], and fit competing models (linear vs. exponential functions of lag τ) to the empirical semivariograms, selecting the best model using the Akaike Information Criterion (AIC). In practice we fitted the BM and OU models, each having a well-established formalisation when working with semivariance [18]. We fitted the OU process to the stationary tracks using the *ctmm.fit* routine in the *ctmm* package [7] available in R [57]. Given that velocity autocorrelation can bias the estimation of the movement magnitude [18], we first fitted an OU-Foraging (OUF; includes velocity autocorrelation time τ_v) model to extract the diffusion parameter (D), position autocorrelation time (τ_p) and movement variance (σ^2). In some cases (1.6% of analyzed tracks), our data did not support the OUF model, probably because the velocity autocorrelation time was smaller or of the same order of magnitude as the sampling interval, thus we fitted the OU model and extracted the same focal parameters. For tracks identified as non-stationary BM, we only extracted the diffusion parameter D from fitting a theoretical semivariogram to the empirical one. All values were $\log_{10}$ transformed. To remove potential outliers, we computed Z-scores for each population:

$$Z = \frac{x_{ip} - \mu_{ip}}{\sigma_{ip}},$$

where x_{ip} is the parameter's i value in the period p, μ_{ip} is the mean of all the parameter's i, values in period p and σ_{ip} (not to be confounded with σ of the OU movement model) is the standard deviation of all the parameter's i values in period p. We removed scores that were < 3 or higher than >3 which represented 1.14% ($N = 90$ out of 7 884) of all tracks and 0.2% ($N = 8$ out of 3 942) of all individual-years [68]. If an OU track was identified as an outlier for a certain parameter, all parameters of that track were subsequently removed because we were interested in variation of both diffusion and return rate. Some individual-years had only one of their periods removed as outliers. In these cases, we ended up removing all the individual-year ($N = 74$ out of 3 934) since analyzing changes in movement required both tracks. For

BM models, only the diffusion coefficient D was used to compare changes between pre- and post-parturition periods.

Following all the above-mentioned criteria, our extensive final data set included 2 342 reproductive females (Tab. A1) with 3 860 female-years covering the pre- and post-parturition periods (*i.e.* 7 720 tracks). Data covered one to seven populations in 23 species, located in a wide range of ecosystems, from the low-productivity biomes of the Mongolian steppes to the highly productive systems found in the temperate regions of Europe (Fig. 2b).

4.4 Covariates

Resource availability and spatial distribution are known to influence animal movement, where individuals in low productive and highly heterogeneous environments move longer distances [46, 72], seeking necessary resources to satisfy their energetic needs. To evaluate the effect of resource productivity and spatial distribution on movement, we used the Normalized-Difference Vegetation Index (NDVI) MOD13Q1 v.006 images with a 250m resolution at a 16-day interval, derived from MODIS satellite imagery and available online from 2000 (https://search.earthdata.nasa.gov/search?q=C194001241-LPDAAC_ECS). NDVI is an index of primary productivity measuring the green biomass of the canopy and grasslands [5, 65], though previous studies [4] also found a correlation between understory biomass and NDVI values in forest habitats. Note that only the study of bison in Prince Albert National Park started before 2000. For the 2 individuals monitored before 2000 (one in 1997, the other in 1997 and 1998), we used the NDVI images from 2000.

We retrieved NDVI composite images spanning from February 2000 to December 2019, which correspond to the year NDVI 250m was first available and the last year of monitoring in our data set, respectively. We rescaled NDVI values to vary between $[-1, 1]$, and modified and removed values based on pixel reliability provided with MOD13Q1. Pixels with reliability values of -1 (no data) and 3 (cloudy) were removed, and those of 2 (snow/ice) were assigned to a NDVI value of 0. Following Teitelbaum et al [72], we set a minimum threshold of 0.05 to all NDVI values below that threshold which do not reflect resource availability for ungulates.

We computed, for each individual-year, the 95% Minimum Convex Polygon (MCP) of all GPS locations from both periods using the *adehabitatHR* package [9] in R. Afterward, we extracted, for each polygon, the mean annual NDVI for the corresponding year of monitoring as a proxy of resource availability. We also measured the spatial range of variation of resources by extracting, for each polygon, the mean annual NDVI (mean interval, derived from MODIS satellite imagery and available online NDVI) values of each pixel for the corresponding year of monitoring and subsequently calculating the spatial range (m) of the autocorrelation in NDVI (range NDVI) values using the *variofit* function from the *geoR* package [61] available in R. High values of the spatial range of NDVI represent broad-scale variation in resources, whereas low values represent fine-scale variation [75]. For 421 out of the 3 860 individual-years, we randomly subsampled 6 000 of the 534 250x250m cells, following Teitelbaum et al [72], to avoid computational limitations due to the high number of cells retrieved in their polygons. Finally, using published papers, we retrieved the mean body mass of adult females for each species in our data set (Table A1) to take into account the allometry of movement, since larger animals have larger range movement and cover larger areas [50].

4.5 Statistical analysis

For all our analyses, we used Bayesian Phylogenetic Mixed-effect Models (BPMM), which are appropriate to perform phylogenetic analyses on large data sets with multiple measurements per species, and implemented in the *MCMCglmm* package [30] for R. It was essential to control for phylogeny as a way to correct for non-independence between species-specific data points that may arise from relatedness among species sharing common traits. We constructed our own phylogenetic tree using full mitogenome sequences retrieved from Genbank [10] (see section "Phylogenetic analysis" in the Supplementary Information B for full details).

We first tested the effect of neonatal tactic (hider vs. follower), resource availability and spatial variation, and period (pre- vs. post-parturition) on the probability of being stationary. We ran BPMM with a binomial distribution specified with the argument family=categorical using the function *MCMCglmm* to investigate the probability of being stationary in each track, defined as a binary response variable (0 = non-stationary BM and 1 = stationary OU/OUF). We included phylogeny (to which we attributed the variance-covariance matrix), species (since multiple measurements for a given species can share biological traits that do not arise from phylogenetic relatedness), population nested in species, year nested in population, and individuals nested in population and species as random factors. We added two three-way interactions in the model as two fixed effects: the first between neonatal tactics, mean NDVI and period, and the second one with the log-transformed spatial range NDVI instead of the mean NDVI. The log-transformed body mass was added as an additive fixed effect to account for the allometric relation of movement [50], along with the monitoring duration of the track (days) and number of locations since a finer and longer sampling procedure has a higher chance of detecting a stationary behavior. Both variables were also log-transformed. We first used a non-informative Inverse Wishart prior ($\nu = 0.02$ and $V = 1$) with a fixed residual variance ($V = 1$ and $fix = 1$). As a second step, we conducted a sensitivity analysis to verify that the prior did not impact our results and re-ran the model using a parameter extended prior ($\nu = 1$, $V = 1$, $alpha.mu = 0$, $alpha.V = 1000$). We observed no difference between the results from each prior. We ran the model three times with 550 000 iterations (burn-in = 50 000 and thinning = 100) and conducted the Gelman-Rubin diagnostic [25] using the *gelman.diag* function from the package *coda* [56] to confirm the convergence of the model. If any difference is observed between the three MCMC chains, the diagnostic concludes that the model did not converge. In our case, we did not detect any difference between our chains.

To assess the effect of parturition and the environment on movement parameters in relation to neonatal tactic, we ran similar BPMM, in terms of random and fixed effects, but with diffusion and return rates as continuous response variables and a Gaussian distribution for the data. In the models on diffusion, we added the attributed model (BM or OU/OUF) as an additive fixed effect to control for differences in diffusion values between BM and OU, the former expressing larger diffusion than the latter. For models on return rate, we only included individuals with tracks identified as stationary Ornstein-Uhlenbeck during both periods. This led to the removal of Mongolian gazelles from the analyses since all individuals were non-stationary during the post-parturition period. We also added, as a statistical weight and for all models, the inverse of the error variance for each data point. We used the non-informative Inverse Wishart prior ($\nu = 0.02$ and $V = 1$) with no fixed residual variance and ran the model with 550 000 iterations (burn-in = 50 000 and thinning = 100). We also conducted a sensitivity analysis with an extended prior ($\nu = 1$, $V = 1$, $alpha.mu = 0$, $alpha.V = 1000$) and found no difference in our results from both priors. We ran the Gelman-Rubin diagnostic and found that our models did converge. To prepare Fig. 4 and 5, we predicted values for each parameter in relation to the 10%, mean and 90% quantiles of every environmental variable (mean and spatial range NDVI) using individuals which were stationary (OU/OUF) during both periods. When predicting values for one environmental variable, we fixed the other at its mean. We fixed the body mass at 60kg, representing the mean body mass of large herbivores [21], and which was log-transformed.

We calculated the phylogenetic heritability [41] H^2 for each model mentioned above, which can be interpreted similarly as Pagel's phylogenetic signal λ [52]. A phylogenetic heritability of $H^2 = 0$ indicates that no phylogenetic relatedness is detected among effect sizes, while an $H^2 = 1$ indicates an exact proportional relationship between effect sizes among species and their phylogenetic relatedness [47]. We reported the mean of the posterior distribution for each effect along with its 95% credible interval of the highest posterior density distribution (HPDI). The significance of an effect was determined by the exclusion of 0 from its credible interval.

Finally, we estimated the consistency of movement parameters at the species, population and individual levels of biological organisation by calculating repeatability (R, see [60] for a review). We also computed the repeatability of diffusion and return rates across years. We estimated Rs according to [48] from the estimated variances associated to the nested random effects of species σ^2_{sp}, population σ^2_{pop}, individual σ^2_{id} and time σ^2_{t} in the GLMMs fitted to individual estimations of movement parameters (σ^2 and τ_p). We extracted inter-individual variance from the residual variance (σ^2_e) and then obtained Rs by dividing one variance component by the sum of all components ($\sigma^2_{\mathrm{sp}} + \sigma^2_{\mathrm{pop}} + \sigma^2_{\mathrm{id}} + \sigma^2_{\mathrm{t}} + \sigma^2_{\mathrm{e}}$). For instance, we calculated repeatability for τ at the species level as:

$$R_{\tau_p} = \frac{\sigma^2_{\mathrm{sp}}}{\sigma^2_{\mathrm{sp}} + \sigma^2_{\mathrm{pop}} + \sigma^2_{\mathrm{id}} + \sigma^2_{\mathrm{t}} + \sigma^2_{\mathrm{e}}}$$

We report all statistics and estimated parameters as the mean and associated 95% credible intervals following [39], whereby $_{\text{95\% lower limit}}$ point estimate $_{\text{95\% upper limit}}$.

Data Availability. The computer code and data used in this paper are available online at the following web address: https://gitlab.in2p3.fr/christophe.bonenfant/neonatal-tactics

Acknowledgments. KA was funded by the French Ministry of Education and Research, and this research took place within a project funded by ANR grant 'Mov-It' (ANR-16-CE02-0010), coordinated by AL We thank members of the 'Mov-It' working group for their helpful comments and inputs on the study. We thank all professionals, PhD and master's students, technical support, and trainees from each collaborating institution for collecting and organizing the respective data sets. We thank Glenn Yannic for his help in constructing the phylogenetic tree. We thank Frédéric Lesmerises and Clara Superbie who provided individual parturition dates for Gaspésie and Saskatchewan Boreal Shield caribou, respectively. We acknowlegde the contribution of Matt Hayes in the collection of mule deer data, Wyoming. This work was performed using the computing facilities of the CC LBBE/PRABI. See also the "Extended acknowledgments" section in the supplementary information (appendix H).

Author Contributions Statement. AL and GP conceived the project, and AL, CB and JMG supervised the revision of the article up to its acceptance. AL, GP and KA assembled existing data that were primary collected and managed by all coauthors. KA performed the statistical analyses, under the supervision of AL, GP, CB and JMG. KA and AL wrote the first draft of the ms. CB, JMG, MG, AJMH, PM, and NM made substantial contribution to the intellectual content of the article and AL, CB and JMG revised the article. All coauthors revised critically, approved the first and revised drafts, and gave their final approval of the version to be published.

Competing Interests Statement. The authors declare no competing interests.

Tables.

Table 1: Glossary of parameters and movement processes of interest, adapted from [54].

Parameters and models	Notations and acronyms	Biological meaning
Brownian motion	BM	An endlessly diffusing movement process described simply by the instantaneous diffusion parameter (D) and representing non-stationarity.
Ornstein-Uhlenbeck position movement process	OU	A stationary home range-bounded movement process described by two parameters (OU: D and τ_p) [18]). Individuals with OU movement patterns are called "resident" in the main text.
Movement process variance	σ^2 (m^2)	The non-random movement magnitude of the movement process, representing a proxy of home range size.
Instantaneous diffusion	D ($m^2.s^{-1}$)	The area covered by an animal per unit of time. Rate representing the area covered when an animal roams away from its position, per time unit. "Diffusion" in the main text.
Position autocorrelation time[18]	τ_p (s)	Time necessary for an animal to revert back to its expected path after a random deviation. Its inverse represents the frequency of return to a central place and is called "return rate" in the main text.
Normalized difference vegetation index	NDVI	The mean NDVI is a proxy of vegetation productivity for large herbivores at large spatial scales [55].
Spatial scale of NDVI variation	SS_{NDVI}	Represents "the distance necessary to travel until NDVI values are uncorrelated" - see [72].

Figure Legends/Captions (for main text figures).

Fig. 1: Conceptual framework and analytical steps for studying the interplay of neonatal tactic (hider vs. follower offspring) and environmental context (resource productivity and spatial scale of resource variation, *sensu* [72]) on residency level, movement metrics and the resulting home range of females before and after giving birth (see introduction for details). Step 1 classifies female movement as fitting a Brownian or an Ornstein-Uhlenbeck (OU) type of model (see Method section, and glossary in Table 1). A female is defined as "resident" if her movement is best described by an OU model. The figure in Step 1 panel displays how the proportion of residents in a population is expected to vary pre- and post-birth in species with hider and follower offspring, across gradients of resource productivity or spatial scale of resource variation. Step 2 corresponds to the predictions for how the 2 movement metrics (diffusion in orange and return rate in purple) and the resulting home range size (in black) should respond pre- and post-birth to the same environmental variables depending on neonatal tactics. Note that when a movement is best descried by a Brownian model (no "residency"), only diffusion (hence neither return rate or home range size) can be estimated.

Fig. 2: Overview of the species and populations. a) Phylogenetic tree of the 23 species of large herbivores included in this study (see the "Phylogenetic analysis" section in the Supplementary Information B). The number of populations for each species is indicated on each pictogram (downloaded from http://www.phylopic.org or from the personal collection of the authors). Blue and red represent followers and hiders, respectively. b) Average location of each population (see Supplementary Table A1) on a composite map of cumulative Normalized Difference Vegetation Index (NDVI) values, retrieved from [58], and used solely for presentation purposes.

Fig. 3: Changes in the propensity for a female to be resident across populations of 23 species of large herbivores (a) in the pre-parturition period and (b) in the post-parturition period, in relation to increasing spatial scale of resource variation (measured by $\mathrm{SS}_{\mathrm{NDVI}}$) with follower (in blue) and hider (in red) offspring. Points, lines, and shading represent mean probability, model fit, and its associated 95% credible intervals, respectively. Point size is proportional to the number of females.

Fig. 4: Changes in expected values of diffusion [a-b] and return rate [c-d] for females across 23 species of large herbivores in relation to mean resource productivity (measured by mean NDVI) and spatial scale of resource variation (measured by $\mathrm{SS}_{\mathrm{NDVI}}$) prior to (dark shading) and following (light shading) parturition with hider (red roe deer fawn) and follower (blue chamois kid) offspring. Low, mean and high categories represent the 10%, mean, and 90% quantiles of each environmental variable. The histogram [e] shows the repeatability of diffusion and return rates according to the different levels of observation (individual, population and species) and time in years.

Fig. 5: Expected mean values of diffusion and return rates of adult females across populations of 23 species of large terrestrial herbivores in relation to (a) mean resource productivity (measured as mean NDVI) and (b) spatial scale of resource variation (measured by $\mathrm{SS}_{\mathrm{NDVI}}$) prior to (start of arrows) and following (arrows' tip) parturition with hider (in red with a deer fawn symbol) and follower (in blue with a chamois kid symbol) offspring. 'Low', 'mean', and 'high' represent the 10%, 50%, and 90% quantiles of each environmental factor (0.18, 0.41, and 0.72 for mean NDVI, and 0.25, 1.33, and 6.5 km for $\mathrm{SS}_{\mathrm{NDVI}}$). Home range size (dotted grey horizontal lines) increases with increasing diffusion and decreasing return rate.

References

[1] Bjørneraas K, Van Moorter B, Rolandsen CM, et al (2010) Screening global positioning system location data for errors using animal movement characteristics. The Journal of Wildlife Management 74(6):1361–1366

[2] Blackwell P (1997) Random diffusion models for animal movement. Ecological Modelling 100(1-3):87–102

[3] Börger L, Fryxell J (2012) Quantifying individual differences in dispersal using net squared displacement. Dispersal ecology and evolution 30:222–230

[4] Borowik T, Pettorelli N, Sönnichsen L, et al (2013) Normalized difference vegetation index (NDVI) as a predictor of forage availability for ungulates in forest and field habitats. European Journal of Wildlife Research 59:675–682

[5] Boschetti M, Bocchi S, Brivio PA (2007) Assessment of pasture production in the Italian Alps using spectrometric and remote sensing information. Agriculture, Ecosystems & Environment 118(1-4):267–272

[6] Bunnefeld N, Börger L, van Moorter B, et al (2011) A model-driven approach to quantify migration patterns: individual, regional and yearly differences. Journal of Animal Ecology 80(2):466–476

[7] Calabrese JM, Fleming CH, Gurarie E (2016) ctmm: An R package for analyzing animal relocation data as a continuous-time stochastic process. Methods in Ecology and Evolution 7(9):1124–1132

[8] Calder WA (1984) Size, function, and life history. Courier Corporation

[9] Calenge C (2006) The package “adehabitat” for the R software: a tool for the analysis of space and habitat use by animals. Ecological modelling 197(3-4):516–519

[10] Clark K, Karsch-Mizrachi I, Lipman DJ, et al (2016) Genbank. Nucleic Acids Research 44(D1):D67–D72

[11] Clutton-Brock T, Albon S, Guinness eF (1989) Fitness costs of gestation and lactation in wild mammals. Nature 337(6204):260–262

[12] Dunn JE, Gipson PS (1977) Analysis of radio telemetry data in studies of home range. Biometrics pp 85–101

[13] English AK, Chauvenet AL, Safi K, et al (2012) Reassessing the determinants of breeding synchrony in ungulates. PLoS One 7(7):e41444

[14] Estes RD, Estes RK (1979) The birth and survival of wildebeest calves. Zeitschrift für Tierpsychologie 50(1):45–95

[15] Fauchald P (1999) Foraging in a hierarchical patch system. American Naturalist 153(6):603–613

[16] Felsenstein J (1985) Phylogenies and the comparative method. American Naturalist 125(1):1–15

[17] Fisher D, Blomberg S, Owens I (2002) Convergent maternal care strategies in ungulates and macropods. Evolution 56(1):167–176

[18] Fleming CH, Calabrese JM, Mueller T, et al (2014) From fine-scale foraging to home ranges: a semivariance approach to identifying movement modes across spatiotemporal scales. American Naturalist 183(5):E154–E167

[19] Fleming CH, Subaşı Y, Calabrese JM (2015) Maximum-entropy description of animal movement. Physical Review E 91(3):032107

[20] Fretwell SD, Lucas Jr. HL (1970) On territorial behavior and other factors influencing habitat distribution in birds I. theoretical development. Acta Biotheor 19:16–36

[21] Fritz H, Loison A (2006) Large herbivores across biomes. In: Danell K, Duncan P, Bergström R, et al (eds) Large Herbivore Ecology, Ecosystem Dynamics and Conservation, vol 11. Cambridge University Press, p 19

[22] Fryxell JM, Hazell M, Börger L, et al (2008) Multiple movement modes by large herbivores at multiple spatiotemporal scales. Proceedings of the National Academy of Sciences 105(49):19114–19119

[23] Gaillard JM, Pontier D, Allaine D, et al (1989) An analysis of demographic tactics in birds and mammals. Oikos pp 59–76

[24] Gaillard JM, Lemaître JF, Berger V, et al (2016) Axes of variation in life histories. In: Kliman R (ed) The Encyclopedia of Evolutionary Biology. Elsevier, Academic Press, p 312–323

[25] Gelman A, Rubin DB (1992) Inference from iterative simulation using multiple sequences. Statistical science pp 457–472

[26] Geremia C, Merkle JA, Eacker DR, et al (2019) Migrating bison engineer the green wave. Proceedings of the National Academy of Sciences 116(51):25707–25713

[27] Van der Graaf A, Stahl J, Klimkowska A, et al (2006) Surfing on a green wave-how plant growth drives spring migration in the Barnacle Goose *Branta leucopsis*. Ardea 94(3):567

[28] Green WC (1992) The development of independence in bison: pre-weaning spatial relations between mothers and calves. Animal behaviour 43(5):759–773

[29] Grémillet D, Lescroël A, Ballard G, et al (2018) Energetic fitness: field metabolic rates assessed via 3D accelerometry complement conventional fitness metrics. Functional Ecology 32(5):1203–1213

[30] Hadfield JD (2010) MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. Journal of Statistical Software 33:1–22

[31] Harestad AS, Bunnel F (1979) Home range and body weight–a reevaluation. Ecology 60(2):389–402

[32] Healy K, Guillerme T, Finlay S, et al (2014) Ecology and mode-of-life explain lifespan variation in birds and mammals. Proceedings of the Royal Society B: Biological Sciences 281(1784):20140298

[33] Higgins SI, Conradi T, Muhoko E (2023) Shifts in vegetation activity of terrestrial ecosystems attributable to climate trends. Nature Geoscience 16(2):147–153

[34] Hofmann RR (1989) Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. Oecologia 78(4):443–457

[35] Jetz W, Carbone C, Fulford J, et al (2004) The scaling of animal space use. Science 306(5694):266–268

[36] Kelt DA, Van Vuren DH (2001) The ecology and macroecology of mammalian home range area. American Naturalist 157(6):637–645

[37] Lent PC (1974) Mother-infant relationships in ungulates. The behaviour of ungulates and its relation to management 1:14–55

[38] Lindström J (1999) Early development and fitness in birds and mammals. Trends in Ecology & Evolution 14(9):343–348

[39] Louis TA, Zeger SL (2009) Effective communication of standard errors and confidence intervals. Biostatistics 10(1):1–2

[40] Lovari S, Sforzi A, Mori E (2013) Habitat richness affects home range size in a monogamous large rodent. Behavioural Processes 99:42–46

[41] Lynch M (1991) Methods for the analysis of comparative data in evolutionary biology. Evolution 45(5):1065–1080

[42] McDonald DW (1983) The ecology of carnivore social behaviour. Nature 301(5899):379–384

[43] McLoughlin P, Gaillard JM, Boyce M, et al (2007) Lifetime reproductive success and composition of the home range in a large herbivore. Ecology 88(12):3192–3201

[44] McMahon TA, Bonner JT (1983) On size and life. Scientific American Books - W. H. Freeman & Co

[45] Mueller T, Fagan WF (2008) Search and navigation in dynamic environments–from individual behaviors to population distributions. Oikos 117(5):654–664

[46] Mueller T, Olson KA, Dressler G, et al (2011) How landscape dynamics link individual-to population-level movement patterns: a multispecies comparison of ungulate relocation data. Global Ecology and Biogeography 20(5):683–694

[47] Nakagawa S, Santos ES (2012) Methodological issues and advances in biological meta-analysis. Evolutionary Ecology 26:1253–1274

[48] Nakagawa S, Schielzeth H (2010) Repeatability for gaussian and non-gaussian data: a practical guide for biologists. Biological Reviews 85(4):935–956

[49] Nathan R (2008) An emerging movement ecology paradigm. Proceedings of the National Academy of Sciences 105(49):19050–19051

[50] Ofstad EG, Herfindal I, Solberg EJ, et al (2016) Home ranges, habitat and body mass: simple correlates of home range size in ungulates. Proceedings of the Royal Society B: Biological Sciences 283(1845):20161234

[51] Oftedal OT, Boness DJ, Tedman RA (1987) The behavior, physiology, and anatomy of lactation in the pinnipedia. Current Mammalogy pp 175–245

[52] Pagel M (1999) Inferring the historical patterns of biological evolution. Nature 401(6756):877–884

[53] Panzacchi M, Herfindal I, Linnell JD, et al (2010) Trade-offs between maternal foraging and fawn predation risk in an income breeder. Behavioral Ecology and Sociobiology 64:1267–1278

[54] Péron G, Fleming CH, de Paula RC, et al (2017) Periodic continuous-time movement models uncover behavioral changes of wild canids along anthropization gradients. Ecological Monographs 87(3):442–456

[55] Pettorelli N, Vik JO, Mysterud A, et al (2005) Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends in ecology & evolution 20(9):503–510

[56] Plummer M, Best N, Cowles K, et al (2006) CODA: convergence diagnosis and output analysis for MCMC. R news 6(1):7–11

[57] R Core Team (2023) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, URL https://www.R-project.org/

[58] Radeloff V, Dubinin M, Coops N, et al (2019) The dynamic habitat indices (DHIs) from MODIS and global biodiversity. Remote Sensing of Environment 222:204–214

[59] Read A, Harvey PH (1989) Life history differences among the eutherian radiations. Journal of Zoology 219(2):329–353

[60] Réale D, Reader SM, Sol D, et al (2007) Integrating animal temperament within ecology and evolution. Biological reviews 82(2):291–318

[61] Ribeiro Jr PJ, Diggle PJ, Ribeiro Jr MPJ, et al (2007) The geoR package. R news 1(2):14–18

[62] Rowcliffe MJ, Carbone C, Kays R, et al (2012) Bias in estimating animal travel distance: the effect of sampling frequency. Methods in Ecology and Evolution 3(4):653–662

[63] Rutberg AT (1987) Adaptive hypotheses of birth synchrony in ruminants: an interspecific test. American Naturalist 130(5):692–710

[64] Sadleir R (1969) The ecology of reproduction in wild and domestic mammals. London, Methuen

[65] Santin-Janin H, Garel M, Chapuis JL, et al (2009) Assessing the performance of NDVI as a proxy for plant biomass using non-linear models: a case study on the Kerguelen archipelago. Polar Biology 32:861–871

[66] Seigle-Ferrand J, Atmeh K, Gaillard JM, et al (2021) A systematic review of within-population variation in the size of home range across ungulates: what do we know after 50 years of telemetry studies? Frontiers in Ecology and Evolution 8:555429

[67] Shepard EL, Wilson RP, Rees WG, et al (2013) Energy landscapes shape animal movement ecology. American Naturalist 182(3):298–312

[68] Shiffler RE (1988) Maximum Z scores and outliers. American Statistician 42(1):79–80

[69] Sinclair A, Mduma SA, Arcese P (2000) What determines phenology and synchrony of ungulate breeding in Serengeti? Ecology 81(8):2100–2111

[70] Stearns SC (1989) Trade-offs in life-history evolution. Functional Ecology 3(3):259–268

[71] Stevens VM, Whitmee S, Le Galliard JF, et al (2014) A comparative analysis of dispersal syndromes in terrestrial and semi-terrestrial animals. Ecology Letters 17(8):1039–1052

[72] Teitelbaum CS, Fagan WF, Fleming CH, et al (2015) How far to go? Determinants of migration distance in land mammals. Ecology Letters 18(6):545–552

[73] Tufto J, Andersen R, Linnell J (1996) Habitat use and ecological correlates of home range size in a small cervid: the roe deer. Journal of Animal Ecology 65:715–724

[74] Van Moorter B, Gaillard JM, McLoughlin PD, et al (2009) Maternal and individual effects in selection of bed sites and their consequences for fawn survival at different spatial scales. Oecologia 159:669–678

[75] Van Moorter B, Bunnefeld N, Panzacchi M, et al (2013) Understanding scales of movement: animals ride waves and ripples of environmental change. Journal of Animal Ecology 82(4):770–780

[76] Venter JA, Vermeulen MM, Brooke CF (2019) Feeding ecology of large browsing and grazing herbivores. In: Gordon IJ, Prince HHT (eds) The ecology of browsing and grazing II. Springer Nature Switzerland, p 127–153

Supplementary information. This article has 8 supplementary sections (appendices A–G).

Appendix A Species and populations

Table A1: Population level data: study site location, GPS sampling schedule, neonatal tactic of newborns (NAP: H – hider; F – follower), average body mass of species (BM), number of monitored individuals (N), range of study years (Time range), and data source for the 54 populations of large herbivores we used in this study. In most cases, captured animals were not weighed for practical reasons. Hence we extracted mean body mass of females from the literature, and assigned the same values for all populations of the same species.

Species	Population	Average animal locations	NAP	BM (kg)	N	sched. (h)	Time range	Data institution
Aepyceros melampus	Serengeti National Park	2.1245S, 34.9456E	H	43.8	17	1	2016–2017	Norwegian Institute for Nature Research (NINA)
Alces alces	Alberta – British Columbia	53.9604N, 118.3382W	H	365	7	4	2008–2009	University of Montana (UMT)
	Alaska – Berners Bay	58.8630N, 134.9196W	H		22	3	2007-2010	Alaska Department of Fish and Game (ADFG)
	Alaska – Gustavus	58.4481N, 135.7300W	H		27	3	2004–2016	
	Jackson	43.8918N, 110.3630W	H		40	1	2005–2009	Wyoming Cooperative Fish and Wildlife Research Unit (WYOCOOP)
	Sublette	42.9813N, 110.2795W	H		56	1	2011–2014	
	Valdres & Hallingdal	60.7035N, 9.0140E	H		22	3	2014–2017	NINA
	Vega Island	65.6589N, 11.9636E	H		48	1	2008–2018	
Antilocapra americana	Northern Sagebrush Steppe	49.2217N, 108.3931W	H	46.844	139	4	2004–2010	UMT
	Red Desert	41.6054N, 107.9508W	H		116	2	2014–2016	University of Wyoming (UWYO)
	Rock Springs	41.5178N, 109.7946W	H		33	2	2017–2018	WYOCOOP
Bison bison	Henry Mountains	38.0000N, 110.8610W	F	274.75	26	6	2011–2013	Utah State University (USU)
	Prince Albert National Park	53.7266N, 106.6663W	F		51	1	1997–2017	Laval University (ULAVAL)
Capra ibex	Bargy mountain range	45.9998N, 6.4642E	F	48.9	24	1	2013–2019	Office Français de la Biodiversité (OFB)
	Swiss National Park	46.6108N, 10.1010E	F		10	2	2008-2017	Swiss National Park (SNP)

Species	Population	Average animal locations	NAP	BM (kg)	N	sched. (h)	Time range	Data institution
Capreolus capreolus	Aurignac	43.2673N, 0.8660E	H	26.5	79	1	2003–2018	National Research Institute for Agriculture, Food and Environment
	Bavarian Forest National Park	48.9388N, 13.3859E	H		21	4	2005–2012	University of Freiburg
	Koberg estate	58.1515N, 12.4307E	H		8	4	2009–2012	Swedish University Of Agricultural Sciences
Cervus elaphus	Bavarian Forest National Park	48.9651N, 13.4393E	H	125	50	1	2002–2013	University of Freiburg
	La Petite Pierre	48.8185N, 7.3309E	H		59	0.25	2002–2016	OFB
	Multiple Norwegian counties	62.9536N, 8.4790E	H		15	1	2007–2010	University of Oslo & Norwegian Institute of Bioeconomy Research
Cervus elaphus canadensis	Canadian Rockies	49.5247N, 114.3009W	H	238.7	98	2	2007–2012	University of Alberta
	Little Mountain	41.1977N, 109.2604W	H		46	1	2016–2019	Wyoming Cooperative Fish and Wildlife Research Unit (WYOCOOP)
	Ya Ha Tinda Ranch	51.7169N, 115.5565W	H		125	0.25	2002–2018	UMT
Connochaetes taurinus	Kenya – 3 National Parks	1.7132S, 36.3246E	F	184.9	19	1	2011–2012	Colorado State University
	Liuwa Plain National Park	14.5594S, 22.5280E	F		13	4	2010–2018	Zambian Carnivore Program
Dama dama	Koberg estate	58.1295N, 12.4135E	H	44	20	1	2007–2012	Swedish University Of Agricultural Sciences
Equus hemionus	Mongolian Gobi	43.0219N, 108.3966E	F	230	17	1	2014–2017	Wildlife Conservation Society Mongolia (WCS Mongolia), University of Veterinary Medicine Vienna (MedVetvienna) & NINA.

Species	Population	Average animal locations	NAP	BM (kg)	N	sched. (h)	Time range	Data institution
Equus quagga	Hwange National Park	18.8889S, 26.8467E	F	322	23	0.5	2009–2016	Centre d'Ecologie Fonctionnelle et Evolutive (CEFE)
Giraffa camelopardalis angolensis	Namib desert	18.9912S, 13.0338E	H	700	5	1	2017–2018	Giraffe Conservation Foundation
Hippotragus niger	Kruger National Park	24.6996S, 31.2303E	H	216.16	7	6	2004–2009	University of Witwatersrand
Odocoileus hemionus	Haida Gwaii	52.8443N, 131.5834W	H	55.5	15	0.5	2011–2013	CEFE
	Little Mountain	41.2305N, 109.1691W	H		92	1	2016–2019	WYOCOOP
	Red Desert	42.2931N, 109.2875W	H		101	2	2014–2019	
	Southwest Colorado	37.7303N, 108.9252W	H		11	3	2012–2013	Colorado Parks and Wildlife (CPW), United State Department of Agriculture-Animal Plant and Health Inspection Service-Wildlife Services (USDA-APHIS-WS), & Pennsylvania Cooperative Fish and Wildlife Research Unit (PACOOP)
	Western Washington	47.1033N, 123.0875W	H		152	5	2009–2017	Washington Department of Fish and Wildlife (WDFW)
	Wyoming Range	42.3342N, 110.6724W	H		143	2	2013–2018	WYOCOOP
Odocoileus virginianus	Pennsylvania	40.2144N, 78.4453W	H	68.5	31	0.5	2018-2018	Pennsylvania Game Commission (PGC) & PACOOP

Species	Population	Average animal locations	NAP	BM (kg)	N	sched. (h)	Time range	Data institution
Oreamnos americanus	Alaska - Klukwan	59.4010N, 135.8817W	F	61	20	6	2011–2016	ADFG
	Alaska – Lynn Canal	59.0049N, 135.0880W	F		18	6	2007–2015	
	Washington	47.6151N, 121.3694W	F		31	3	2003–2007	WDFW
Ovibos moschatus	Zackenberg	74.4654N, 20.6262W	F	266	28	1	2014–2017	Aarhus University
	Quebec	58.1965N, 73.5548W	F	225	18	3.5	2017–2018	ULAVAL & Ministry of Forests, Fauna and Parks
Ovis canadensis	Grand Teton	43.7210N, 110.8562W	F	57.9	2	0.5	2009–2009	WYOCOOP
Ovis gmelini musimon	Bauges hunting reserve	45.6970N, 6.2004E	F	37.1	16	0.33	2005–2013	OFB
	Caroux reserve	43.6321N, 2.9619E	F		75	2	2004–2018	
Procapra gutturosa	Mongolian Steppe	47.2447N, 115.4887E	H	24	6	1	2009–2017	WCS Mongolia
Rangifer tarandus caribou	Côte du Nord	50.8335N, 68.7283W	F	132	53	1	2005–2018	ULAVAL
	Gaspésie	48.9583N, 66.1316W	F		25	2	2013–2016	Université du Québec à Rimouski
	Saskatchewan Boreal Shield	57.1532N, 104.3711W	F		86	5	2014–2017	University of Saskatchewan – McLoughlin Lab in Population Ecology
Rangifer tarandus platyrhynchus	Svalbard	78.0478N, 15.4607E	F		49	2	2009–2018	Norwegian University of Life Sciences
Rupicapra rupicapra	Bauges hunting reserve	45.6582N, 6.2190E	F	31.7	89	0.33	2004–2018	OFB
	Swiss National Park	46.6464N, 10.1566E	F		22	2	2007–2016	SNP
Saiga tatarica	Mongolian Steppe	47.0629N, 93.8708E	H	32.3	16	5	2007–2018	WWF & WCS Mongolia

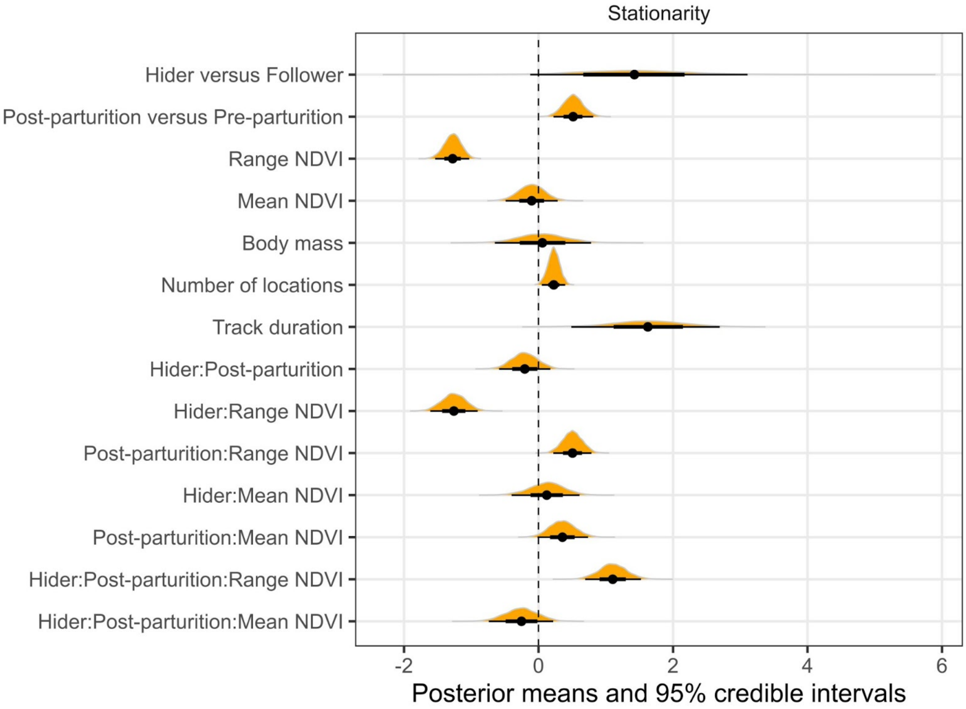
Appendix B Phylogenetic analysis

We retrieved full mitogenome sequences from Genbank. Sequences were aligned using Kalign 2.072, edited and visually inspected with SeaView 4.3.31. The models of DNA substitution were selected using the software “Smart Model Selection” (SMS)2, based on the Akaike Information Criterion (AIC). The GTR + G + I substitution model best fitted our mitogenome data set. Based on this selected substitution model, a phylogenetic tree was constructed using a Maximum Likelihood (ML) approach applied on $>$ 16000 aligned base pairs of full mitogenomes. ML heuristic searches were performed using PHYML 3.33, optimizing the tree topology with SPR, using a BioNJ starting tree and adding 5 SPR tree searches using random starting trees. The resulting unrooted tree was visualized and edited with FigTree 1.3.1 (http://tree.bio.ed.ac.uk/software/figtree/; Fig. 2.a). Finally, we extracted the covariance matrix among the species from the phylogenetic tree.

Appendix C Stationarity

Fig. C1: Percentage of Ornstein-Uhlenbeck models (stationarity) for pre-parturition (plain bars) and post-parturition (dashed bars) for each studied population. Horizontal lines represent the mean percentage of stationarity for each tactic and period. Blue and red represent followers and hiders, respectively. BIS: American bison; BGS: Bighorn sheep; CA: Caribou; CH: Alpine chamois; ELK: Elk; FD: Fallow deer; GI: Giraffe; IB; Alpine ibex; IMP: Impala; KL: Khulan; MG: Mountain goat; MK: Muskox; MOG: Mongolian gazelle; MOU: European mouflon; MS: Moose; MUL: Mule deer; PG: Pronghorn; RD: Red deer; RN: Svalbard reindeer; ROE: Roe deer; SA: Saiga antelope; SAB: Sable antelope; WIL: Wildebeest; WTD: White-tailed deer; ZR: Plains zebra.

Fig. C2: Means of the posterior distribution for phylogenetic heritability $\mathbf{H^2}$ and fixed effects, along with their 95% highest posterior density intervals (HPDI), extracted from Bayesian Phylogenetic Mixed Models assessing the relationship between neonatal tactic, reproductive period, seasonality, and the probability of being stationary. Values excluding 0 are statistically significant. We estimated the parameters from a dataset of 23 species and $N = 2\,386$ monitored individuals.



Appendix D Bayesian phylogenetic linear mixed effect models

Fig. D3: Means of the posterior distribution and 95% highest posterior density intervals (HPDI) of the fixed effects retrieved from the most parsimonious Bayesian Phylogenetic Mixed Models determining factors impacting the variation of home range size, diffusion, and the frequency of return to a central place. Values excluding 0 are statistically significant. We estimated the parameters from a dataset of 23 species and $N = 2\,386$ monitored individuals.

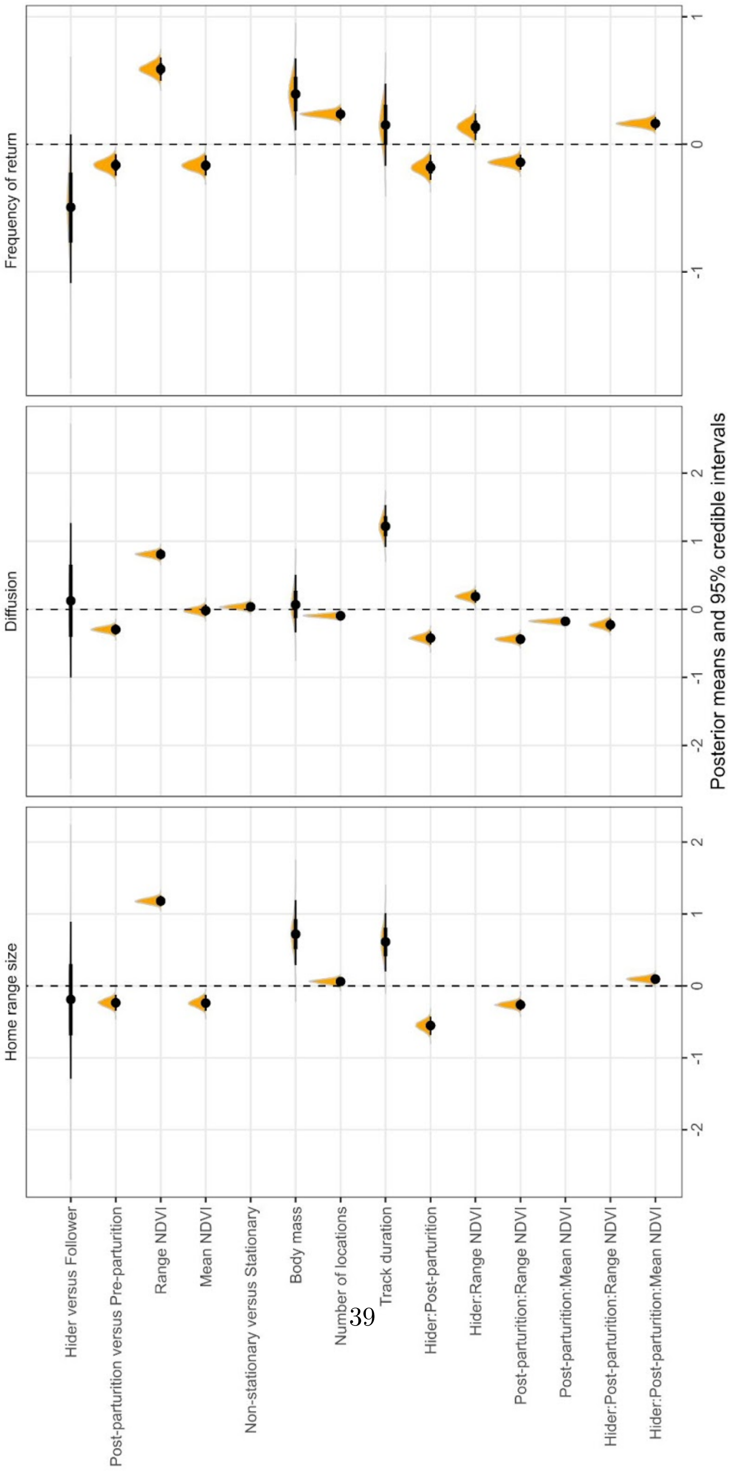


Fig. D4: Reconstructed slopes for mean (a-b-c) and range (d-e-f) NDVI from the most parsimonious Bayesian Phylogenetic Mixed models for home range size, diffusion, and frequency of return for each neonatal anti-predator tactic and period. Bars associated to point estimates are the 95% credible intervals. Blue chamois kid and red roe deer fawn represent followers and hiders, respectively. Greek letters (α, β and γ) highlight statistically different parameters at the 5% risk (parameters with the same letter are not distinguishable). We estimated those parameters from a dataset of 23 species and $N = 2\,386$ monitored individuals.

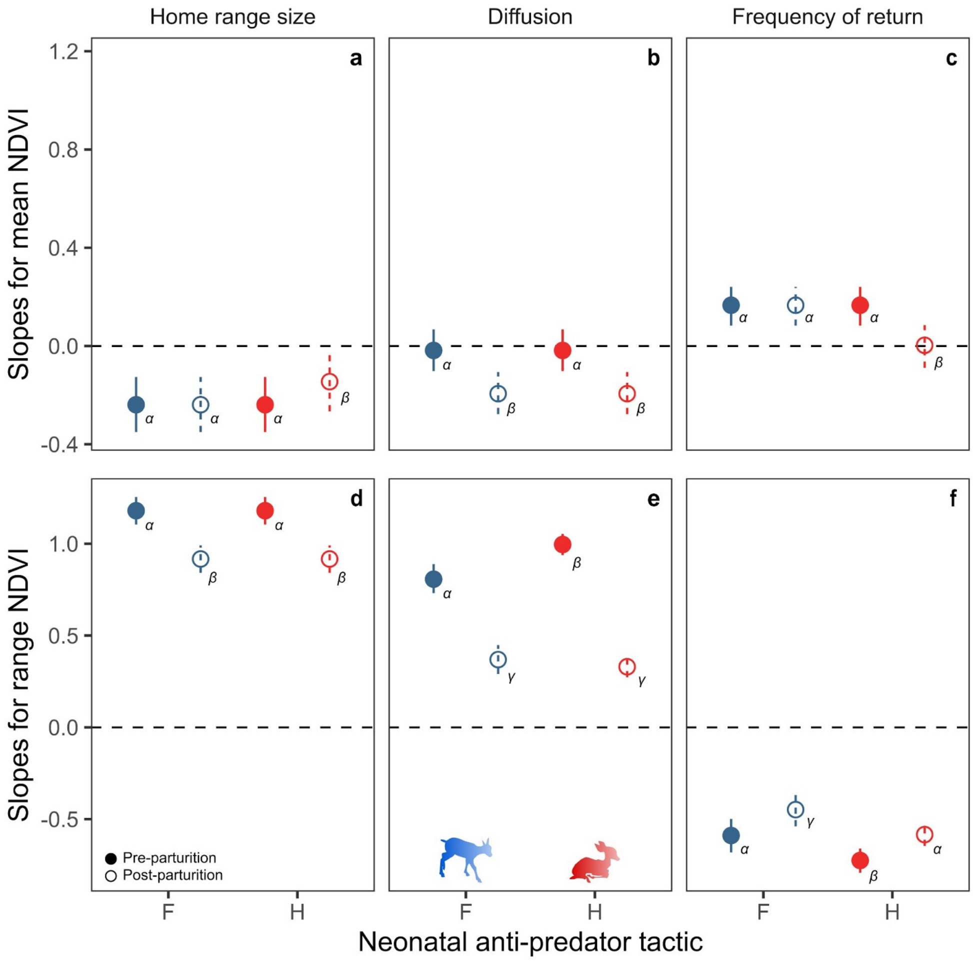


Fig. D5: Predicted values of the three movement components (home range size [a-b], diffusion [c-d], and frequency of return [e-f]) of 23 species of large herbivores ($N = 2\,386$), retrieved from the most parsimonious Bayesian phylogenetic mixed models depicting the effect of the interplay between neonatal anti-predator tactic, pre- and post-parturition, productivity (mean NDVI; left panels) and spatial range of resource variation (range NDVI; right panels). Low, mean, and high classes represent the 10%, mean and 90% quantiles of each environmental variable (0.18, 0.41 and 0.72 for mean NDVI, and 0.25, 1.33 and 6.5 km for range NDVI). Predicted values for each parameter were computed for an animal of 60 kg, and the mean value of one environmental variable was fixed when predicting the effect of the other environmental variable for each class. Solid and blank points represent mean predicted values for pre- and post-parturition, respectively. Dark and light shadings represent pre- and post-parturition, respectively. Red roe deer fawn and blue chamois kid represent hider and follower species, respectively. The increase in the size of points represent higher values of environmental variables.

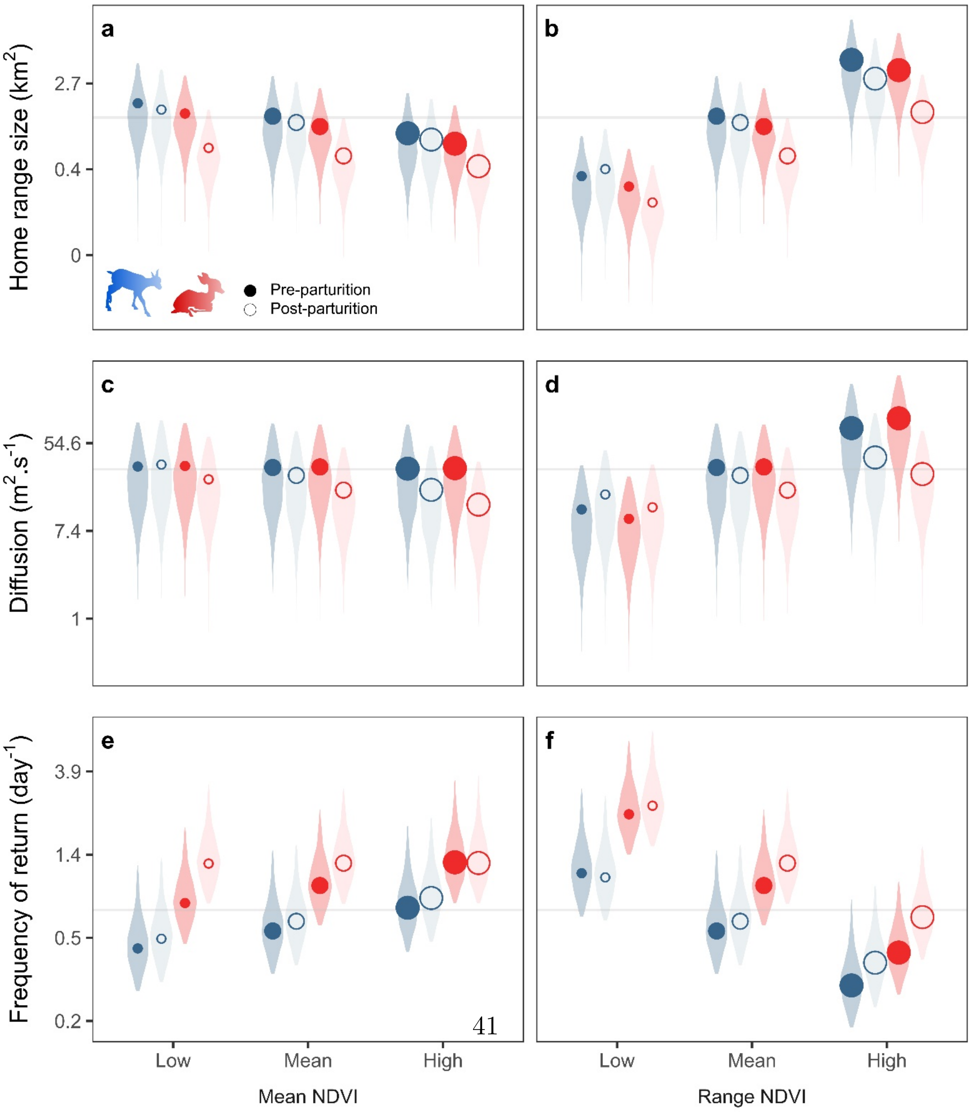


Fig. D6: Predicted values of the three movement components (home range [a, b, c, d], diffusion [e, f, g, h], and frequency of return [i, j k, l]) of 23 species of large herbivores, retrieved from Bayesian phylogenetic mixed models depicting the effect of the interplay between neonatal anti-predator tactic (blue vs. red plots), reproductive period (plain vs. dashed line), productivity [a–j], and spatial range of resource variation [c–l]. Points and shades represent mean predicted values and 95% credible intervals, respectively. Blue and red represent followers and hiders, respectively, also represented by chamois kid and roe deerfawnsilhouettes.

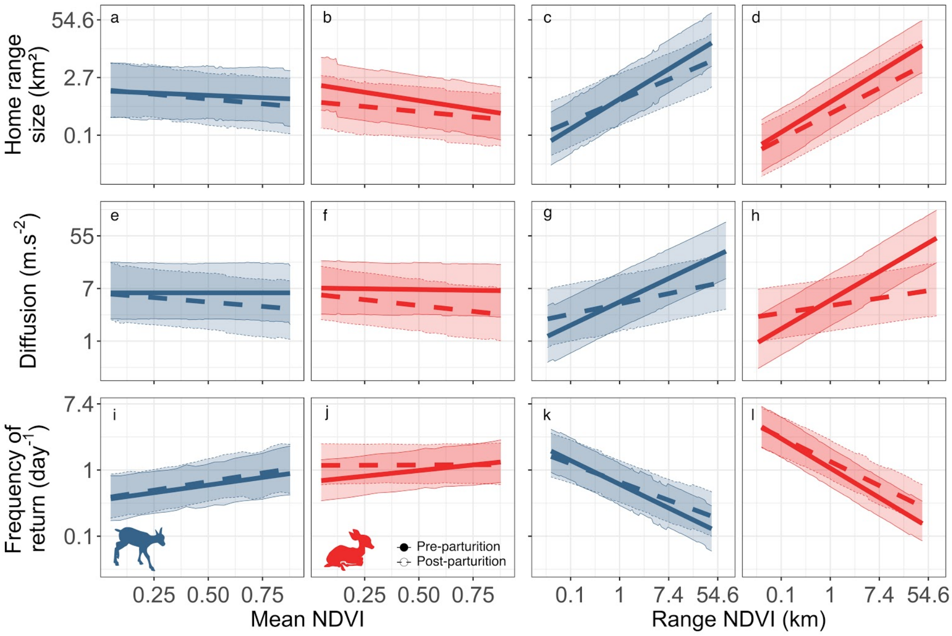
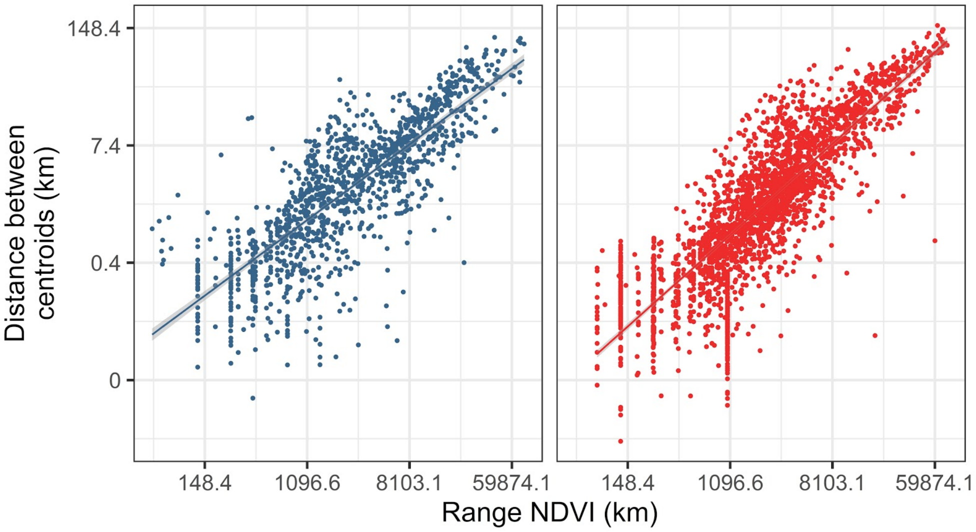
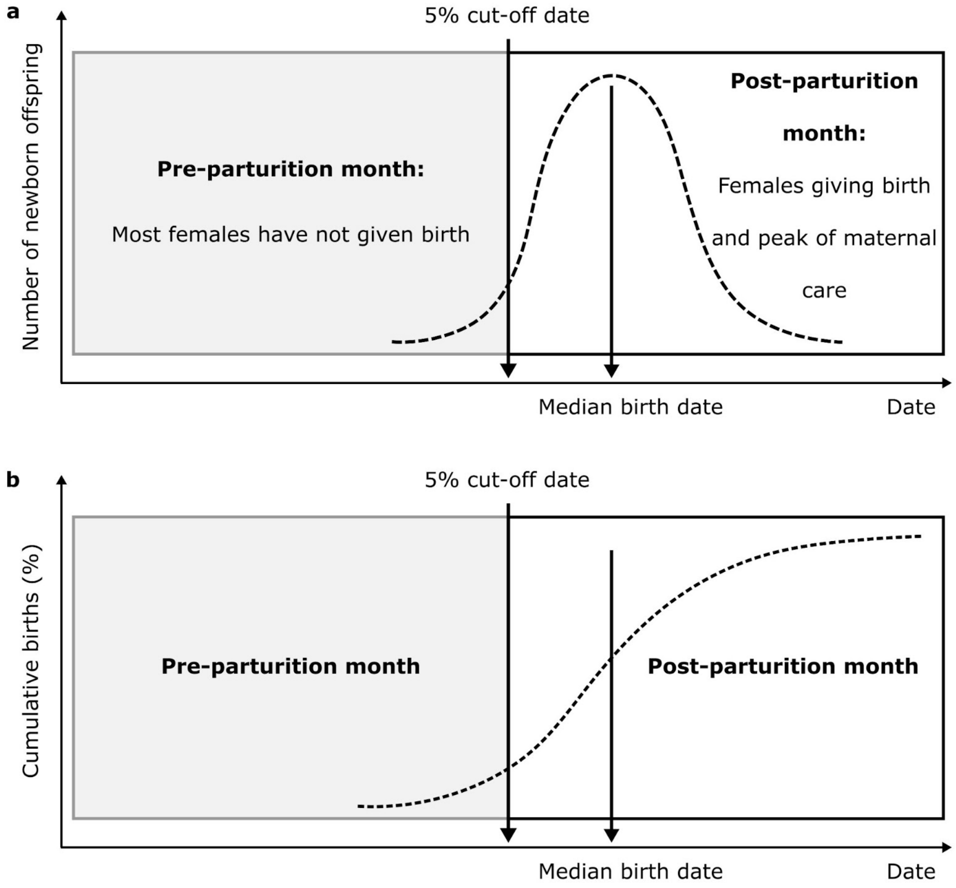


Fig. D7: Linear regression between the range of NDVI and the euclidean distance between the centroïds of the locations of each period for every individual year. Plain colored lines are the predicted values from the regression model, and the shaded area covers the 95% credible intervals of the predictions. Blue and red represent followers and hiders respectively.



Appendix E Cut-off date

Fig. E8: Representing the 5% cut-off date from (a) the distribution of numbers of newborn offspring or from (b) cumulative percentage of birth events to determine pre- and post-parturition periods. The shape of both curves is hypothetical.



Appendix F Semi-variograms of movement models

Fig. F9: GPS location (points) and semivariograms of Brownian Motion and Ornstein-Uhlenbeck movement behavior. Only the diffusion coefficient can be estimated from BM tracks. Ornstein-Uhlenbeck leads to a home range with spatially bounded movements where σ^2 represents the asymptotic movement variance scaling to home range size, τ_p represents the home range crossing time or the time needed to reach the asymptote, and the diffusion coefficient D represents the rate of increase in the Mean Squared Displacement.

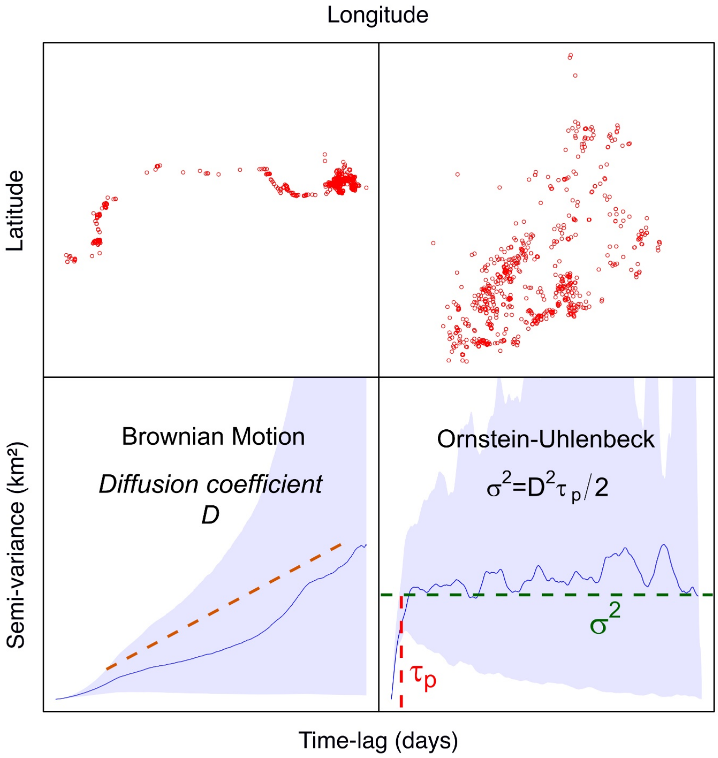


Table E2: Information on reproduction for each study population along with the type of cut-off date used for the analysis. The 5% cut-off dates were retrieved either using published data or using material provided by the data owners.

Species	Population	Reproduction information	Type of cut-off date	5% cut-off date	References
Aepyceros melampus	Serengeti National Park	Pregnancy	Population	1-October	Ogutu et al. 2014[4]
Alces alces	Alberta – British Columbia	None	Population	1-June	Sigouin et al. 1997[5]
	Alaska – Berners Bay	Birth	Population	13-May	Guesstimate provided by data owner
	Alaska – Gustavus	Birth	Population	13-May	Guesstimate provided by data owner
	Jackson	Pregnancy & Birth	Population	14-May	Guesstimate provided by data owner
	Sublette	Pregnancy & Birth	Population	14-May	Guesstimate provided by data owner
	Valdres & Hallingdal	Birth	Population	20-May	Guesstimate provided by data owner
	Vega Island	Birth	Individual & Population	20-May	Computed using individual birth dates
Antilocapra americana	Northern Sagebrush Steppe	None	Population	12-May	Barrett 1981[6]
	Red Desert	Birth	Population	12-May	Panting 2018[7]
	Rock Springs	None	Population	22-May	Guesstimate provided by data owner
Bison bison	Henry Mountains	None	Population	1-April	Fuller et al. 2007[8]
	Prince Albert National Park	Pregnancy at capture	Population	25-April	Meagher 1986[9]
Capra ibex	Bargy mountain range	Birth	Population	19-May	Couturier 1961[10], Catusse et al. 1996[11]
	Swiss National Park	Birth	Population	1-June	Guesstimate provided by data owner
Capreolus capreolus	Aurignac	Birth	Individual & Population	1-May	Computed using individual birth dates
	Bavarian Forest National Park	None	Population	1-May	Guesstimate provided by data owner
	Koberg estate	None	Population	15-May	Guesstimate provided by data owner
Cervus elaphus	Bavarian Forest National Park	None	Population	1-June	Guesstimate provided by data owner
	La Petite Pierre National Hunting and Wildlife Reserve	None	Population	11-May	Loe et al. 2005[12]
	Multiple Norwegian counties	Birth	Individual & Population	1-June	Computed using individual birth dates

Species	Population	Reproduction information	Type of cut-off date	5% cut-off date	References
Cervus elaphus canadensis	Canadian Rockies	Pregnancy at capture	Population	20-May	Berg 2019
	Little Mountain	Birth	Individual & Population	1-June	Computed using individual birth dates
	Ya Ha Tinda Ranch	Birth	Individual & Population	22-May	Berg 2019
Connochaetes taurinus	Kenya – 3 National Parks	None	Population	1-February	Hopcraft 2010[14]
	Liuwa Plain National Park	RS	Population	10-October	Guesstimate provided by data owner
Dama dama	Koberg estate	Birth	Individual & Population	1-July	Computed using individual birth dates
Equus hemionus	Mongolian Gobi	None	Population	1-July	Guesstimate provided by data owner
Equus quagga	Hwange National Park	Birth	Population	1-October	Grange et al. 2015[15]
Giraffa camelopardalis angolensis	Namib desert	None	Population	1-March	Guesstimate provided by data owner
Hippotragus niger	Kruger National Park	None	Population	1-February	Guesstimate provided by data owner
Odocoileus hemionus	Haida Gwaii	None	Population	1-June	Guesstimate provided by data owner
	Little Mountain	Birth	Individual & Population	1-June	Computed using individual birth dates
	Red Desert	None	Population	1-June	Guesstimate provided by data owner
	Southwest Colorado	None	Population	1-June	Pojar and Bowden 2004[16]
	Western Washington	Birth	Individual & Population	20-May	Computed using individual birth dates
	Wyoming Range	Birth	Individual & Population	1-June	Computed using individual birth dates
Odocoileus virginianus	Pennsylvania	None	Population	15-May	Diefenbach et al. 2019[17]
Oreamnos americanus	Alaska - Klukwan	Birth	Population	13-May	Guesstimate provided by data owner
	Alaska – Lynn Canal	Birth	Population	13-May	Guesstimate provided by data owner
	Washington	None	Population	18-May	Côté and Festa-Bianchet 2001[18]
Ovibos moschatus	Zackenberg	None	Population	15-April	Thing et al. 1987[19]

Species	Population	Reproduction information	Type of cut-off date	5% cut-off date	References
Ovibos moschatus	Quebec	Pregnancy at capture	Population	1-May	Guesstimate provided by data owner
Ovis canadensis	Grand Teton	None	Population	1-May	Guesstimate provided by data owner
Ovis gmelini musimon	Bauges hunting reserve	None	Population	1-April	Bon et al. 1993, Bourgoin et al. 2018
	Caroux reserve	None	Population	1-April	Bourgoin et al. 2018[21]
Procapra gutturosa	Mongolian Steppe	None	Population	1-July	Olson et al. 2005[22]
Rangifer tarandus caribou	Côte du Nord	Pregnancy at capture	Population	20-May	Pinard et al. 2012[23]
	Gaspésie	Birth	Individual & Population	20-May	Computed using individual birth dates
	Saskatchewan Boreal Shield	Birth	Individual & Population	1-May	Computed using individual birth dates
Rangifer tarandus platyrhynchus	Svalbard	Birth	Individual & Population	1-June	Computed using individual birth dates
Rupicapra rupicapra	Bauges hunting reserve	None	Population	15-May	Loison 1995[24]
	Swiss National Park	Birth	Population	15-May	Guesstimate provided by data owner
Saiga tatarica	Mongolian Steppe	Birth	Population	13-June	Buuveibaatar et al. 2013[25]

Appendix G Length of hider phase in large herbivores

Table G3: Duration of the hiding phase period of newborns in large herbivores retrieved from the literature. BM stands for body mass in kilograms, GL for gestation length in days, and D for the duration of the hiding phase of newborns in weeks. Note that we could find an estimate of the hiding phase duration for 52% (13/25) of the species we studied in this paper.

Species	BM (kg)	GL (d)	D (w)	Polytocous	Reference
Aepyceros melampus	44	196	1	m	Mooring & Rubin (1991)
Alces alces	365	240	3	p	Altman(1958)
Antilocapra americana	47	250	3	p	Byers (1997)
Bison bison	275	278	—	m	—
Capreolus capreolus	26	144	8	p	Linnell et al. (1998)
Capra ibex	49	167	—	m	—
Cervus elaphus	239	255	2.5	m	Altman (1963)
Cervus elaphus	125	235	3	m	Clutton-Brock & Guinness (1975)
Connochaetes taurinus	185	250	—	m	—
Dama dama	44	236	1	m	San Jose & Braza (1992)
Equus hemionus	230	406	—	m	—
Equus quagga	322	371	—	m	—
Giraffa camelopardalis	700	450	2	m	Pratt & Anderson (1979)
Hippotragus niger	216	270	2.5	m	Thompson (1998)
Odocoileus hemionus	56	205	6	p	Riley & Dood (1984)
Odocoileus virginianus	68	200	8	p	Schwede et al. (1994)
Oreamnos americanus	61	186	—	m	—
Ovis canadensis	58	180	—	m	—
Ovibis moschatus	246	250	—	m	—
Ovis ?	37	150	—	m	—
Rangifer tarandus	132	210	—	m	—
Rangifer tarandus	132	210	—	m	—
Rupicapra rupicapra	32	170	—	m	—
Saiga tatarica	32	140	1	p	Bekenov et al. (1998)
Procapra gutturosa	22	158	1.5	p	Habibi et al. (1993)

Appendix H Extended Acknowledgments

Species	Population	Acknowledgments
Aepyceros melampus	Serengeti National Park	This research was supported by the European Union's Horizon 2020 research and innovation program under grant agreement No. 641918 (AfricanBioServices).
Alces alces	Alberta – British Columbia	Funding provided by Alberta Fish and Wildlife, Canadian Association of Petroleum Producers, University of Montana, Alberta Conservation Asssociation, and World Wildlife Fund.
	Alaska – Berners Bay & Gustavus	This research was funded by the Alaska Department of Fish and Game and the Alaska Department of Transportation and Public Facilities.
	Jackson & Sublette	Wyoming Cooperative Fish and Wildlife Research Unit (WYOCOOP)
	Valdres & Hallingdal – Vega Island	The study was supported by the Research Council of Norway (project SUSTAIN 244647 and SFF-III 223257)
Antilocapra americana	Northern Sagebrush Steppe	The NSS Pronghorn study was funded by the Alberta Antelope Guides, Alberta Conservation Association (ACA), Alberta Fish and Game Association, (Zone 1), Alberta Professional Outfitters Society, Alberta Sport Recreation Parks and Wildlife Foundation, Canadian Forces Base Suffield, Foundation for North American Wild Sheep - Eastern Chapter, MITACS Inc. - Accelerate Program, Montana Chapter of the Wildlife Society with Counter Assualt Inc., Montana Fish, Wildlife & Parks (FWP), National Fish and Wildlife Foundation, Petro-Canada Sustainable Greasslands Applied Research Program, Safari Club International, Safari Club International Alberta Chapter & Northern Alberta Chapter, Sagebrush Science Initiative (a collaboration between U.S. Fish and Wildlife Services and Western Association of Fish and Wildlife Agencies), Saskaatchewan Ministry of Environment, University of Calgary, University of Montana, U.S. Bureau of Land Management (BLM), and World Wildlife Fund (WWF). Additional in-kind support was provided by The Miistakis Institute, The Nature Conservancy, FWP, ACA, BLM and WWF.
	Red Desert	Anadarko Petroleum Corporation, Black Diamond Minerals LLC, British Petroleum North America, Devon Energy, Linn Energy, Memorial Resource Development, Samson Resources, Warren Resources, Incorporated, the Bureau of Land Management-Rawlins Field Office, Wyoming Game and Fish Department, Wyoming Governor's Big Game License Coalition, and the University of Wyoming (Department of Ecosystem Science and Management, Office of Academic Affairs, and Wyoming Reclamation and Restoration Center) funded our research.
	Rock Springs	WYOCOOP

Species	Population	Acknowledgments
Bison bison	Henry Mountains	Utah State University (USU)
	Prince Albert National Park	Laval University (ULAVAL)
Capra ibex	Bargy mountain range	Office Français de la Biodiversité (OFB)
	Swiss National Park	Swiss National Park (SNP)
Capreolus capreolus	Aurignac	We would like to thank the local hunting associations, the Fédération Départementale des Chasseurs de la Haute Garonne, as well as all co-workers and volunteers for their involvement and the field technicians B. Cargnelutti, N. Cebe, J. Merlet, D. Picot and J.L Rames, for their assistance in roe deer captures and tagging.
	Bavarian Forest National Park	The project was funded by the program Ziel ETZ Free State of Bavaria-Czech Republic (2014-2020) Interreg V (project number 184).
	Koberg estate	Swedish University Of Agricultural Sciences
Cervus elaphus	Bavarian Forest National Park	This project was funded by the program Ziel ETZ Free State of Bavaria – Czech Republic 2014–2020 (INTERREG V)" (project number 184).
	La Petite Pierre National Hunting and Wildlife Reserve	This data collection was funded by the Office Français de la Biodiversité. We would like to thank the wildlife technicians (J.-L. Hamann and V. Siat), the foresters, the 67 Départemental Service and the many volunteers for their help in the capture of deer.
	Multiple Norwegian counties	University of Oslo & Norwegian Institute of Bioeconomy Research
Cervus elaphus canadensis	Canadian Rockies	This research was supported by the Natural Sciences and Engineering Research Council of Canada (NSERC) and the Alberta Conservation Association.
	Little Mountain	Funding for this project was provided by Wyoming Game and Fish Department, Bureau of Land Management, Muley Fanatic Foundation Headquarters and the Southwest, Upper Green, Casper, and Flaming Gorge chapters of Muley Fanatic Foundation, Safari Club International Foundation, Rocky Mountain Elk Foundation, Wyoming Wildlife and Natural Resource Trust, Wyoming Animal Damage Management Board, Bowhunters of Wyoming, Wyoming Governor's Big Game License Coalition. KSH was funded by National Science Foundation Graduate Research Fellowship.
	Ya Ha Tinda Ranch	Funding was provided by NSF LTREB Grant 1556248, Parks Canada, Alberta Conservation Association, Natural Sciences and Engineering Research Council, Rocky Mountain Elk Foundation, Safar Club International Foundation, Alberta Environment and Parks, University of Alberta, University of Montana.

Species	Population	Acknowledgments
Connochaetes taurinus	Kenya – 3 National Parks	This research was supported by the National Scoience Foundation (DEB Grant 0919383).
	Liuwa Plain National Park	Zambian Carnivore Programme
Dama dama	Koberg estate	The Swedish Environmental Protection Agency and The Marie-Claire Cronstedt foundation
Equus hemionus	Mongolian Gobi	Movement data on khulan was collected within the framework of the Oyu Tolgoi LLC Core Biodiversity Monitoring Program, implemented by the Wildlife Conservation Society through a cooperative agreement with Sustainability East Asia LLC. During manuscript preparation, Petra Kaczensky was funded by the Research Council of Norway (grant 251112).
Equus quagga	Hwange National Park	We thank the Director General of the Zimbabwe Parks and Wildlife Management Authority for providing the opportunity to carry out this research in Hwange National Park. This research was partly funded by the grants ANR-08-BLAN-0022, ANR-11-CEPS-003, ANR-16-CE02-0001-01. The support from the CNRS LTSER Zone Atelier program is also acknowledged.
Giraffa camelopardalis angolensis	Namib desert	Giraffe Conservation Foundation
Hippotragus niger	Kruger National Park	University of Witwatersrand
Odocoileus hemionus	Haida Gwaii	Funding was provided by grant BAMBI-2010-BLAN-1718-0 of the French 'Agence Nationale de la Recherche', by Forest Renewal BC, South Moresby Forest Replacement Account, International Research Group (GRDI) Dynamics of Biodiversity and Life-History Traits, the French Ministry of Foreign Affairs, and the French Ecological Society (SFE). Logistic support was provided by the Haida Gwaii Watchmen, the Gwaii Haanas National Park Reserve, National Marine Conservation Area Reserve, and Haida Heritage Site, the Research Group on Introduced Species and the Laskeek Bay Conservation Society.
	Little Mountain	Funding for this project was provided by Wyoming Game and Fish Department, Bureau of Land Management, Muley Fanatic Foundation Headquarters and the Southwest, Upper Green, Casper, and Flaming Gorge chapters of Muley Fanatic Foundation, Safari Club International Foundation, Rocky Mountain Elk Foundation, Wyoming Wildlife and Natural Resource Trust, Wyoming Animal Damage Management Board, Bowhunters of Wyoming, Wyoming Governor's Big Game License Coalition. KSH was funded by National Science Foundation Graduate Research Fellowship.

Species	Population	Acknowledgments
Odocoileus hemionus	Red Desert	
	Southwest Colorado	The USDA National Wildlife Research Center, Colorado Habitat Partnership Program, Montelores Habitat Partnership Program, Rocky Mountain Elk Foundation, and the Colorado Auction/Raffle Grant program provided funding for this project. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.
	Western Washington	Support for this work was from U.S. Fish and Wildlife Service under the State Wildlife Grants Program and Federal Aid in Wildlife Restoration.
	Wyoming Range	The Wyoming Range Mule Deer project is supported by Wyoming Game and Fish Department, Wyoming Game and Fish Commission, Bureau of Land Management, Muley Fanatic Foundation (including Southwest, Kemmerer, Upper Green, and Blue Ridge Chapters), Boone and Crockett Club, Wyoming Wildlife and Natural Resources Trust, Knobloch Family Foundation, Wyoming Animal Damage Management Board, Wyoming Governor's Big Game License Coalition, Bowhunters of Wyoming, Wyoming Outfitters and Guides Association, Pope and Young Club, U.S. Forest Service, and U.S. Fish and Wildlife Service.
Odocoileus virginianus	Pennsylvania	Work was approved by an Institutional Animal Care and Use Committee (IACUC) at The Pennsylvania State University under protocol numbers PROTO201800639 and 47054. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.
Oreamnos americanus	Alaska – Klukwan & Lynn Canal	Research was supported by the Alaska Department of Fish and Game, Alaska Department of Transportation and Public Facilities, Bureau of Land Management and Coeur Alaska.
	Washington	Support for this work was from U.S. Fish and Wildlife Service under the State Wildlife Grants Program and Federal Aid in Wildlife Restoration, the Wildlife Research Program of Seattle City Light, the Sauk-Suiattle Tribe, and the United States Forest Service Challenge Cost Share program.
Ovibos moschatus	Zackenberg	Research was supported by 15. Juni Foundation, Copenhagen Zoo, the Danish Environmental Protection Agency and the Aarhus University Research Fund

Species	Population	Acknowledgments
Ovibos moschatus	Quebec	Our research is supported by the Québec Ministère des forêts, de la faune et des parcs and Caribou Ungava partners (in alphabetical order) : Air Inuit, ArcticNet, Azimut Exploration, Centre d'Études Nordiques, Grand Council of Crees, Exploration Osisko, Canada Foundation for Innovation, GlenCore-Mine Raglan, Hydro-Québec, Makivik Corporation, TataSteel Minerals Canada Limited. Caribou Ungava was supported by the Natural Sciences and Engineering Research Council of Canada (NSERC RDCPJ 46512-14). We thank V. Brodeur, C. Jutras, B. Lamglait, S. Lair, M. Leblond and A. Brodeur for assistance with the muskox project. We thank all the professionals and wildlife technicians of the Ministère des forêts, de la faune et des parcs of Québec government from the for assistance with the muskox project, fieldwork and data collection. In particular, C. Jutras and V. Brodeur. We thank the Centre québécois sur la santé des animaux sauvages for help and support, in particular B. Lamglait and S. Lair.
Ovis canadensis	Grand Teton	WYOCOOP
Ovis gmelini musimon	Bauges hunting reserve & Caroux reserve	We thank all the professionals and trainees from the Office Français de la Biodiversité who performed the monitoring of this population.
Procapra gutturosa	Mongolian Steppe	We are grateful to field assistants as well as World Wide Fund for Nature, Mongolia (WWF) for gazelle capture permissions. All animals were captured following standard protocols approved by the Ministry of Environment and Green Development in Mongolia (licenses: 6/5621, 5/4275). The project was funded by Robert Bosch Foundation.
Rangifer tarandus caribou	Côte du Nord	This research was supported by the Sentinel North program of Université Laval, made possible, in part, thanks to funding from the Canada First Research Excellence Fund, together with the Fonds de Recherche du Québec—Nature et Technologies, the Ministère des Forêts, de la Faune et des Parcs (MFFP), and the Université Laval Industrial Research Chair in Boreal Forest Silviculture.

Species	Population	Acknowledgments
Rangifer tarandus caribou	Gaspésie	Thanks to B. Baillargeon, D. Grenier, J. Mainguy, and G. Tremblay for the capture and collaring of Atlantic-Gaspésie caribou. This work was supported by the Fonds de Recherche du Québec – Nature et Technologies (FRQNT), the Ministère des Forêts, de la Faune et des Parcs, the Canada Foundation for Innovation (John R. Evans Leaders Fund Grant # 26442 to M.-H. St-Laurent), the Natural Sciences and Engineering Research Council of Canada (NSERC Discovery Grant #386661-2010 to M.-H. St-Laurent), the Société des Établissements de Plein Air du Québec, the Fondation de la Faune du Québec and the Université du Québec à Rimouski (Fonds Institutionnel de Recherche).
	Saskatchewan Boreal Shield	Funded by a Collaborative Research and Development Grant from the Natural Sciences and Engineering Research Council (NSERC) Canada (CRDPJ 449509), with additionasupertabular l financial and in-kind support from Cameco Corporation, Environment and Climate Change Canada, the Government of Saskatchewan, the Saskatchewan Mining Association, SaskPower Inc., Golder Associates Ltd., Claude Resources Inc., Rio Tinto Group, Orano Resources Canada Inc., Golden Band Resources Inc., Masuparia Gold Corporation, Western Economic Diversification Canada, Omnia Ecological Services, and the University of Saskatchewan.
Rangifer tarandus platyrhynchus	Svalbard	COAT - Climate-ecological Observatory for Arctic Tundra; SIOS - Svalbard Integrated Arctic Earth Observing System
Rupicapra rupicapra	Bauges hunting reserve	We also thank all the professionals and trainees from the Office Français de la Biodiversité who performed the monitoring of this population.
	Swiss National Park	We thank the rangers of the Swiss National Park for marking and observing the individuals.
Saiga tatarica	Mongolian Steppe	The capture and collaring efforts of Mongolian saiga were funded by World Wide Fund for Nature (WWF)'s Mongolia Program Office and Wildlife Conservation Society (WCS)'s Mongolia Program. The animal captures were approved by the Ministry of Environment and Tourism of Mongolia.