Phenology of births in ungulates: insights on its measure and its ecological determinants

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Abstract

The phenology of births corresponds to the study of the position and duration of the period of births, related to its drivers and consequences on individuals and populations. Mainly regulated by environmental, biotic and internal factors through evolutionary processes and phenotypic adjustments, the date of birth has short- and long-term implications on individual survival and reproductive success. The phenology of births also affects population dynamics. Although the study of the phenology of births is an old discipline, it still arouses strong interest nowadays because of its sensitivity to climate change. The methods employed to study phenology are constantly progressing, but numerous interrogations remain regarding the diversity of phenology of births encountered *in natura* and the modifications to which they are exposed. The aim of this thesis is to study the phenology of births, from the validation of sampling methods to the identification of the ecological and evolutionary processes associated, with large herbivores as a case study.

In the first chapter, I studied the ability of non-specialist volunteers to identify the presence or absence of young individuals in pictures produced by a camera trap grid located in Serengeti National Park, Tanzania. Some limitations still need to be accounted for before using such dataset to reconstruct phenology of births. In the second chapter, I explored and compared the different methods used to describe the phenology of births in large herbivores using simulated data. I reassessed the framework for studying phenology in terms of concepts and mathematical description, discussed the diversity of metrics, and proposed guidelines to help identify the most suitable method. In the third chapter, I explored the consequences of the timing of birth on the juveniles, yearlings and mares survival in plain zebras living in Hwange National Park, Zimbabwe. Survival decreased with an increasing proportion of time spent in dry season. Thus, climate change could have a detrimental effect on the population dynamics because of their phenology of births.

Using direct observation data can be associated with several methodological limitations, but it is possible to account for them. Allometric relationships can also reduce the comparability of the studies between small and large organisms, and it could be interesting to account for this factor. Eventually, the study of the phenology of births is of major interest to understand the risks to which wild populations are exposed because of climate change. Involving the general public through citizen science is a great tool to raise awareness about such issues.

Key words: camera trapping, capture-mark-recapture, citizen science, large herbivores, metrics, phenology, reproduction, survival, tropical ecosystem

Résumé

La phénologie des naissances est l'étude du positionnement et de la durée des périodes de naissance en lien avec ses facteurs directeurs et les conséquences qu'elle peut avoir sur les individus et les populations. Principalement régulée par des facteurs environnementaux, biotiques et internes à travers des processus évolutifs et des ajustements phénotypiques, la date de naissance a des répercussions à court et long terme sur la survie et le succès reproducteur des individus et sur la dynamique des populations. Discipline à l'origine ancienne, l'étude de la phénologie suscite à l'heure actuelle un vif intérêt en raison de sa sensibilité aux changements climatiques. Les méthodes employées pour l'étudier sont nombreuses et en constante évolution, mais des interrogations subsistent quant à la diversité des phénologies observables dans la nature et aux modifications auxquelles elles sont exposées. L'objectif de cette thèse est d'étudier la phénologie des naissances, depuis la validation des méthodes de collecte des données jusqu'à la mise en évidence des processus écologiques et évolutifs associés, avec pour objet d'étude les grands mammifères herbivores.

Dans le premier chapitre, j'ai étudié la capacité des volontaires non-spécialistes à identifier la présence ou absence de jeunes individus sur des photographies produites par piégeage photographique dans le Parc National du Serengeti, en Tanzanie. Certaines limitations doivent encore être prises en compte afin d'utiliser ce type de données pour reconstruire une phénologie des naissances. Dans le deuxième chapitre, j'ai exploré et comparé les différentes méthodes utilisées pour décrire la phénologie des naissances chez les grands herbivores sur la base de simulations. J'ai ainsi réexaminé le cadre d'étude de la phénologie en termes de concepts et descripteurs mathématiques, discuté la diversité des métriques, et proposé des guides pour aider au choix de la méthode la plus adaptée. Dans le troisième chapitre, j'ai exploré l'effet de la date de naissance sur la survie des poulains, des jeunes d'un à deux ans et des juments chez les zèbres du Parc National de Hwange, au Zimbabwe. Leur survie diminuant à mesure que le temps passé en saison sèche augmente, les changements climatiques pourraient avoir des conséquences néfastes sur la dynamique de la population en lien avec leur phénologie des naissances.

L'utilisation de données d'observation directe va de pair avec certaines limitations méthodologiques, qui peuvent néanmoins être corrigées ou prise en compte. Les relations allométriques peuvent réduire la comparabilité des études entre petits et grands organismes, et il pourrait être intéressant de prendre compte de ce facteur. Enfin, l'étude de la phénologie des naissances revêt un intérêt majeur dans la compréhension des risques encourus par les populations sauvages face aux changements climatiques, et l'inclusion du grand public à travers les sciences participatives permet une sensibilisation vis-à-vis de ces enjeux.

Mots clés : capture-marquage-recapture, écosystèmes tropicaux, grands herbivores, métriques, phénologie, piégeage photographique, reproduction, sciences participatives, survie

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Résumé substantiel en Français

Introduction générale

Les premières mentions à l'étude des cycles de la nature, que ce soit en lien avec l'agriculture ou des rites religieux, remontent à plusieurs siècles avant notre ère. Ce n'est qu'à partir du 18ème siècle que des auteurs tels que Charles Morren formalisent le concept de « phénologie », l'étude de la récurrence des évènements biologiques périodiques, de leurs causes et de leurs conséquences sur le cycle de vie des organismes. A travers le recensement de plus en plus normalisé et fréquent d'évènements tels que les dates de floraison ou encore l'arrivée et le départ des oiseaux migrateurs, la phénologie devient progressivement une discipline scientifique à part entière, dont les facteurs directeurs s'étudient par l'observation *in natura* mais aussi en conditions contrôlées en laboratoire. Avec la mise en évidence des effets des changements globaux sur la biodiversité, l'étude de la phénologie devient au 20ème siècle un enjeu de recherche majeur. Les concepts et méthodes d'analyse associés se multiplient rapidement, source de confusion et de brouillage des messages généraux à tirer des études empiriques.

La phénologie de la reproduction, au cœur du cycle de vie des organismes, revêt un aspect majeur car c'est par ce biais que ceux-ci transmettent leur patrimoine génétique. Les organismes ont évolué selon différentes stratégies d'allocation des ressources énergétiques à la reproduction et à l'élevage des jeunes (stratèges r et K) selon leur environnement et diverses sources de compromis. Chez les mammifères placentaires, le cycle de reproduction s'étend de l'initiation de la préparation des organes reproducteurs à la production d'un ou plusieurs individus autonomes, en passant par de nombreux stades intermédiaires tels que la fécondation, la gestation et la mise bas. Ces processus sont régulés par des mécanismes hormonaux fins qui permettent l'interaction entre des facteurs externes et internes et les organes reproducteurs. Dans la plupart des cas, le cycle de reproduction est régulé par la date de mise bas (ou de naissance), l'évènement charnière du cycle qui concentre les coûts énergétiques les plus forts chez la mère. Des processus évolutifs lents et des ajustements phénotypiques à l'échelle de la vie des organismes, plus ou moins facile à mettre en évidence empiriquement, permettent une régulation précise du cycle de cette date cruciale. Le manque de données et de méthodes de mesure efficaces limite en effet la compréhension de ces mécanismes, particulièrement des processus évolutifs observables seulement sur le long terme et à travers des comparaisons multi-spécifiques rares.

Il est néanmoins évident que le positionnement des naissances dans l'année est en premier lieux régulé par la disponibilité de la ressource alimentaire et par les conditions extérieures rencontrées à la naissance par les jeunes. Chaque espèce répond à ces facteurs environnementaux de façon directe dans les environnements imprévisibles, ou indirecte au moyen de prédicteurs tels que les changements de photopériode dans les environnements saisonniers. Des facteurs biotiques tels que les interactions inter-spécifiques (*e.g.,* la prédation) régulent l'étalement des naissances en favorisant des comportements qui limitent le risque de prédation. Les interactions intra-spécifiques (*e.g.,* harcèlement par les mâles) agissent eux aussi sur l'étalement des naissances au niveau de la population. Enfin, des facteurs individuels viennent dans un second temps réguler la phénologie des naissances de façon plus fine. Cependant, les hypothèses théoriques ne rencontrent pas toujours de support empirique, ou n'ont pas encore été testées de façon robuste faute de moyens et de méthodes adaptés.

La date de naissance a des répercussions à court et long terme sur la valeur sélective et la survie des jeunes, mais aussi sur la mère. Le taux de croissance, la masse corporelle à l'âge adulte ou encore le rang social des individus sont étroitement liés à sa période de naissance, qui est susceptible de varier selon des compromis entre les intérêts de la mère et ceux du jeune. De façon plus générale, la dynamique de la population étant affectée par la survie et le taux de recrutement de jeunes, elle est donc dépendante de la phénologie des naissances. Les cohortes de mauvaise qualité produisant moins de jeunes, eux aussi de moindre qualité, ont des répercussions sur le taux de croissance et la taille de la population. Une phénologie des naissances inadaptée à la taille de la population peut même théoriquement conduire à son extinction dans des cas extrêmes. Avec les changements globaux, de plus en plus d'espèces voient se creuser l'écart entre la période favorable de naissance et la période de naissance effective, ce qui a des conséquences négatives sur la démographie des populations qui se propagent d'un niveau trophique à l'autre. Ces transferts et leurs conséquences, particulièrement chez les espèces dont le temps de génération est long, sont encore sous-explorés et méconnus.

Dans ce contexte, les objectifs de cette thèse sont d'étudier la phénologie des naissances, depuis la validation des méthodes de collecte des données jusqu'à la mise en évidence des processus écologiques et évolutifs associés. Les grands herbivores, regroupant ici les artiodactyles (incluant les suidés), les périssodactyles et les proboscidiens, forment un groupe d'étude adapté car ils regroupent de nombreux traits d'histoire de vie des mammifères et vivent dans des habitats très variés couvrant presque toutes les latitudes et continents.

L'étude de la phénologie des naissances nécessite des données à long terme disponibles pour une portion aussi large que possible de la population. Pour répondre à ces attentes, de nombreuses méthodes se développent, mais il est nécessaire de tester leur validité avant de les généraliser. Dans le premier chapitre, je vérifie l'efficacité du piégeage photographique couplé aux sciences participatives pour établir des phénologies des naissances chez trois espèces de grands herbivores Africains. Une fois que les données sont récoltées, il est nécessaire de les synthétiser en utilisant des concepts et descripteurs mathématiques adaptés. Dans le contexte de la phénologie des naissances chez les grands herbivores, de nombreux termes et métriques sont employés et rendent la comparaison et la compréhension des mécanismes généraux complexes. Dans le deuxième chapitre, j'explore la diversité des métriques utilisées pour décrire la phénologie des naissances chez les grands herbivores afin de les comparer et de proposer des lignes directrices pour favoriser la comparaison entre les études. Une fois que les questions méthodologiques sont résolues, il est possible de documenter les causes et conséquences de la phénologie des naissances sur les organismes. La phénologie des naissances de nombreuses espèces tropicales est encore sous-étudiée, alors que les changements globaux menacent ces écosystèmes par des bouleversements majeurs. Dans le troisième chapitre, j'utilise un suivi à long terme d'une population de zèbres pour évaluer les effets de la phénologie des naissances sur la survie des jeunes et des juments à travers l'effet des conditions environnementales rencontrées à la naissance.

Les sciences participatives couplées au piégeage photographique permettent-elles d'étudier la reproduction ? Les leçons à tirer du programme Snapshot Serengeti

A l'heure actuelle, les écologues ont de plus en plus fréquemment recours au piégeage photographique pour estimer de nombreux paramètres écologiques tels que l'occupation et l'abondance des espèces sur un site donné, ou encore leurs patrons d'activité. Du fait de la grande quantité de données collectées par de tels procédés, des volontaires non-spécialistes sont souvent invités à participer au processus de traitement des données par le moyen des sciences participatives. Cependant, la vérification de la qualité des données produites et un prérequis majeur à leur utilisation. Dans le premier chapitre de cette thèse, l'objectif est d'évaluer si les données obtenues à partir d'un programme de piégeage photographique faisant intervenir les sciences participatives pour la phase d'analyse du contenu des photographies, le programme Snapshot Serengeti, peuvent servir à étudier la phénologie de la reproduction chez les grands

herbivores. Nous évaluons en particulier si la présence de juvénile (moins d'un mois ou moins de 12 mois) appartenant à trois espèces de grands herbivores vivant dans le Parc National du Serengeti en Tanzanie (le topi *Damaliscus jimela*, le kongoni *Alcelaphus cokii*, et la gazelle de Grant *Nanger granti*) peut être détectées de façon fiable par les volontaires. Une corrélation positive entre la proportion de volontaires identifiant des juvéniles et la présence effective de ces individus sur les photographies, évaluée par trois observateurs entraînés à détecter leur présence, est attendue. L'accord entre les observateurs entraînés sur l'identification des classes d'âge et des espèces est tout d'abord vérifié, mettant en évidence un bon accord entre eux (κ de Fleiss > 0.61 pour les juvéniles de moins d'un mois et de moins de 12 mois). Ceci suggère que des critères morphologiques peuvent être utilisés avec succès pour déterminer l'âge des individus sur les photographies. De plus, la probabilité d'observer des juvéniles de moins d'un mois quand leur présence est avérée plafonne à 0.45 pour les gazelles de Grant, mais peut atteindre 0.56 pour les kongonis et même 0.70 pour les topis. Les mêmes relations sont d'autant plus fortes pour les juvéniles de moins de 12 mois, au point que leur présence est parfaitement détectée par les volontaires en ce qui concerne les topis et les kongonis. Ainsi, la classification des photographies issues du piégeage photographique par des volontaires non-spécialistes permet un tri modérément précis mais rapide, mettant en évidence de façon efficace la présence et l'absence de juvéniles. Cependant, obtenir des données plus précises à partir de cette méthode semble difficile. Les limitations relatives à l'utilisation des sciences participatives couplées au piégeage photographique pour étudier la phénologie de la reproduction, ainsi que les options envisageables pour aider à la détection des juvéniles sont discutées. L'addition de critères d'âge sur les plateformes en ligne de sciences participatives ou encore l'utilisation des intelligences artificielles en support des volontaires pourraient notamment être des pistes d'amélioration.

Comment décrire et mesurer la phénologie ? Une investigation de la diversité des métriques avec la phénologie des naissances chez les grands herbivores comme cadre d'analyse

Charles Morren a proposé en 1849 le terme « phénologie » pour décrire les phénomènes périodiques régulés par la succession des saisons. Le terme s'est par la suite répandu dans de nombreux domaines scientifiques, allant de la biologie de l'évolution à la biologie moléculaire. L'adoption du concept de phénologie dans une telle diversité de champs disciplinaires a participé au développement d'une grande diversité de métriques mathématiques et a une certaine confusion autour des notions associées. Dans le deuxième chapitre de cette thèse, nous

étudions la diversité des mesures associées à la phénologie des naissances chez les grands herbivores. Nous identifions 52 métriques utilisées jusqu'à présent pour quantifier la phénologie. Une analyse quantitative est conduite sur la base de simulations, ainsi qu'une comparaison et une classification des métriques, en utilisant une matrice de corrélations. La capacité de chaque métrique à capturer la variation d'une des caractéristiques de la phénologie est évaluée grâce à des analyses de sensibilité. Finalement un score est attribué à chaque métrique selon huit critères qui semblent important pour décrire la phénologie de façon complète et adaptée. Quatre caractéristiques de la phénologie semblent importantes et peuvent être clairement définies : le positionnement des naissances dans le temps (ou « timing »), la synchronie (*i.e.,* le degré d'étalement des naissances), la rythmicité et la régularité (*i.e.,* la répétabilité du timing et de la synchronie respectivement). Une corrélation élevée existe entre les métriques décrivant la même caractéristique de la phénologie, ce qui suggère qu'une telle diversité de métriques n'est pas nécessaire. De plus, les meilleures métriques ne sont pas nécessairement les plus communément employées, et les métriques les plus simples sont souvent les meilleures. En effet, les métriques faciles à implémenter obtiennent généralement les meilleurs scores. Les statistiques circulaires semblent particulièrement adaptées pour décrire le timing et la synchronie des naissances dans le contexte d'une analyse comparative qui regrouperait des distributions de forme variée. Le degré de répétabilité de ces deux descripteurs est encore peu étudié, mais des tests non-paramétriques tels que le test de Mood ou le test de Kolmogorov-Smirnov permettent une première quantification de cette variabilité au cours des années. Finalement, des guides et conseils sont proposés afin de favoriser la répétabilité des études et la comparaison des patrons de phénologie entre celles-ci. Certains pièges à éviter lors du choix des métriques sont mis en lumière. Ainsi, l'objectif de cette étude est de faciliter l'utilisation de concepts clairs et de métriques robustes pour étudier la phénologie, en particulier dans le contexte des changements globaux.

La date de naissance affecte-t-elle la survie du jeune et de la mère chez le zèbre des plaines ?

Chez les grands herbivores, la localisation des naissances dans le temps est principalement régulée par la disponibilité saisonnière de leurs ressources alimentaires. La dynamique des populations est fortement influencée par la survie et le recrutement des jeunes, qui dépend fortement de la date de naissance, celle-ci déterminant si les individus naissent pendant une période favorable ou non. Si les naissances ont lieu pendant la période la plus

favorable dans l'hémisphère nord, caractérisé par des environnements très saisonniers et prévisibles, comme c'est le cas pour la majorité des grands herbivores vivant sous ces latitudes, le zèbre quant à lui donne naissance toute l'année au Parc National de Hwange, au Zimbabwe. Il s'agit d'une savane tropicale caractérisée par la succession d'une saison humide favorable et d'une saison sèche moins favorable. Nous utilisons des modèles de capture-marquage-recapture sur des données de suivi individuel à long terme de cette population et collectées entre 2008 et 2019, pour évaluer l'effet de la date de naissance sur la survie de plusieurs classes d'âge d'individus. Nous explorons ainsi l'effet de la saison (comme variable catégorielle) et de la proportion de temps passé en saison sèche sur la survie de trois catégories de juvéniles (les jeunes poulains de moins de six mois, les poulains plus vieux de six à 12 mois, et les jeunes d'un à deux ans) et des juments, en les distinguant selon leur statut reproducteur (*i.e.,* accompagnée ou non d'un poulain dépendant, soit de moins de six mois). La saison n'a pas d'effet sur les survies annuelles estimées. La survie annuelle des poulains les plus jeunes n'est également pas affectées par la proportion de temps passé en saison sèche. En revanche, la survie annuelle des poulains les plus âgés et des jeunes entre un et deux ans diminue à mesure que l'exposition à la saison sèche augmente chez ces individus. La survie annuelle des juments diminue elle aussi avec un temps croissant passé en saison sèche, quel que soit le statut reproducteur, mais dans une plus large mesure quand les juments sont non-reproductrices. La date de naissance, en déterminant les conditions extérieures expérimentées par les poulains et leurs mères pendant une phase critique de leur cycle de vie, joue donc un rôle déterminant dans leur survie. Comme il est attendu que les changements climatiques conduisent à des sécheresses plus fréquentes, mais aussi à des saisons sèches plus longues et plus difficile dans les écosystèmes tropicaux, nous formulons l'hypothèse que ces phénomènes auront probablement un effet négatif sur la dynamique de la population de zèbres dans un futur plus ou moins proche.

Discussion générale

Les observations directes sur des populations sauvages permettent d'étudier la phénologie des naissances dans toute sa complexité. Cependant la date de naissance est souvent imprécise, conduisant à des phénologies elles-mêmes imprécises. Le piégeage photographique permet un suivi continu mais il est nécessaire de prendre en compte les caractéristiques biologiques des espèces dans les protocoles de suivi et d'analyse. Des études en conditions contrôlées peuvent permettre de comprendre l'effet d'un facteur ciblé sur la phénologie en s'affranchissant des autres. Enfin, l'étude de populations suivies sur le long terme, dont les

caractéristiques démographiques et de l'environnement sont bien connues telle que pour la population de chevreuils du Territoire d'Étude et d'Expérimentation de Trois Fontaines (France), peuvent permettre de relier facteurs environnementaux et phénologie des naissances de façon précise.

D'autre part, les relations allométriques qui relient les caractéristiques des individus à leur masse corporelle par des relations de proportionnalité interviennent aussi dans notre capacité de suivi et dans la détermination de la phénologie des naissances selon la taille des organismes d'intérêt. Les méthodes de suivi des petites et grandes espèces peuvent être similaires mais un suivi simultané n'est pas possible. De plus, la prise en compte de ces facteurs de proportionnalité dans la mesure du niveau de synchronie des naissances n'a jusqu'alors pas été considérée dans les analyses comparatives. De façon générale, des comparaisons multi-spécifiques de la réponse des phénologies des naissances à différents types de facteurs directeurs peuvent permettre de mettre en évidence les grands processus évolutifs qui restent encore à élucider au sein des mammifères et de tirer des conclusions générales pour ceux qui sont déjà bien connus.

Si l'on veut pouvoir étudier l'effet des changements globaux sur la phénologie des naissances, il est nécessaire d'obtenir des jeux de données à long terme, encore rares pour les écosystèmes de l'hémisphère sud, et des données historiques qui peuvent servir de base de comparaison avec la période actuelle. A l'heure des changements globaux, l'étude de la phénologie des naissances peut renseigner sur la capacité d'une population à s'ajuster à un environnement changeant, et à orienter les politiques de conservations vers les espèces les plus fragiles. Les sciences participatives, en plus d'aider à la collecte de données de phénologie, sont un vecteur majeur de sensibilisation du grand public aux questions environnementales.

Dans cette thèse, j'ai testé la validité d'une nouvelle méthode de collecte de données de phénologie, l'utilisation du piégeage photographique associé aux sciences participatives, qui nécessite encore d'être perfectionnée mais reste une voie prometteuse pour l'avenir. J'ai aussi réalisé un état de l'art en termes de mesure de la phénologie des naissances sur la base duquel j'ai pu proposer des lignes directrices pour les analyses futures. J'ai enfin complété les connaissances sur la phénologie des naissances des espèces tropicales, en mettant en évidence la relation entre date de naissance, environnement et survie chez le zèbre. De futurs axes de recherche pourraient concerner des populations suivies individuellement sur le long terme ainsi que des comparaisons multi-spécifiques, afin de mieux comprendre la phénologie des naissances chez les mammifères, ses déterminants, ses conséquences, et les évolutions que l'on peut attendre en réponse aux changements globaux.

Foreword

The initial aim of this thesis was to explore the ecological and evolutionary causes and consequences of the phenology of births in the context of a multi-specific and multi-site assemblage of large herbivores living in southern Africa, using camera trapping and citizen science as the principal method of data collection. However, it appeared that camera trapping together with the identification of the presence of newborn individuals in the pictures by non-specialist volunteers did not meet the prerequisites to conduct such study yet. This led to the necessity to find another source of data to pursue the ecological and evolutionary analyses, and to publish a first article explaining the limitations associated with those methods in the context of the phenology of births. In parallel to this methodological limitation, I faced the large diversity of metrics used so far to describe and study the phenology of births in the literature on large herbivores (but also in other groups). This raised the question of "which one to choose *a priori*?". Thus, it appeared appropriate to produce a second article to provide a state of the art and a comparison, associated with guidelines to choose the most relevant metric. After those methodological considerations, I moved back to the initial ecological and evolutionary questions and explored the consequences of the timing of births in a selected species of tropical ungulate, the plains zebra, for which a long-term individual-based dataset collected by direct observations in the field was available. Eventually, the objectives of this PhD thesis evolved and led to what this work is today. The thesis is divided into two main axes, one dealing with the two methodological questions (chapters 1 and 2), and the second one dealing with the eco-evolutionary questions (chapter 3). A fourth chapter (at a too early stage to appear in this manuscript) is in preparation to complete the second axis. It will focus on the environmental determinants of the phenology of births in an intensively followed population of individually known roe deer. The objective of a fifth project will be to provide an overview of the determinants of the phenology of births in mammals by reviewing the literature and to provide insights into the well and marginally documented theoretical hypotheses in this field of research.

This thesis was supported by a grant from the French "Ministère de la Recherche" through the "Ecole Doctorale E2M2" at the University "Claude Bernard Lyon 1". This thesis was written in English to facilitate the diffusion of this work within the international scientific community, and to allow all the members of the jury to fully benefit from the content.

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General introduction

Historical approach of the notion of phenology

The first mentions of periodic phenomena and phenology

Since the very first written records, human beings have proven to feel concerned about the natural cycles regulating their environment. Observations of the annual changes in the vegetation and climate are reported since as early as the 11th century B.C.E. in China, primarily for agricultural or a religious purposes related to harvests and religious rites timing (Puppi 2007). Since then, and especially since the 16th century, records of phenology observations have spread out. These observations focused on the description of the succession of different plant phases such as leafing or flowering (Lechowicz 1995), but also of arrival dates of birds related to their migration (Sparks 1999). In the 18th century, naturalists such as Carl Linnaeus started to systemically record observations and formalize relationships between the latter and climatic variables (Puppi 2007).

Adolphe Quetelet was the first to publish, in 1842, sets of instructions to guide the record of what he called "periodical phenomena" in plants and animals (Demarée 2011). After that, the notion of "phenology" appeared in 1849 with Charles Morren as "a particular science having the goal to understand the manifestations of life governed by time" (Morren 1849, Demarée 2009). Since then, phenology has become a major topic of research (Visser *et al.* 2010). Among many others, an updated and generalist definition of the term has been given by the US/IBP Phenology Committee as "the study of the timing of recurring biological events, the causes of their timing with regard to biotic and abiotic forces, and the interrelation among phases of the same or different species" (Puppi 2007).

From Morren to the 20th century, the outburst of the study of phenology as a science

Since Morren, phenology has been the subject of an increasing number of studies. Naturalists recorded a wide variety of periodic phenomena on a yearly basis, ranging from the reproductive cycle of mosses to the annual development of deer antlers, including the winter diapause of spiders and even the annual distribution of births in humans (*e.g.,* McCook 1885, Clarke 1896, Robertson 1924, Huxley 1926, Conard 1946, Cowgill 1966). Concomitantly, the vocabulary associated to the description of phenology, such as "seasonality" or "frequency", has been

progressively defined in the scientific literature, also expanding to irregular and supra-annual patterns (*e.g.,* Newstrom *et al.* 1994, Battey 2000). The same applied to specific terms, such as "breeding season" or "breeding synchrony" in the context of the study of animal reproduction (Ansell 1960, Findlay and Cooke 1982). Purely descriptive in the first place, those studies progressively started to question the relationship between such phenomena and biotic or abiotic factors, leading to a more scientific approach of phenology (Puppi 2007).

Phenology began to be studied not only in the wild in relation to the seasons (*e.g.,* Allsopp 1971), but also in controlled conditions in terms of environmental variables (*e.g.,* temperature in Bentz *et al.* 1991). If the physiologists and geneticists explored the underlying mechanisms responsible for the regulation of phenology in organisms in relation to their environment (Desjardins *et al.* 1986, Sempéré *et al.* 1992), the chronobiologists rather highlighted the persistence of biological rhythms even in the absence of environmental triggers (Gwinner and Dittami 1990). Hence, phenology has emerged as a central concept in biology and ecology, at the junction between various disciplines such as physiology, genetics, chronobiology or evolutionary ecology (Visser *et al.* 2010).

The study of phenology today: the recognition of anthropogenic climate change as a milestone

Even if the first mentions of the impacts of climate change on biodiversity appeared lately in the scientific literature (Parmesan 2006), anthropogenic climate change has been demonstrated to be significant since the mid-19th century (Abram *et al.* 2016). Climate change modifies numerous natural phenomena such as biogeochemical cycles (*e.g.,* Chen *et al.* 2013), geographical and temporal distribution of species (*e.g.,* Lenoir *et al.* 2008), and above all, phenology of living organisms (*e.g.,* Visser and Both 2005). With the modifications induced by climate change, the study of phenology has progressed at all ecological levels: from the individual level through the life cycle of the organisms, to the community level through trophic interactions, including the population level through the synchronization of a given life cycle phase between individuals (Forrest and Miller-Rushing 2010). Hundreds of scientific papers have now documented the consequences of climate change on phenology in terms of phenotypic and evolutionary adaptations and ecological mismatches (Walther *et al.* 2002, Parmesan 2006, Halupka and Halupka 2017).

Such a renewed interest went hand in hand with practical and methodological developments. The use of new technologies, such as remote-sensing, GPS tracking or even

camera trapping, have allowed to monitor more precisely the environment and the individuals spatially and temporally (Pettorelli *et al.* 2005, Hebblewhite and Haydon 2010, Hofmeester *et al.* 2020). In other respects, citizen science has provided perhaps less accurate but large-scale and long-term data (Jiguet *et al.* 2011). However, the implementation of new methods in fields of research such as the study of phenology, especially when the participation of non-specialists is at stake, needs to be tested and validated before being generalized (see **chapter 1**).

The description and quantification of phenology have also improved over time, going from the simple association of a discrete phenomenon to a climatic season, up to the precise characterization of a continuous pattern using generalized additive models, cosinor analysis or spectral decomposition for instance (*e.g.,* Cancho-Candela *et al.* 2007, Winder and Cloern 2010). Between both extremes (*i.e.,* coarse descriptive approach and precise quantification of the complete pattern), a wide range of methods to describe phenology have arisen, depending on the objectives of the studies and the quality of the associated datasets (Moussus *et al.* 2010). Numerous mathematical metrics have been developed to describe the position, the duration, the skewness, the repeatability and other characteristics of a periodical phenomenon, with the ultimate goal to relate it to its explanatory factors (Forrest and Miller-Rushing 2010). Nonetheless, with such a diversity of methods used to quantify phenology and its relationship with explanatory factors, comes a lack of consistency between studies which can scramble the general message when comparing them (Visser and Both 2005, see **chapter 2**).

In essence, phenology is a very ancient subject of questioning, which has evolved a lot since its beginnings and continues to raise new interrogations today in the context of a changing world. If the study of phenology developed a lot in the plant kingdom, it also concerns the animal kingdom, addressing subjects as diverse as migration, diapause or moulting, but above all reproduction. I will now focus on the phenology of reproduction in animals.

The phenology of births, nested inside the life cycle of the organisms

Reproduction within the life cycle, a source of various trade-offs

Reproduction is a central part of the life cycle of animals because it is through this mechanism that they transmit their genetic heritage. But reproduction is also a costly process in terms of energy (Bronson 1985). According to the principle of energy allocation, an individual has a limited amount of energy that it can invest in either growth, maintenance or reproduction throughout its life to maximize its fitness (Williams 1966). Therefore, reproduction is subject

to a crucial energetic trade-off (Stearns 1989). According to its life history traits and its environment, each species (even each population and individual) invests differently in reproduction during its life (Hirshfield and Tinkle 1975). The K strategists, for instance, generally live in a predictable environment and tend to invest less in reproduction, *via* a late sexual maturity and a low fecundity, than the r strategists, which are expected to do the opposite due to the unpredictable environment in which they live (Wilson and MacArthur 1967, Pianka 1970). With their long lifespan, K strategists can attempt several reproductive events. They are iteroparous (whereas r strategists breed only once in their life and are known as semelparous), distributing by this way the costs and benefits of reproduction throughout their life. Age at first and last reproduction, inter-birth interval, litter size are crucial variables in the lifetime reproductive success of such species (Clutton-Brock 1988).

Moreover, K strategists tend to invest a lot in their offspring *via* high parental care, leading to high offspring survival (Wilson and MacArthur 1967, Pianka 1970). They have a low number of offspring at once: they can be either monotocous such as large herbivores, which often have a single offspring at once, or polytocous such as carnivores, which have several young at once. Thus, reproduction is also the source of an inter-generational trade-off between parents and offspring. Parents should equilibrate their energetic investments to maximize their offspring survival and also sustain their own needs to insure maintenance and future reproduction. In the well-known example of the kestrel falcon *Falco tinnunculus*, the survival and future reproductive success of the parents with experimentally increased litter size tends to decrease (Dijkstra *et al.* 1990).

The reproductive cycle per se

The reproductive cycle of placental mammals is divided into several ordered phases (Fig. 1). It is initiated when the reproductive organs start to produce the gametes in females (oogenesis) and males (spermatogenesis) in response to internal and/or external factors (detailed later). Copulation occurs when both sexes are sexually receptive, generally after courtship and mate selection, and allows male's sperm deposition into the female's tract. Then, the fertilization phase consists in the combination of male's sperm and female's eggs, leading to the formation of a zygote. According to the species, the two previous steps (*i.e.,* copulation and fertilization) can be successive in time or delayed, such as in some bats whose females can store sperm during a variable period of time before fertilization (Mori and Uchida 1980). After that, the zygote develops to form an embryo (embryogenesis). This period can also be characterized by an

interruption for a various amount of time at the blastocyst stage, called the embryonic diapause (*e.g.,* in roe deer *Capreolus capreolus*, van der Weijden and Ulbrich 2020). The gestation corresponds to the period of development of the embryo. Its length can vary at the intra-specific level (Kiltie 1982), but the amplitude of variation is often considered to be slight. Gestation ends with parturition, the delivery of the offspring. It is followed by a period of rearing, during which the offspring is fed exclusively or not (*i.e.,* additional solid food intakes) by its mother *via* lactation, which can last a few days in some seals to a few years in some great apes (Hayssen 1993). The mother also provides care to the young during lactation. Such maternal behaviour can end with weaning or persist longer, but not later than the birth of the next offspring. The female is either able to return to a fertile stage right after parturition, this is the post-partum oestrus (*e.g.,* in pinnipeds, Boyd 1991), or reaches this stage only when her current young becomes independent. This cycle can be repeated several times during the year for polyoestrous mammals, every year for monoestrous mammals, or even at a larger time span (*e.g.,* in orangutans *Pongo spp.*, van Noordwijk *et al.* 2018).

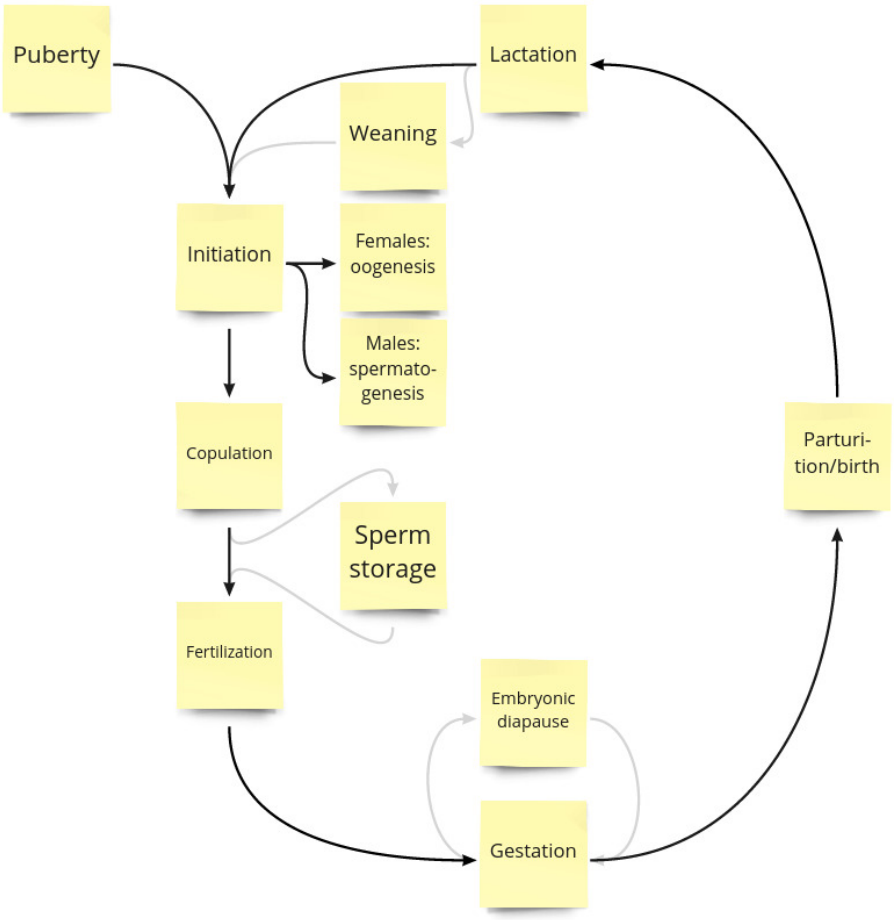

Figure 1: The reproductive cycle in mammals. Black arrows: obligatory transitions; grey arrows: non obligatory steps.

In mammals, male and female reproductive cycles are both regulated by the interaction between hormones produced in the brain (by the pineal gland, the hypothalamus and the pituitary gland) and hormones produced in the reproductive organs, together known as the gonadotropic axis. The pineal gland, sensitive to changes in photoperiod (*i.e.,* the variation of the relative duration of day and night during a 24-hours period), produces melatonin accordingly, which stimulates the hypothalamus (Reiter 1980). It is also worth noting the existence of a self-sustained internal clock, called endogenous rhythm, regulating life and reproductive processes (Reiter 1980, Heideman and Bronson 1994). In turn, the hypothalamus produces the gonadotropin-releasing hormone (GnRH) to monitor and induce the release of hormones from the pituitary gland: the follicle stimulating hormone (FSH) and the luteinizing hormone (LH) (Bronson 2009). Both hormones circulate through the bloodstream and reach the gonads (testes and ovaries, in males and females respectively) to stimulate gametogenesis (Palermo 2007). FSH and LH are involved in a negative feedback system as their secretion, as well as the secretion of GnRH, is mainly regulated by testosterone in males (Hayes *et al.* 2001), and progesterone and oestrogens in females (which also play a role in the preparation of the body for pregnancy and lactation). Those three main hormones, secreted by the reproductive organs, act concomitantly with numerous others (depending on the sex and the species of interest) in this regulation axis, and are responsible for the morphological changes of male and female gonads to prepare for reproduction (see Pearson 1944, Spinage 1969, Webley and Johnson 1983 for some examples). Internal and external factors also interact with this endocrine pathway to regulate the reproductive cycle (Bronson 1989).

The date of parturition is the linchpin of the reproductive cycle

Most of the environments on Earth are not constant, even between the tropics (Borchert *et al.* 2015). Thus, the conditions provided to the organisms are variable across the year, creating more or less favourable periods to breed. Therefore, individuals often do not reproduce any time of the year, but rather adjust the beginning and/or the termination of their reproductive cycle to match the most suitable period (Bronson 1989). In mammals as in other taxa, the reproductive cycle is mainly driven by the female's cycle, because it is the most constrained sex. More specifically, it is generally accepted that the reproductive cycle is timed by the costliest phase in terms of energetic costs inside the female's cycle (Bronson 1989). Lactation is the most expensive phase for the mother (Gittleman and Thompson 1988, Clutton-Brock *et al.* 1989), and it is a critical period for the physical and psychosocial development of the

offspring too (Hayssen 1993). When the size of the organism increases, the costs of lactation decrease: females of large species feed smaller offspring compared to their own body size; lactation lasts longer so the costs associated are spread more evenly. As early and mid-lactation is less costly for females of large species, late lactation and weaning become increasingly critical (for the offspring) in the reproductive cycle (Bronson 1989). The pivotal event which regulates those stages is the date of parturition (or the date of birth, from the offspring perspective).

Evolutionary processes are at stake here, as the date of parturition is heritable (*e.g.,* Réale *et al.* 2003a, Feder *et al.* 2008, Clements *et al.* 2010). Natural selection favours individuals that breed at the right time to ensure their offspring survival and transmit efficiently their genetic heritage, including the date of parturition. Food resource, predation pressure and some social cues, as it will be discussed extensively in the following sections, are the main ultimate factors driving the phenology of reproduction by directly acting on offspring survival. Moreover, even if the date of parturition is fairly conservative for a given female (*e.g.,* Plard *et al.* 2013), it can also be subject to phenotypic adjustments occurring at the individual scale and depending on external and internal constraints encountered by the female at the time of a given reproductive event (*e.g.,* Renaud *et al.* 2019). The internal clock, but also food resource and environmental cues are proximal factors regulating the phenology of reproduction too. Ultimate factors are less easily ascertainable than proximal factors because they require multi-generational data and cannot be tested at the individual scale. Multi-specific comparison can provide an adapted framework to test such hypotheses (see Rutberg 1987 and Brockman and van Schaik 2005 addressed later in this introduction for examples), but remain too marginal yet, because i) a large number of studies treating various species are needed, ii) those studies should use at best the same, at least similar descriptors of the phenology of births to be comparable.

However, the date of parturition takes place at the end of the reproductive cycle and relies on the timing of the previous events that are highly temporally constrained (*e.g.,* low flexibility in the duration of the oogenesis between oestrus initiation and conception, or in the gestation length between fertilization and parturition, but see Berger 1992). Therefore, numerous factors intervene throughout the whole reproductive cycle to adjust the timing of parturition. On the one hand, indirect factors can be used at the time of initiation of the reproductive cycle or conception as predictors to anticipate conditions at the time of parturition (Visser *et al.* 2010). On the other hand, direct factors during gestation can play a role in the timing of parturition too (Rowell and Shipka 2009). The balance between the effect of both regulation types depends, among others, on the mean gestation length of the species: according

to Owen-Smith and Ogutu, organisms with long gestation (> 1 year) are supposed to rely on proximal cues around conception, whereas organisms with short gestation (≤ 1 year) could exploit ultimate factors around parturition (Owen-Smith and Ogutu 2013). So, even if the crucial moment often lies in the date of parturition in mammals, it is important to bear in mind that the reproductive cycle is regulated as a whole.

Reproduction is part of the life cycle of the individuals, and critical in the determination of their fitness. It is divided into several steps, among which the most energetically costly is lactation. Through its initiation date corresponding to the date of parturition/birth, lactation generally determines the timing of the entire cycle in mammals. I will now explore the numerous drivers which act directly or indirectly at the individual, but also at the population scale, to time the reproductive cycle of an entire population *via* the regulation of the phenology of births.

The drivers of the phenology of births

The regulation of the timing of parturition/birth intervenes at the individual scale, and the addition of all individual timings in a population leads to the phenology of births, *i.e.,* the distribution of births of all the newborn in the population during a given reproductive cycle. Phenology of births can be described using two simple descriptors, commonly used in the literature and voluntarily kept broad in their definition here: timing (*i.e.,* the global position of births in a given year for a given population) and synchrony (*i.e.,* the spread of births in a given year for a given population). Both aspects of the phenology of births are regulated at the population scale, with the particularity that synchrony emerges from the collective response of all the individuals of the population (*i.e.,* cannot be defined at the individual scale), contrary to timing which is also an individual property (*i.e.,* the individual date of birth).

The environmental factors are the main drivers of the phenology of births

Food resource and abiotic conditions

Food resource is generally considered as one of the main forces driving the phenology of births in herbivores (*e.g.,* Sinclair *et al.* 2000 in ungulates, DiBitetti and Janson 2000 in primates, Heideman and Utzurrum 2003 in nectarivorous bats), but also in carnivores (*e.g.,* Cumming and Bernard 1997 in insectivorous bats, Beja 1996 in otter *Lutra lutra*) and also suspected in other groups (*e.g.,* Carone *et al.* 2019 in fin whale *Balaenoptera physalus*). It is critical in the

determination of the timing of births both as a proximal determinant, by acting on female body condition before parturition (Adams and Dale 1998), and as an ultimate determinant, by acting on the ability of the offspring to feed after birth and thus to survive (Festa-Bianchet 1988). Specific compounds in the food resource can be used by the individuals to time the initiation and/or the termination of the reproductive cycle, as cues of the timing of quality food supply (*e.g.,* in montane vole *Microtus montanus*, Berger and Cain 1977). In herbivores, the impact of several aspects of food resource is not often directly measurable and as a consequence, have been explored *via* various proxies such as food quality (*e.g.,* crude protein content, Sinclair *et al.* 2000; Normalized Difference Vegetation Index (NDVI), Ryan *et al.* 2007) and food quantity (*e.g.,* evapotranspiration, Rutberg 1987; green biomass, Sinclair *et al.* 2000; rainfall, Ogutu *et al.* 2010). Food resource is also an evolutionary constraint governing the selection of specific life history traits related to reproduction, by simultaneously impacting the ability of parents and offspring to maintain and grow respectively (Box 1).

Although abiotic conditions mainly drive the phenology of births *via* the regulation of food availability, they can also play a direct role in shaping the phenology of births through the modification of the conditions experienced by parents and offspring around the period of birth. Temperature, for instance, drives the phenology of births through its direct impact on thermoregulation in offspring (in Dall's sheep *Ovis dalli dalli*, Bunnell 1980), foraging ability of the parents (in wild dog *Lycaon pictus*, McNutt *et al.* 2019), or female condition in general (in European rabbit *Oryctolagus cuniculus,* Rodel *et al.* 2005). More marginally, the timing of ice availability, which provides a breeding ground for some arctic species, seems to be critical in their phenology of births too (*e.g.,* in harbour seals *Phoca vitulina*, Temte 1994). Nevertheless, both drivers (food resource and abiotic conditions) are intrinsically related, and it is often hard to disentangle their individual effects on the phenology of births. A general approach of this duality in predictable environments lies in global predictors, such as photoperiod.

Box 1: The capital-income breeder continuum, a life history trait acting on the phenology of births and evolving in response to environmental seasonality.

Capital breeders are generally defined as organisms which rely on the energy acquired and stored during the non-reproductive period to ensure their reproduction, whereas **income breeders** essentially rely on the available resources at the time of their reproduction to pursue it (Jönsson 1997). Such strategies have evolved in response to the predictability of food resource availability, to optimally adjust reproduction to the environment (Sun *et al.* 2020). Thus, capital breeders living in unpredictable environments are characterized by a variable conception window, high inter-annual variation in birth rates, high prenatal mortality rates and low variation in infant mortality rates. To the contrary, income breeders living in predictable environments have a narrow conception window, low inter-annual variation in birth rates, low prenatal mortality rates and high inter-annual variation in infant mortality rates (Brockman and van Schaik 2005).

Tracking environmental conditions in predictable and unpredictable environments

Among the numerous definitions lent to the term "seasonality", a broad and largely accepted one (and the one I use here) is "the phenomenon of recurrent fluctuations in climatic conditions and environmental productivity over the year" (Heldstab *et al.* 2018 from Lindstedt and Boyce 1985). The degree of seasonality follows a latitudinal gradient, from the poles, the most seasonal environments, to the equator, the least seasonal environment. Populations of various (English *et al.* 2012) or even the same (Neumann *et al.* 2020) species demonstrate variable patterns of births according to the latitude, but also the elevation (Millar and Innes 1985), in response to the associated gradient of environmental seasonality.

In seasonal environments, the succession of the seasons and the associated environmental conditions is highly conservative from one year to another. It can thus be predicted well before the birthing period by indirect cues such as photoperiod (Bradshaw and Holzapfel 2007). Numerous species have evolved at a long-term scale to respond to changes in photoperiod to time their reproductive cycle (*e.g.,* McAllan *et al.* 1991, Desjardins *et al.* 1986, Sempéré *et al.* 1995). Even if populations living in seasonal environments remain susceptible to short term cues and are able to adjust phenotypically (*e.g.*, bighorn sheep *Ovis canadensis* individually adjust their calving date in response to the amount of precipitation Renaud *et al.* 2019) and even genetically (*e.g.,* increased food abundance advances breeding in North

American red squirrels *Tamiasciurus hudsonicus*, Réale *et al.* 2003b), the ability to adjust vary among individuals (*e.g.,* reindeer *Rangifer tarandus*, Paoli *et al.* 2020). More concerning, some species seem to almost exclusively depend on photoperiodic cues rather than on actual environmental signals (*e.g.,* roe deer, Rehnus *et al.* 2020). Such species are of particular research interest in the context of climate change, as the simultaneous impact of static (*i.e.,* photoperiod) and changing (*i.e.,* climatic factors) cues is still poorly understood and exposes them to maladaptation.

To the contrary, in unpredictable or constant environments (*e.g.,* at the equator or even inside cave environments), photoperiod changes are minimal and not necessarily representative of the environmental seasonality, which can be more dictated by rainfall patterns, for instance. In these environments, organisms are more dependent on direct environmental cues (*e.g.,* sporadic rainfalls in desert rodents Beatley 1969) preferentially acting on the initiation or the termination of the reproductive cycle than on the phenology of births *per se* (Bronson 1989). Some species living in such environments do not even show any response to photoperiodic cues (Bronson and Heideman 1992).

Environmental factors mainly drive the timing of births, but this control over timing also implies an indirect effect on synchrony (Findley and Cooke 1982). Indeed, the adequate conditions to breed are fulfilled for a given period of time, which can possibly range from a very short duration (*e.g.,* in arctic environments), leading to high synchrony, to the whole year (*e.g.,* in some tropical forests), leading to low synchrony. In the latter case, births can still be highly synchronous, but then environmental factors are not necessarily the main drivers of the phenology of births.

The biotic factors are the second order drivers of the phenology of births

How to synchronize reproductive events?

In the context of reproduction, synchrony is often defined as "the phenomenon caused by biological interactions operating to produce a tighter clustering of reproductive events than would have been imposed by environmental seasonality alone" (Ims 1990a). Thus, in some populations, phenology of births should have evolved from a slightly synchronous (in response to the environment) to a highly synchronous distribution under the pressure of supplementary forces. The synchrony of births is often less largely studied than the timing because of the difficulties to quantify it. Indeed, the evaluation of synchrony necessitates information about as many individuals in the population as possible, whereas timing can be condensed by the first

date or the peak date (even if it is not necessarily the best measure available, Forrest and Miller-Rushing 2010). Thus, the proximal and ultimate causes of the timing of births are presently more generally explored and better known than the causes of the synchrony of births. Moreover, until now, synchrony has been described with many different descriptors according to i) the group of species (generally the period gathering 80% of births since the first birth in ungulates, Rutberg 1987; using the mean vector length in primates, DiBitetti and Janson 2000), ii) the shape of the distribution (mostly the proportion of births around a central measure such as the mean birth date for peak distributions, Estes 1976; and heterogeneity indexes such as the evenness index when studying spread out distribution, Sinclair *et al.* 2000), or iii) to the resolution of the data (general season of births for coarse data, Fairall 1968; smallest number of successive blocks of five days for fine data, Zerbe *et al.* 2012). Such diversity of measures of the synchrony of births severely limits our ability to compare it among mammals.

From a mechanistic point of view, females can actively synchronize their reproductive events such as conception, but also ovulation or even parturition to answer various constraints. But the precise underlying mechanisms are not always clearly understood yet. It has been observed that external factors such as moon phases (Sinclair 1977, Murray 1982) or social cues such as flehmen displayed by females (Berger 1992) can play a role in such behaviours, but chemical mechanisms are probably at stake too (McClintock 1978, Porter and Wilkinson 2001).

Inter-specific interactions

The role of predation, perhaps the main biotic factor proposed to explain the synchrony of births, initially comes from the literature on birds (Darling 1938). The historical example in mammals was provided by Estes in 1976: the author hypothesized that the predation of spotted hyena *Crocuta crocuta* on blue wildebeest *Connochaetes taurinus* in Ngorongoro crater, Tanzania, acts as an ultimate factor and should lead to synchronous births in the prey by selecting against early and late births (Estes 1976, see also Testa 2002). Similar results have been observed in other mammals (*e.g.,* in the snowshoe hare *Lepus americanus*, O'Donoghue and Boutin 1995). More generally, four main theoretical strategies link the synchrony of births with predation (Ims 1990a): i) the predator satiation strategy, ii) the predator swamping strategy, iii) the predator avoidance strategy, and iv) the collective vigilance and defence of the offspring (displayed by the adults, contrary to the three previous hypotheses which concerns mainly newborn, Estes 1976). Both predator satiation and swamping strategies run concurrently to favour the synchrony of births: the high number of simultaneous newborn provides enough preys at the same time to reduce individual predation risk (Karban 1982, for a historical example

in cicadas), and reduces predators hunting efficiency by overwhelming them as they can only handle a limited number of preys at a time (but it also depends on the predator behaviour, see Ims 1990b). To the contrary, the predator avoidance strategy is supposed to favour asynchronous births: the low number of simultaneous newborn dispersed in the landscape should force predators to actively search for preys and reduce the individual risk of being detected (Gosling 1969).

In ungulates, the combination of the hypotheses stated above with species and predator characteristics, but also environmental factors, has led to the evolution of a gradient of life history traits known as the hider-follower continuum (Box 2). However, the relationship between behaviour of the young and phenology of births is often solely partially explored. Theoretical hypotheses are empirically tested by comparing the level of synchrony of several species regarding the hider-follower dichotomy, without considering the fact that it is rather a continuum, or without taking into account the predatory and environmental context.

Besides predation, a relatively recent evolutionary force acting on the synchrony of births is the anthropogenic pressure. Hunting pressure, for instance, has advanced the timing of births up to 12 days in 22 years in a highly hunted population of wild boar *Sus scrofa scrofa* (Gamelon *et al.* 2011). More marginally, active control of the phenology of births *via* population regulation (*e.g.,* forced-weaning) and environment management (*e.g.,* cessation of grazing by livestock) has also been attempted in highly managed populations such as bison *Bison bison* (Kaze *et al.* 2016). However, the results on the enhancement of the synchrony of births do not seem conclusive.

The impact of inter-specific competition (*e.g.,* for the access to food resource) on the phenology of births has never been empirically explored in mammals, but such effects are theoretically supported by the existence of a high variability in the distribution of births among large African herbivores living in the same environment and exploiting similar resources (Bronson 1989 with the example of Dasmann and Mossman 1962, see also Drickamer 1978 for two sympatric species of *Peromyscus* displaying different patterns of reproduction). Moreover, even if it does not directly affect the phenology of births, there are evidence that juvenile survival and recruitment can be affected by species competition (*e.g.,* negative effect of the presence of red deer *Cervus elaphus* on chamois *Rupicapra rupicapra rupicapra* birth rate, Donini *et al.* 2021) but also mutualism (*e.g.,* positive effect of the presence of migratory herds on calf survival in giraffe *Giraffa camelopardalis*, Lee *et al.* 2016).

Finally, a last form of species interaction which could act on the phenology of births is parasitism. There is currently no evidence of the impact of parasitism (or even more generally,

diseases) on the phenology of births either, but these themes remain largely under-investigated (but see Berger and Cain 1999 for an exploration in a brucellosis-exposed population of bison).

Box 2: The hider-follower continuum, a life history trait evolving in response to predation, shapes the phenology of births.

Follower species are mainly characterized by the early ability of the offspring to stand and follow its mother, whereas **hider** species are able to hide and spend a long time separated from their mother during their first days of life (Lent 1974). Such behaviours are supposed to have evolved in response to the type of predation (specialist or generalist predators, Ims 1990b), the environment (open or closed landscape) and other life history traits of the focal population (*e.g.,* migratory or resident). They are associated with different levels of synchrony of births (Rutberg 1987, Linnell and Andersen 1998): followers should give birth in a very limited period of time to benefit from group vigilance and protection, predator satiation and swamping strategies; hiders should demonstrate a variable level of births synchrony because they primarily rely on food resource, and secondly on predator pressure *via* the predator avoidance strategy. However, predation pressure is not necessarily the main force driving the level of synchrony between births, and studies exploring synchrony relatively to the behaviour of the young can provide inconsistent results (see Green and Rothstein 1993b for a follower species giving birth asynchronously, and Michel *et al.* 2020 for a hider species giving birth synchronously).

Intra-specific interactions

Intra-specific competition has been proven to be a major driver of the phenology of births, sometimes even disrupting the phenology dictated by the environment (Tinsley Johnson *et al.* 2018). As an example, a high synchrony of births is observed in small mammals displaying communal breeding to limit the risk of infanticide and competition between offspring (in banded mongoose *Mungos mungo*, Hodge *et al.* 2011). To the contrary, the same phenomenon can be observed in large mammals living in social units, to benefit from communal rearing this time (in lion *Panthera leo*, Bertram 1975). Male harassment, in turn, has also been proposed as an evolutionary force explaining the high synchrony of births in pinnipeds: by giving birth at the same time, females reduce the individual harassment undergone (in grey seal *Halichoerus grypus*, Boness *et al.* 1995). Such adaptations are intrinsically related to the mating system of the species (Box 3). In other respects, males can actively synchronize births via the

synchronization of ovulation, when taking over a group of females (in gelada *Theropithecus gelada* in Tinsley Johnson *et al.* 2018, and in lion in Bertram 1975), males perform infanticide and induce abortion in females, causing a resetting of their reproductive cycles), or even by their vocalizations (Calabrese *et al.* 2018), in order to increase their own reproductive success.

Furthermore, intra-specific competition not only constraints synchrony, but also affects timing of births. An increased population density generally leads to later births by decreasing female condition and delaying their reproductive cycle (Clutton-Brock 1987). To conclude, male vocalizations can also advance the timing of births by advancing the timing of oestrus in females (McComb 1987).

Box 3: The mating system, a life history trait related to the phenology of births.

The mating system not only relates to the type of association between males and females (monogamy, polygamy regrouping polyandry and polygyny, or promiscuity), but also to the sexual dimorphism between both sexes (Jarman 1983). The mating system is highly dependent on the environment through the cost of acquisition and defences of food and mate resources (Emlen and Oring 1977), but it is also related to the phenology of reproduction. Indeed, birth phenology and mating system should act reciprocally on each other (but see Heldstab *et al.* 2018 for a counterexample). The "marginal male effect" (in pinnipeds, McLaren 1967) states that subordinate males occupying peripheral areas of the colony should be of lower quality than central males and have fewer mating opportunities, leading to an increasing spatial concentration of breeding females around dominant males. Miller proposed a temporal equivalent of this effect which explains why polygyny should favour reproductive synchrony (Miller 1975): females ready to breed early or late during the breeding season are less susceptible to be fertilized, and if so, should be fertilized by less competitive marginal males which are not able to breed inside the reproductive season. In the former case, the parturition date of the females will not be transmitted, and in the latter case, daughters will be equally limited and sons of low competitive value. To the contrary, a highly synchronous reproductive cycle among females can enhance monogamy because of a reduced accessibility to several spatially dispersed females by a given male (Emlen and Oring 1977).

Individual factors also play a role in shaping the phenology of births

Lastly, one can suppose that individual factors should shape the phenology of births at the population scale too. The age structure of the female section of the population, for instance, can

lead to a variable level of synchrony, and even to a variation in the timing of births. Because young females tend to give birth later than prime-age females (*e.g.,* in caribou *Rangifer tarandus* Adams and Dale 1998), an increasing number of young females in the population could reduce the synchrony of births. In Geoffroy's rousette *Rousettus amplexicaudatus*, primigravid females have only one reproductive event during their first reproductive year, which falls between the two peaks of older females, disrupting the pattern of births of the population (Heideman and Utzurrum 2003). In other respects, failure to conceive during the first oestrus in polyoestrous species can delay the timing of fertilization, and thus the timing of parturition, for the concerned individuals (Guinness *et al.* 1978). A skewed sex ratio against males may also delay the timing of births by reducing the availability of reproductive males (*e.g.,* in red deer, Holand *et al.* 2003).

Female condition and quality are major sources of variation in the individual timing of parturition: females in poor body condition give birth later than females in good condition (Cameron *et al.* 1993, and the other way round: Plard *et al.* 2014a), as well as females which weaned an offspring during the previous reproductive cycle (Feder *et al.* 2008), because the reproductive effort depleted their resources. The effect of inbreeding has also been explored, but results are inconsistent. Some authors found an advancement of the date of birth for inbred individuals (in female bighorn sheep, Rioux-Paquette *et al.* 2011), whereas others found no evidence for an effect of either maternal or offspring inbreeding level on the date of birth (in red deer, Walling *et al.* 2011) or a delay in the date of births (Hogg *et al.* 2006). The variable proportion of females concerned by either situation in a given population is hence susceptible to modify the pattern of births at the population scale.

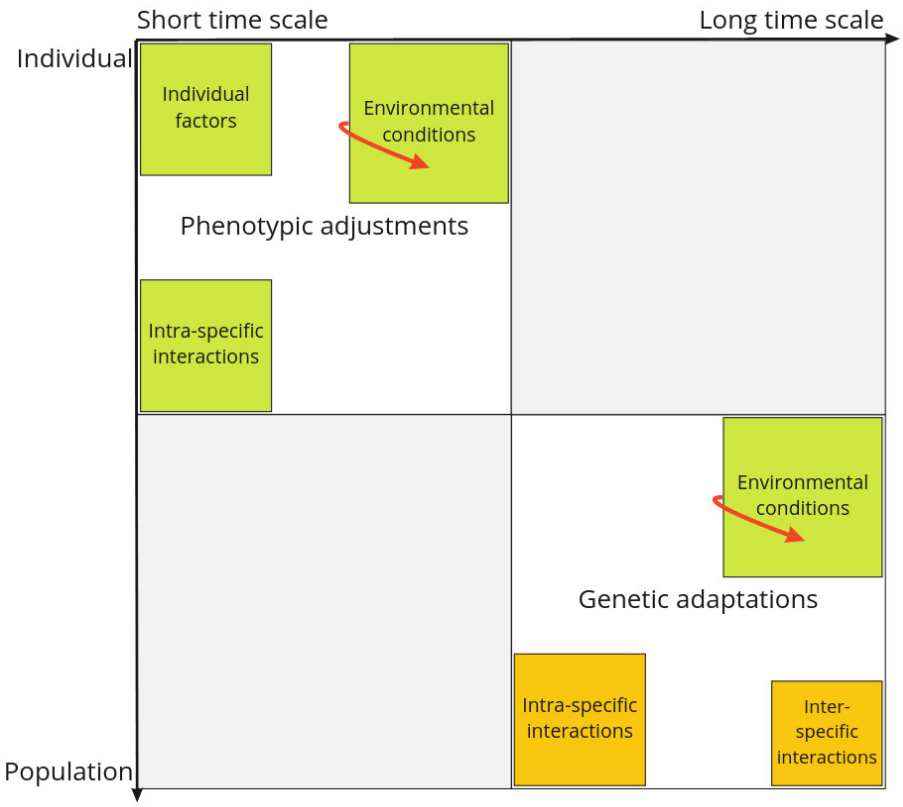

Figure 2 : The main drivers of the phenology of births in mammals act at different scales. Phenotypic adjustments occur at the individual scale during a given year, whereas genetic adaptations occur at the population scale on the long term. The drivers of the phenology of births can act both on the timing of birth (which is more related to individuals, in green) and on the synchrony of births (which mainly depends on the population response, in orange). Some drivers are directly acting on the phenology of births, whereas others act as indirect predictors (red arrows in the graph). The relative importance generally associated with each driver in shaping the phenology of births is represented by the size of the box. See text for a detailed description of the drivers.

Environmental, biotic and individual factors act concurrently to shape the distribution of births (Fig. 2), but the relative part of each factor is not easy to disentangle, and varies according to the species and even to the population studied (*e.g.,* Rutberg 1984, Lambin 1993, Post *et al.* 2003). Nevertheless, those complex interactions play a major role in the determination of the phenology of births in mammals, which in turn will impact the individuals, the populations, and even the communities.

The consequences of the phenology of births...

... On the individuals: the offspring and the mother survival and fitness

The evolutionary forces mentioned above, which determine the individual timing of birth, have evidently direct consequences on offspring survival. Hence, in synchronized populations,

juveniles born outside the birthing peak are exposed to a higher risk of predation (Estes 1976, O'Donoghue and Boutin 1995) or infanticide (Hodges 2008). In seasonal environments where births are generally restricted to the favourable season, individuals born early have a better survival rate. Indeed, offspring growth rate is affected by the quality of food resource and the duration of its availability after their birth, a longer exposure to a good resource before the next unfavourable season therefore allowing a better growth (Festa-Bianchet 1988, Feder *et al.* 2008). In addition, according to the level of synchrony of births of the cohort (*i.e.,* the group of individuals born during the same reproductive cycle and sharing the same early conditions for their development) and the density of the population, offspring are more or less subject to competition (Hodges 2008, Rasmussen and Rudolf 2015). More generally, the timing of birth is an indicator of the condition experienced by the mother during pregnancy, and thus determines critical components of the offspring survival, such as birth mass, mediated by environmental and maternal effects (Wolcott *et al.* 2015). Early survival is generally the result of an interaction between all those factors (*e.g.*, Lee *et al.* 2017).

The environmental conditions experienced during early life, which have been proven to have evident short-term effects, also have long-term effects on survival, reproductive success, and eventually fitness of the individuals (Lindström 1999). Indeed, the timing of births often determines weaning mass, which in turn determines later body mass and survival (*e.g.,* winter survival in bighorn sheep lambs, Feder *et al.* 2008; adult body mass in roe deer, Plard *et al.* 2015; or even disease susceptibility during adulthood, Muñoz-Tuduri and Garcia 2008). Sexual maturation duration (Iason 1989) and acquisition of a social rank (Green and Rothstein 1993a) depend on the timing of birth of the individual too. Such long-term reproductive consequences resulting from early life conditions, when advantageous, are known as the "silver spoon effect" (Grafen 1988). However, the date of birth acts in interaction with other individual factors such as sex or compensatory mechanisms, sometimes scrambling the general trends (*e.g.,* there is no influence of the date of birth on survival to weaning in Fairbanks 1993, nor on growth rate in Gaillard *et al.* 1993a).

Besides, it should not be forgotten that the date of birth is the result of a trade-off between the offspring and the mother interests (*e.g.,* minimizing the inter-birth interval for the mother and maximizing offspring survival, Dezeure *et al.* 2021), although both of them are not necessarily exclusive (offspring survival and recruitment participate in enhancing the fitness of the mother). Thus, even if the date of parturition does not seem to directly affect the survival of the mother (but engaging reproduction or not has consequences on maternal survival: Clutton-Brock *et al.* 1983), it can at least influence her reproductive success. Females giving birth earlier

are more likely to breed again the next year (Clutton-Brock *et al.* 1983, Guinness *et al.* 1978). In species practicing post-partum oestrus, they are even more likely to breed again during the current year in case of early litter loss (Williams *et al.* 2013). Here again, covariables such as the age of the mother or the reproductive success during the previous year can interact with the date of parturition and influence the reproductive success. This can be explained by reproductive costs that are variable among females according to their age or quality (*e.g.,* Hamel *et al.* 2009, Descamps *et al.* 2009).

Such diversity in the consequences of the timing of birth on offspring and mothers according to individual covariables might indicate that generalizations from model organisms to predict general trends is not advisable. There is a particular need to explore further the consequences of the timing of births in species living in the Southern hemisphere, where little is currently known (Lee *et al.* 2017, see **chapter 3**). This is mainly due to the lack of long-term and individual-based studies (Clutton-Brock and Sheldon 2010).

… On the population: implications for demography

Population dynamics relies on several characteristics such as the size of the population, its growth rate, the age structure and the survival associated with each age category. The temporal component of reproduction, namely the phenology of births, plays a role in the population dynamics through its effects on several of those components (Fig. 3). As seen previously, the timing of births has consequences on juvenile survival at the individual scale. However, such effects are also detectable at the population scale: a mistimed phenology of births implies a lower cohort survival in roe deer, for instance (Plard *et al.* 2014b). Even if juvenile survival has low elasticity (*i.e.,* relative sensitivity) as regard to population growth rate, it is characterized by a high variability, sufficient to affect the growth rate of the population, and even being one of its critical components for some species such as large herbivores (Gaillard *et al.* 2000). The survival of juveniles born during a given reproductive cycle determines the later recruitment of this cohort in the adult section of the population. The effects of a low juvenile survival and recruitment on the population growth rate can be masked in the short term and appear solely on the long term, especially for long-living species where decreasing growth rate can be buffered (Morris *et al.* 2008). A mistimed phenology of births can also induce long lasting effects in the newborn individuals, such as a reduced reproductive success, which can affect the entire cohort. Low quality cohorts have lower reproductive success at the adult stage (Gaillard *et al.* 2003), which in turn could lead to a lower recruitment of the subsequent generations. Eventually, the

synchrony of births could also play a role in the population dynamics through long-term effects on the offspring maturation. A lack of synchrony in the individual timing of birth can propagate to other phenological stages such as reproductive maturation, which could cause a lack of reproductive synchrony between individuals of the same cohort, or even inside the whole population. This could be particularly true in short-living species.

Additionally, density naturally acts as a retroactive control loop on the population dynamics through the phenology of births. A high population density generally leads to a higher competition between females. They consequently give birth later, inducing a lower juvenile survival (see development above), which can ultimately lead to a decrease in the population density (Clutton-Brock *et al.* 1987). But population dynamics can suffer from disruptions of this loop. In species with a naturally low reproductive synchrony, an advantageous strategy in unpredictable environments, the reduction of the population density also reduces the opportunity of mating with congeners by temporally isolating them (*i.e.,* incompatible reproductive timing between individuals of the same population) when the population becomes too small. Such phenomena can lead to Allee effects, which could ultimately cause the extinction of the population (see Calabrese and Fagan 2004 for a theoretical demonstration in the context of plant and insect life history traits). While this phenomenon is illustrated through non-mammal species examples here, it is likely to happen in small mammals adopting similar reproductive strategies.

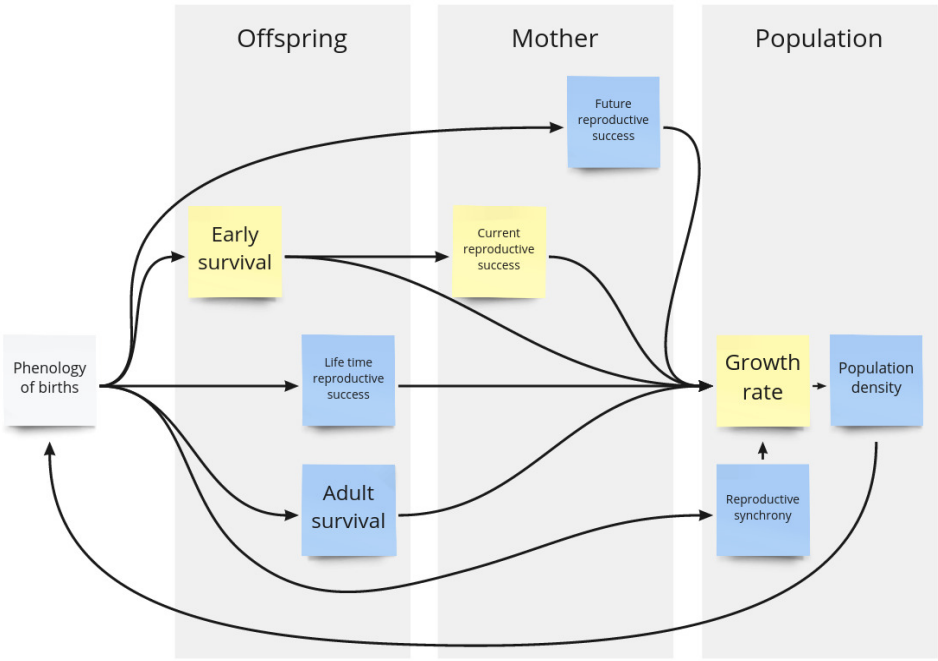

Figure 3 : The multi-scale consequences of the phenology of births in mammals. Yellow: immediate consequences; blue: delayed consequences.

Climate change is currently one of the major sources of disturbance of the phenology of births, acting on the population dynamics through the increasing frequency of mismatches between the timing of births and the food resource availability in primary consumers (Visser and Both 2005, but the effects of climate change have also proven to be not as detrimental as expected for the population dynamics of some species like reindeer: Hansen *et al.* 2019). Although such effects are predominant and have been largely documented in species breeding during a restricted period of the year (*e.g.,* Plard *et al.* 2014b), they are also present in year-round breeders (*e.g.,* Burthe *et al.* 2011). The response of each population in terms of reproductive phenology depends on its life history traits and demographic characteristics, but also on the local environmental variations experienced, and all of these need to be taken into account in risk analyses (Campos *et al.* 2017). To properly explore the effects of climate change on the phenology of births, long-term data, and thus perennial and cost-effective methods of data collection are needed. In line with these requirements, automated and cost-effective methods such as camera trapping and citizen science, respectively, are developing, but their relevance still needs to be assessed. Then, even if the direct effects of climate change on secondary consumers have already started to be explored (*e.g.,* McNutt *et al.* 2019), the propagation of the impacts of a mismatch between the reproductive phenology of an organism and its food resource through trophic levels has received less attention yet.

… On the communities

The propagation of mismatches through trophic levels is still poorly understood, mainly because of a lack of long-term data, but also of an imperfect knowledge of the species ecology and inter-specific relationships (Miller-Rushing *et al.* 2010). The phenology of births is part of the mechanisms at stake here. A well-known pathway is the change in secondary consumer occupancy in response to the change of the occupancy of its prey, a primary consumer, which responds itself to a change in primary productivity (*e.g.,* Stoner *et al.* 2018). One can theoretically expect similar mechanisms in the context of the phenology of reproduction, as the timing of conception of some predator seems to be regulated by the timing of births of their prey (Maruping-Mzileni *et al.* 2020), which in turn depends on the phenology of the vegetation. A lack of responsiveness at one or several levels of such pathways could cause a destabilisation of the complete trophic chain through the phenology of births.

The phenology of births relies on the phenotypic and evolutionary responses of the individuals and the populations to internal and external factors. Those factors allow the individuals to optimally time their reproductive cycle, in order to enhance the offspring survival and increase the offspring and the parent fitness. Large herbivores constitute a perfect study case to explore the multiple questions related to the phenology of births in mammals in several respects.

Large herbivores as a case study

Large herbivores are a well-known group

The large herbivores are nowadays often defined as the herbivorous mammals with a body mass > 2 kg, including essentially the ungulates and some large marsupials (Danell *et al.* 2006). The ungulates constitute a polyphyletic group generally employed to describe hoofed mammals: the orders *Artiodactyla* (*i.e.,* even number of fingers) and *Perissodactyla* (*i.e.,* uneven number of fingers). According to the definition selected, ungulates can also include the *Proboscidea* (*i.e.,* characterised by a trunk) (Danell *et al.* 2006), and the *Suina* (*i.e.,* pigs and peccaries) and *Cetacea* (*i.e.,* aquatic mammals), which are not strictly herbivorous. Here I retain the term "large herbivores" to refer exclusively to *Artiodactyla* (including *Suina*), *Perissodactyla* and *Proboscidea*.

Large herbivores have been extensively studied for several decades now, for management and ecological purposes (*e.g.,* Holloway et al. 1950). Thus, they constitute a well-known group, with long-term data currently available (*e.g.,* red deer of the Isle of Rum are studied since 1953, https://rumdeer.bio.ed.ac.uk/). Such datasets allow temporal comparisons, particularly valuable in the context of climate change. Numerous studies have explored their distribution, behaviour, reproductive and demographic parameters, and many of those parameters are now available in large syntheses (*e.g.,* Wilson and Mittermeier 2011).

Large herbivores concentrate a high diversity

Large herbivores naturally occupy almost all latitudes, from the poles (*e.g.,* caribou, Post *et al.* 2003) to the equator (*e.g.,* Bornean yellow muntjac *Muntiacus atherodes*, Giman *et al.* 2007), and all continents except Antarctica and Australia (but see Forsyth *et al.* 2018). They also occur in habitats ranging from sea level (*e.g.,* moose *Alces alces*, Singh *et al.* 2012) to as much as 5 000 m a.s.l (*e.g.,* alpine musk deer *Moschus chrysogaster*, Buzzard *et al.* 2018). Thus, they experience a large variety of conditions and climates. Consequently, they are characterised by

various life history traits related to their environment, such as their diet, anti-predator behaviours or mode of energy allocation to reproduction. Through their high diversity, large herbivores regroup a lot of characteristics found in mammals.

The result of such a variability of environmental conditions, additionally to intrinsic characteristics such as body mass or mating system, has led to a wide diversity of phenology of reproduction, ranging from intra-annual (*e.g.,* dikdik *Rynchotragus (Madoqua) kirki*, Sinclair *et al.* 2000) to supra-annual (*e.g.,* elephant *Africana loxodonta*, Moss 2001) patterns, with a high diversity of species characterized by various annual patterns (Sinclair *et al.* 2000). At the population scale, the phenology of births is also highly variable, ranging from highly synchronous (*e.g.,* roe deer, Gaillard *et al.* 1993b) to asynchronous (*e.g.,* giraffe, Lee *et al.* 2017) patterns. As the same species sometimes occupies a wide latitudinal gradient (*e.g.,* moose), and some others occur in poly-specific assemblages (*e.g.,* large herbivores of the Serengeti), it is possible to study the phenology of births according to a variety of ecological conditions within the same species (Neumann *et al.* 2020), but also according to similar ecological conditions with various life history traits (Sinclair *et al.* 2000).

Large herbivores are easy to monitor

Large herbivores are relatively easy to study because of their consequent body mass and size, diurnality (for a large amount of them), terrestriality, which make them easy to identify and track in the field *via* direct observations but also indirect monitoring such as camera trapping or GPS tracking. Moreover, most of them occur in quite large populations and are not endangered yet (unlike carnivores), and thus can be monitored for scientific purposes without major risk of threatening the populations (but see Kock *et al.* 1987).

Large herbivores constitute a highly diverse, well known and easy to monitor group inside the taxa of mammals. Thus, they are the perfect candidate to study the different aspects of the phenology of births in mammals. On this basis, the objectives of my thesis are to explore the phenology of births throughout a complete scientific approach, from the methodological questions associated with data collection and description, to the evolutionary and ecological significance of the phenology of births.

Thesis aims and structure

Methodological approach of the phenology of births

How to record the phenology of births?

The phenology of births is not an easy subject to study for two main reasons: first, it requires long-term data, and second, it necessitates being able to monitor a large fraction of the population. Consequently, numerous ways of monitoring wildlife have been developed for this purpose, ranging from direct observations in the field (Ogutu *et al.* 2010, Plard *et al.* 2015), to automated surveys using GPS tracking (Marchand *et al.* 2021, Walton and Mattisson 2021), including camera trapping (Hofmeester *et al.* 2020) and participatory programs. However, all the methods developed until now face a trade-off between time-consumption and monetary cost on the one hand, and temporal (is the survey lasting?) and coverage (is the population well covered?) efficiency on the other hand. A way to simultaneously maximize several items is to combine several methods. Nonetheless, if temporal and monetary cost can be easily determined upstream, efficiency needs to be tested afterward.

In **chapter 1** (*Can citizen science analysis of camera trap data be used to study reproduction? Lessons from Snapshot Serengeti program*), I explored the reliability of a combination of two methods, camera trapping and citizen science, to determine the presence of juveniles in the wild for three species of African antelopes, the topi *Damaliscus jimela*, the kongoni *Alcelaphus cokii* and the Grant's gazelle *Nanger granti*, and then extrapolate their phenology of births. To do so, I used the Snapshot Serengeti program, Tanzania (Swanson *et al.* 2015), currently the world's largest program of its kind.

How to describe the phenology of births?

Once the data is collected, the next step is to make it speak. To do so, the global information should be synthesized into handy concepts and mathematical descriptors. As a result of the variety of patterns encountered in the wild and the prolificity of this research topic, the study of phenology of reproduction has led to a bulk of terms and metrics, with similar objectives but not necessarily easy to bring together or comparable. Many measures are specific to one paper, conceived for the very specific purpose and context of the study and never used again. Several studies have proposed clarifications of the general definitions and concepts associated with phenology to favour dialogue between related disciplines (Visser *et al.* 2010, Forrest and Miller-Rushing 2010). Other studies have compared a limited number of metrics used to measure a very specific component of phenology to encourage the generalization of the use of

the best one (Moussus *et al.* 2010, Landler *et al.* 2018). However, there is currently no comprehensive study simultaneously reviewing the diversity of metrics used to describe the various components of phenology and providing guidance to choose the most suitable ones. However, this is particularly important to fill the gaps in terms of multi-specific comparisons to better understand the role of ultimate factors and in the context of climate change to better assess their consequences on the shape of the phenology of births.

In **chapter 2** (*How to describe and measure phenology? An investigation on the diversity of metrics using phenology of births in large herbivores*), I explored the diversity of metrics used to describe the phenology of births in the literature on large herbivores. Based on simulated data, I compared the behaviour of more than 50 metrics and assessed their ability to describe timing, synchrony and their repeatability for a given phenology. I finally reassessed a general framework to study the phenology of births and favour comparisons between studies.

Ecological and evolutionary approach of the phenology of births

What are the consequences of the phenology of births?

As seen previously, the timing of birth has consequences on the individual survival and fitness. In offspring, this can be directly related to the environmental conditions at birth, namely food resource and abiotic conditions, which determine the ability of the offspring to grow (Festa-Bianchet 1988). In the Northern hemisphere, even if it is not directly a matter of survival, mothers can suffer from those conditions too, in their ability to engage the next reproduction for instance (Clutton-Brock *et al.* 1983). In the Southern hemisphere in turn, where tropical mammals live in less predictable environments with a more complex seasonality, the selection of the timing of birth and its consequences on both juveniles and mothers still remain poorly explored and understood (Lee *et al.* 2017). Nevertheless, dramatic changes related to climate change are expected in those environments, which have already started to be visible (Richard *et al.* 2001). Thus, there is a real need to better understand the phenology of births of tropical species. Although some datasets are available to address those questions, they were until now often ancient and patchy (*e.g.,* Allsopp 1971), based on population metrics only (*e.g.,* Ogutu *et al.* 2014), or limited to a small number of individuals (*e.g.,* Calabrese *et al.* 2018).

In **chapter 3** (*Does timing of birth affect juvenile and mare survival in wild plains zebras?*), I used an individual-based dataset of more than 10 years to explore the consequences of the timing of birth relatively to the duration of the dry season, on juvenile and mother survival in a tropical large herbivore, the plain zebra *Equus quagga*. Although living in a seasonal

environment in Hwange National Park, Zimbabwe, this population breeds year-round. In the context of climate change, the seasonality should become even more pronounced, potentially exposing the population to maladaptation.

Axis 1

Methodological approach of the phenology of births

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Chapter 1

Can citizen science analysis of camera trap data be used to study reproduction? Lessons from Snapshot Serengeti program

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Abstract

Ecologists increasingly rely on camera-trap data to estimate biological parameters such as population abundance. Because of the huge amount of data camera trap can generate, the assistance of non-scientists is often sought after, but an assessment of the data quality is necessary. We tested whether volunteers' data from one of the largest citizen science projects – Snapshot Serengeti – could be used to study breeding phenology. We tested whether the presence of juveniles (less than one or 12 months old) of species of large herbivores in the Serengeti: topi, kongoni, Grant's gazelle, could be reliably detected by the 'naive' volunteers versus trained observers. We expected a positive correlation between the proportion of volunteers identifying juveniles and their effective presence within photographs, assessed by the trained observers. The agreement between the trained observers was good (Fleiss' $\kappa > 0.61$ for juveniles of less than one and 12 month(s) old), suggesting that morphological criteria can be used to determine age of juveniles. The relationship between the proportion of volunteers detecting juveniles less than a month old and their actual presence plateaued at 0.45 for Grant's gazelle, reached 0.70 for topi and 0.56 for kongoni. The same relationships were much stronger for juveniles younger than 12 months, reaching 1 for topi and kongoni. The absence of individuals < one month and the presence of juveniles < 12 months could be reliably assumed, respectively, when no volunteer and when all volunteers reported a presence of a young. In contrast, the presence of very young individuals and the absence of juveniles appeared more difficult to ascertain from volunteers' classification, given how the classification task was presented to them. Volunteers' classification allows a moderately accurate but quick sorting of photograph with/without juveniles. We discuss the limitations of using citizen science camera-traps data to study breeding phenology, and the options to improve the detection of juveniles.

Keywords: African ungulates, age determination, *Alcelaphus cokii*, *Damaliscus jimela*, *Nanger granti*

Introduction

Camera trapping is increasingly used for ecological monitoring due to its low cost, relative ease of use and the variety of data it can supply (O'Connell *et al.* 2010). For instance, camera trap data are used to study species' occupancy and co-occurrence (Anderson *et al.* 2016), population dynamics (Karanth *et al.* 2006) or individual behaviour (*e.g.,* vigilance behaviour: Chamaillé-Jammes *et al.* 2014, or diel activity patterns: Luo *et al.* 2019). A potential drawback of camera traps is the huge amounts of data that are generated (> 7 millions photographs for the Snapshot Serengeti initiative alone). Ecologists have realized that the benefits of continuously collecting data in the field can quickly be negated by the burden of database management, and visual inspection and analysis of photographs to record the desired data (Wearn and Glover-Kapfer 2017).

To process such a massive amount of information in a reasonable time, scientists have sought the help of non-specialists who perform diverse tasks like counting objects in photographs, describing picture content or identifying animal and plant species (McShea *et al.* 2015). Initially, part of the scientific community was sceptical about citizen science, in particular questioning data quality (Riesch and Potter 2014). However, volunteers have sometimes proven to be as efficient as experts, for instance for the identification of large herbivore species in savanna ecosystems (Swanson *et al.* 2016). More recently, the advances in deep learning have led computers to become as efficient as people at identifying species, and, sometimes, behaviour classification problems (Norouzzadeh *et al.* 2018). However, human judgment is still valuable in particular cases where too little data are available to train models (*e.g.,* active learning, Joshi *et al.* 2009), or when differences among the objects to be classified are subtle and classification requires some subjectivity (Miele *et al.* 2021). We believe this is the case for age classification problems, for which to the best of our knowledge the number of precisely labelled pictures taken in the wild is currently too small to allow an efficient and reliable automatization of the process.

Under the assumption that the detectability of juveniles and adult females segments of the population is not biased by camera traps methodology, classifying individuals into age classes such as juveniles and adults would allow estimates of key demographic parameters (*e.g.,* reproductive rates) or life history traits (*e.g.,* breeding phenology). For instance, Ogutu and colleagues (2008) highlighted that rainfall influences the abundance of several large herbivore species of the Mara-Serengeti ecosystem, by acting differently on each segment of the populations at specific periods of the year. Furthermore, it would facilitate the study of the

relationships between population characteristics and their environments such as between birth phenology, diet and food resource availability (Sinclair *et al.* 2000), or their potential evolution in the context of climate change (Visser and Both 2005). Until now, the study of those key demographic parameters has been mainly conducted by direct field observations (Côté and Festa-Bianchet 2001 in mountain goats, Plard *et al.* 2013 in roe deer). However, this methodology still requires an intensive and often costly field effort. Identifying and counting juveniles from camera traps could reduce this field effort, or allow larger-scale or longer-term studies, as suggested by Hofmeester *et al.* (2020), but could also be time-consuming because of tedious data processing. With the help of citizen science, data handling time could be substantially reduced, but the accuracy of non-specialists in detecting juveniles of large mammals from photographs has not yet been explored.

Here, we evaluate the usefulness of camera trap data annotated by citizen scientists online to assess the presence of juveniles of large herbivores in the photographs. We use photographs and citizen classifications from the Snapshot Serengeti project (Swanson *et al.* 2015), one of the world's largest citizen science programs, on a subset of the data. We focus on the detection of juveniles in three species found in the Serengeti National Park, Tanzania with contrasting social and neonatal behaviours: topi *Damaliscus jimela*, kongoni *Alcelaphus cokii* and Grant's gazelle *Nanger granti*. We first evaluate the agreement between trained observers from our research team, and then test the ability of the volunteers to detect juveniles by comparing their classification with ours. We predict a better agreement between trained observers for the youngest age class because determination criteria are clearer and easier to identify than for older juveniles (*e.g.,* absence of horns). Consequently, the level of agreement should decrease for age classes that are based on more subjective or difficult-to-assess criteria (*e.g.,* shape of the horns). Under the hypothesis that volunteers could generally identify juveniles correctly, we expect a positive relationship between the proportion of volunteers reporting a juvenile on a photograph and the probability of the actual presence of a juvenile, as determined by the trained observers. Again, we expect the correlation to be stronger for the youngest age class of juveniles because they are easier to differentiate from adults. Across species, we expect a higher agreement and correlation for topi and kongoni than for Grant's gazelle because the former are larger, live in smaller groups and have similar body growth rate between males and females (Wilson and Mittermeier 2011), hence reducing the risk of confusion between young males and older females. Overall, our study details the strengths and weaknesses of camera trap data, in particular when classified by citizen scientists, for the study of reproductive traits such as reproductive rates or breeding phenology.

Materials and methods

Study site

The surveyed area within the Serengeti National Park, Tanzania, is composed of open plains and savanna woodlands. Rain mostly occurs between November and June (wet season), with mean annual rainfall increasing from 500 mm in the southeast to 1100 mm in the northwest. This area harbours a rich community of large herbivores, composed of gregarious and migratory wildebeest *Connochaetes mearnsi*, zebra *Equus sp.* and Thomson's gazelle *Eudorcas nasalis*, but also resident populations such as Cape buffalo *Syncerus caffer* or warthog *Phacochoerus africanus* (Sinclair and Norton-Griffiths 1995). Community dynamics are driven both by herbivores, maintaining an open state of the grassland by intensive grazing (McNaughton 1985, Sinclair and Norton-Griffiths 1995) as well as large predators (*e.g.,* lion *Panthera leo* and hyena *Crocuta crocuta*, Sinclair and Norton-Griffiths 1995).

Camera trap data

The Snapshot Serengeti camera trap grid was deployed in 2010 in Serengeti National Park, Tanzania, to monitor lions and their prey, though the bycatch of numerous other species has proven useful as well. Running continuously since 2010, the grid spans 1125 km^2 in the centre of the park. We used data provided by Snapshot Serengeti camera survey recorded between July 2010 and April 2013 (Supporting information 1). The camera traps were set ~ 50 cm above ground in the centre of a 5 km2 grid cell. The detection radius was approximately 45° and their field of view about 14 m (Swanson *et al.* 2015). Cameras took a rapid series of three pictures upon trigger of the motion and heat sensors ('capture event' in Swanson *et al.* 2015, hereafter called a 'sequence' following Meek *et al.* 2014) in a few seconds interval, with a one-minute delay between sequences.

Choice of studied species and sorting steps of the dataset

Among the many large herbivore species present in the study site, we selected topi, kongoni and Grant's gazelle due to their contrasting biology and characteristics useful to assess the age classes of individuals. The criteria considered were 1) number of available sequences, 2) relatively small group size, 3) presence of horns in males and females, 4) relatively large size of the young (young of larger species are larger, and therefore criteria like horns are easier to detect), 5) contrasting anti-predator of behaviour of the young (Supporting information 2).

We selected the final dataset (n = 2359 sequences) to conduct the analyses following several sorting steps, based on the detection of the species of interest and of the presence of juveniles from the initial complete dataset (n = 1 184 657 sequences) by the volunteers. We then corrected this dataset thanks to the trained observers' reclassifications (details in Table 1).

Assessing the presence or absence of juveniles in photographs

All Snapshot Serengeti photographs have been uploaded to the online citizen science platform 'The Zooniverse' (<www.zooniverse.org>) to be classified by volunteers. Each sequence was processed by as many as 25 volunteers (minimum = 11, maximum = 57, Swanson *et al.* 2016), who each identified what species was present in the sequence and recorded whether at least one juvenile was present or not. Note that no formal definition of a juvenile was provided to volunteers, nor were there any particular guidelines about how to identify a juvenile. Volunteers simply searched and checked 'young' in the Zooniverse interface when they suspected the presence of non-adult individuals. Regarding age classes, the only question volunteers had to reply to was: 'Are there any young present?'. For each sequence, the volunteers' classifications were then compiled via a plurality algorithm to yield a consensus classification, leading to a proportion of volunteers (Pv) who identified at least one juvenile in each sequence (details in Swanson *et al.* 2015). Here, we used all sequences where volunteers identified topi, kongoni and Grant's gazelle, with at least one volunteer ($Pv > 0\%$) having annotated the presence of a juvenile. We could not analyse all sequences for which no volunteer had reported a juvenile, as these were too many (n = 2018, 11 141 and 6628 for topi, kongoni and Grant's gazelle respectively) to be reviewed individually. However, we checked a subset of them (n = 1000 for each species), and the chance that a trained observer observed a 'true' juvenile (*i.e.,* of less than 12 months old, see age classes definition below) was < 6.5% for all three species studied when no volunteer did report one. We did not correct observations for recaptures of the same individuals as we were only interested in the ability of volunteers to detect the presence of juveniles on the sequences, but not the actual number of juveniles.

Three of us (LT, LK and MC), considered here as trained observers, searched all sequences retained for juveniles, which were assigned to an age class when detected. We used previously published morphological descriptions of the studied species (*e.g.,* shape and size of horns, size relating to the adult; Supporting information 3) to identify and age individuals. We distinguished between 1) juveniles < one month, 2) between one and six months, 3) between six and 12 months, 4) between 12 and 24 months, termed yearling hereafter and 5) individuals

over two years old, termed adults hereafter. We defined age classes according to biological characteristics relevant to juvenile identification for each species (*e.g.,* very young individuals for birth phenology identification, juveniles under one year for recruitment estimation). We recorded observers' classifications with Aardwolf software (Krishnappa and Turner 2014). Ultimately, we produced a dataset describing the presence or absence ($M_{i,s,j}$), in each sequence of individuals of any of the five age categories *i*, for the species *s*, by trained observer *j*.

Table 1: Number of sequences at each sorting step from the extraction of raw data to the selection of all the independent sequences with at least one individual < 1 month old, for the three species of the study: topi, kongoni and Grant's gazelle (pictures from Snapshot Serengeti program, Tanzania, between July 2010 and April 2013). Standard deviations are calculated on the basis of the classifications of the three trained observers.

Step n°	**Step name**	**Consists in**	**Classifier**	**Number of sequences**		
				Topi	**Kongoni**	**Grant's gazelle**
1	Row data	all sequences produced during the survey	none	1,184,657		
2	Blank sorting	sequences with animals	volunteers	319,915		
3	Species sorting 1	sequences with study species	volunteers	2,299	12,431	7,723
4	Young sorting 1	sequences with at least more than 0% of volunteers identifying young	volunteers	281	1,290	1,095
5	Species sorting 2	sequences with study species corrected by trained observers	trained observers	324	1,281	754
6	Young sorting 2	sequences with at least one young	trained observers	216 ± 1	830 ± 17	348 ± 18
7	Young sorting 3	sequences with at least one young less than one month old	trained observers	59 ± 9	137 ± 33	58 ± 3
8	Re-sight sorting 1	independent sequences (remove of resights notified by the observers)	trained observers	39 ± 7	71 ± 27	50 ± 5
8'	Re-sight sorting 2	independent sequences (remove of sequences taken less than 10 minutes after the previous one by the same camera trap)	theoretical sorting	42 ± 8	70 ± 22	40 ± 4

Statistical analyses

We first evaluated the agreement between the three trained observers on the detection of individuals assigned to each age class for each species. We measured this agreement with the Fleiss' κ, implemented in the '*raters'* R package (Quatto and Ripamonti 2014). Fleiss' κ (Fleiss 1971) is the comparison of agreement between 2+ judges and the level of agreement expected by chance alone. It takes values between −1 and 1, values < 0 indicating an agreement lower to

what could be expected by chance, values > 0 indicating a greater agreement than expected by chance, and values = 0 indicating an agreement close to random. We tested for significance of the difference between the Fleiss' κ using a bootstrap procedure following Vanbelle and Albert (2008) (Supporting information 4).

We tested the relationship between the proportion of volunteers identifying at least one juvenile (*Pv*) and the probability that trained observers had identified at least one juvenile < 1 month (category i = 1). We also explored the same relationship with juveniles < 12 months (therefore including juveniles of categories 1–3 above). We fitted three generalized estimating equation models: one linear (Eq. 1 below) and two piecewise models. The first piecewise model was characterized by a slope on both sides of the threshold (Eq. 2), the second by a slope before and a plateau after the threshold (Eq. 3). We fitted piecewise models to search for a potential 'saturation' phenomenon, whereby beyond a specific proportion of volunteers the probability to effectively observe a juvenile does not increase anymore. We also fitted the null model for comparison. All the models were fitted for the two age classes and for each species individually, using the *wgee* function implemented in the '*wgeesel'* R package (Xu *et al.* 2018). We selected the best model using the Quasi-likelihood under the independence model criterion QIC (thresholds selected by comparison of QIC of the models for each species and age class as well). It is a modification of the Akaike information criterion AICc, suitable when quasi-likelihood is used instead of likelihood (Pan 2001), implemented in the '*MuMIn'* R package (Bartoń 2019). We used a logit link function and a binomial distribution of errors (Agresti 2002), considering the proportion of volunteers identifying at least one juvenile as fixed effect, and the identity of the sequence as clustering variable with an exchangeable correlation structure:

$$logit\left(M_{s,i,j}\right) = \mu + \beta_{s,i} \times Pv_s \qquad \textit{(Eq. 1 – linear model)}$$

$$logit\left(M_{s,i,j}\right) = \begin{cases} \mu + \beta 1_{s,i} \times Pv_s \;\; if \; Pv_s \leq \; \theta \\ \mu + \beta 2_{s,i} \times Pv_s \;\; if \; Pv_s > \theta \end{cases} \qquad \textit{(Eq. 2 – piecewise model 1)}$$

$$logit\left(M_{s,i,j}\right) = \begin{cases} \mu\theta + \beta 1_{s,i} \times Pv_s \;\; if \; Pv_s \leq \; \theta \\ \mu 2 \;\; if \; Pv_s > \theta \end{cases} \qquad \textit{(Eq. 3 – piecewise model 2)}$$

where $M_{s,i,j}$ denotes the presence or absence of at least one juvenile of the age class i (< 1 or 12 months) for a given sequence, for the species s and the observer j, μ is the expected mean probability of actual presence of at least one juvenile of the age class i when none of the volunteers identified the presence of a juvenile, Pv_s is the proportion of volunteers identifying at least one juvenile for a given sequence, for the species s and θ is the best threshold. We performed all analyses using the R statistical software (<www.r-project.org>).

Results

From the Snapshot Serengeti monitoring program, we obtained 281, 1290 and 1095 sequences for topi, kongoni and Grant's gazelle respectively (Fig. 1a) sorting step 'Young sorting 1' and Table 1. Our selection process led to a dramatic drop in the number of usable sequences (*i.e.,* those containing at least one < 1 month old juvenile), with a tenfold reduction at the species level: it only remained between 7.7% and 18.1% of the complete dataset available for the species (n = 59 ± 9 SD, 137 ± 33 SD and 58 ± 3 SD for each species respectively, Fig. 1a) sorting step 'young sorting 3' and Table 1). The largest losses of sequences happened during the phases of selection of sequences containing the studied species and then juveniles (Fig. 1a and Table 1). Figure 1b suggests that we would obtain similar results concerning the loss of sequences after selection for sequences containing juveniles for any large herbivore species recorded in the Snapshot Serengeti program.

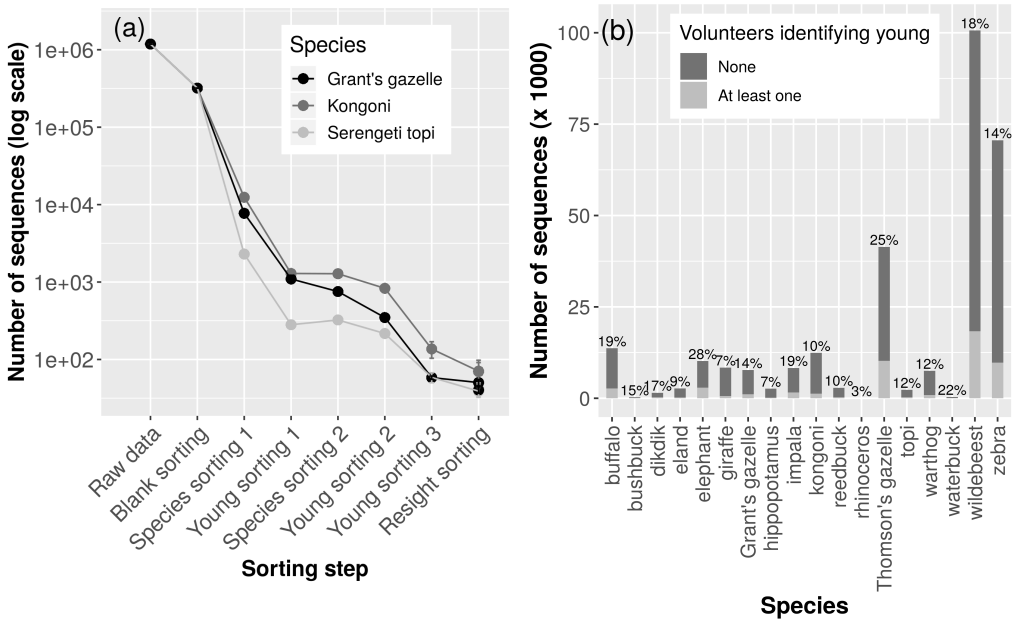

Figure 1: (a) Number of sequences available at each sorting step from the extraction of raw data to the selection of all the independent sequences with at least one individual < 1 month old, for the three species of the study: topi, kongoni, Grant's gazelle. Pictures from Snapshot Serengeti, Tanzania, between July 2010 and April 2013. Raw data: all sequences produced during the survey; blank sorting: sequences with animals; species sorting 1: sequences with study species according to the volunteers; young sorting 1: sequences with at least one volunteer identifying 'young'; species sorting 2: sequences with study species corrected by trained observers; young sorting 2: sequences with at least one young according to the trained observers; young sorting 3: sequences with at least one young < 1 month old according to the trained observers; resight sorting: independent sequences once sequences taken less than 10 minutes after the previous one by the same camera trap and presenting the same species have been removed (following Palmer et al. 2018). Note the log scale for the ordinate axis, vertical bars represent the standard deviations. (b) Number of sequences available for all the large herbivore species present in the study site. The proportions indicate the proportion of sequences where at least one volunteer identified juveniles for a given species.

The three trained observers identified 993 ± 49 SD, 3020 ± 180 SD and 2128 ± 224 SD individuals of any age class. On average, they could not assign an age class to ~11% (n = 118 ± 68 SD), ~20% (n = 775 ± 256 SD) and 32% (n = 1026 ± 492 SD) of the individuals for topi, kongoni and Grant's gazelle respectively, a significant between-species difference ($\chi^2 = 262.83$, $df = 2$, $p < 0.001$).

For all species, and as expected, the agreement between trained observers was highest for the youngest age class, then declined with age until the yearling class was reached (Fig. 2). Yearlings were reasonably well classified in kongoni, but overly misclassified in topi and Grant's gazelle (Fig. 2). As expected, the agreement among trained observers was the highest for the youngest age class of juveniles, but also for the second age class and the adults, with Fleiss' κ values almost always > 0.61 (denoting a substantial agreement, following Landis and Koch 1977), except for Grant's gazelle aged between one and six months and adult topi. Agreement among observers was the highest for topi aged < 1 month old (Fleiss' $\kappa = 0.78$ [0.72; 0.84]). In support of our prediction, we observed the lowest agreement for juveniles aged six months and older, and more obviously so for Grant's gazelle. Agreement among observers concerning the three first age classes pooled together (representing the juveniles) was very good, with Fleiss' κ values largely > 0.61 for all the species. The same holds true for juveniles between one and 12 months old when pooled together. Our results were globally consistent among the three species studied, with the highest agreement for topi, and the least for Grant's gazelle (Fig. 2). All estimated Fleiss' κ were significantly different from an agreement obtained by chance ($p < 0.001$, see Supporting information 4).

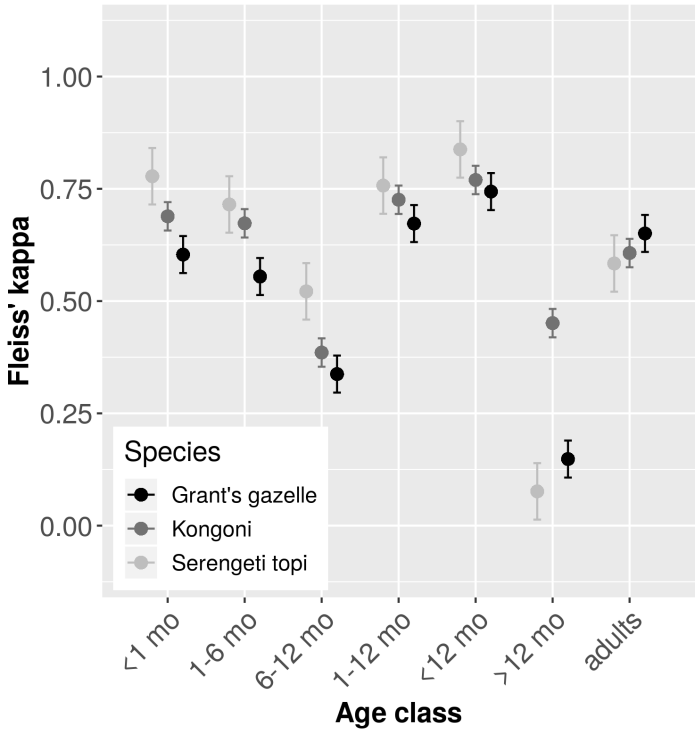

Figure 2: Fleiss' κ denoting the level of agreement between the three trained observers (LT, LK and MC) in the identification of presence or absence of at least one individual belonging to any of the five age classes (< 1 month, 1–6 months, 6–12 months, > 12 months, adults), for the three species of interest. Pictures from Snapshot Serengeti Program, Tanzania, between July 2010 and April 2013. The two combined age classes '1–12 months' and '< 12 months' are also presented. Light grey dots: topi, dark grey dots: kongoni, black dots: Grant's gazelle. Vertical bars represent the confidence intervals of the points estimates. A Fleiss' κ near 1 denotes an almost perfect agreement, whereas a value near or < 0 means a very poor agreement between raters.

The model best describing our data for the age class < 1 month was the linear model for topi, the piecewise model with slopes on both sides of the threshold for kongoni and the piecewise model with slope before and plateau after the threshold for Grant's gazelle (Table 2). The model best describing our data for the age class < 12 months was the threshold model with slopes on both sides of the threshold for topi, kongoni and Grant's gazelle (Table 2).

The probability of observing a juvenile when all volunteers reported one was near 1 for juveniles < 12 months for topi and kongoni. Concerning Grant's gazelle, this probability only reached 0.90 when 41% of the volunteers recorded the presence of young. Between 41% and 100% of volunteers identifying young in the sequences, the probability decreased (Fig. 3d–f). When investigating the presence of juveniles < 1 month, the probability that a juvenile was actually present was never greater than 70% (Fig. 3a–c). On the other hand, the model predicted that when no volunteer reported the presence of juveniles, the probability that there was juveniles < 1 month was under 1.8%, but there was at least 9.6% chance to observe a juvenile < 12 months.

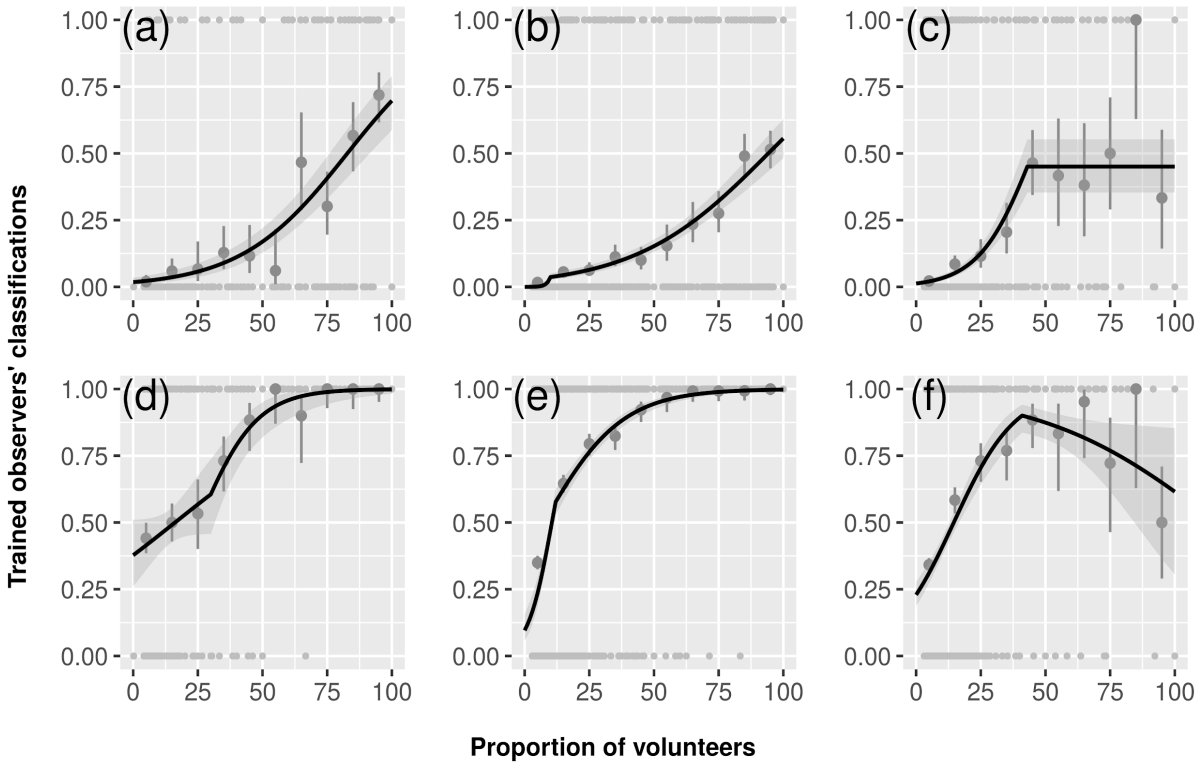

Figure 3: Relationship, as predicted from the best model (see text for details), between the proportion of volunteers identifying the presence of 'young' and the probability of presence of at least one individual < 1 (a–c) and < 12 (d–f) months assessed by the trained observers in a given sequence of photographs (0 < proportion of volunteers identifying 'young' ≤ 1), for the three species of interest: (a) and (d) topi, (b) and (e) kongoni and (c) and (f) Grant's gazelle. Pictures from Snapshot Serengeti Program, Tanzania, between July 2010 and April 2013. Light grey dots represent the probability of presence of at least one individual < selected age class in each sequence assessed by the three trained observers, dark grey dots represent the mean of those probabilities for each 10% volunteers interval, vertical bars represent 95% confidence intervals. Solid line represents predicted values from the best model. Shaded areas represent 95% confidence interval of these predicted values.

Contrary to our expectations, the piecewise model characterized by two slopes was almost always selected as the best model for the three species and both age classes. This denotes a sudden change in the rate of detection from a certain percentage of volunteers. The detection rate decreases for kongoni and Grant's gazelle for young < 12 months beyond 12 and 41% of volunteers voting for the presence of young respectively. The number of volunteers who did classify a photograph was independent from the probability to detect a young.

Table 2: Statistics of models investigating the relationship between the proportion of volunteers identifying at least one 'young' and the probability of presence of at least one individual < 1 or 12 months, assessed by the trained observers on a given sequence for the three species of interest: topi, kongoni and Grant's gazelle. Best models are in bold. θ=estimated threshold (% of volunteers), QIC=Quasi-likelihood under the Independence model Criterion, estimates ± standard error. Best models are in bold type.

Age class	Species	Model type	θ	QIC	Quasi-likelihood	Estimates
< 1 month	Topi	Null		924.6	-459.77	in. = -1.509 ± 0.133
		Linear		**630.9**	**-311.05**	**in. = -4.013 ± 0.342** **β = 0.048 ± 0.005**
		Piecewise - slope/plateau	90	635.2	-313.23	in. = -4.102 ± 0.362 β1 = 0.051 ± 0.005 μ2 = 0.626 [0.523; 0.720]
		Piecewise - slope/slope	78	634.7	-310.49	in. = -8.863 ± 1.763 β1 = 0.045 ± 0.007 β2 = 0.064 ± 0.023
	Kongoni	Null		2614.4	-1304.83	in. = -2.125 ± 0.081
		Linear		1993.0	-992.05	in. = -3.977 ± 0.174 β = 0.043 ± 0.003
		Piecewise - slope/plateau	90	2005.8	-998.42	in. = -4.007 ± 0.178 β1 = 0.044 ± 0.003 μ2 = 0.498 [0.434; 0.563]
		Piecewise - slope/slope	**10**	**1966.7**	**-977.58**	**in. = -10.522 ± 1.740** **β1 = 0.687 ± 0.178** **β2 = 0.039 ± 0.003**
	Grant's gazelle	Null		1236.2	-615.91	in. = -2.479 ± 0.117
		Linear		1016.6	-501.81	in. = -3.653 ± 0.181 β = 0.055 ± 0.007
		Piecewise - slope/plateau	**43**	**969.7**	**-480.75**	**in. = -4.355 ± 0.227** **β1 = 0.097 ± 0.008** **μ2 = 0.451 [0.353; 0.552]**
		Piecewise - slope/slope	43	974.6	-480.48	in. = -4.573 ± 0.544 β1 = 0.094 ± 0.010 β2 = 0.006 ± 0.013

Table 2: continued.

Age class	Species	Model type	θ	QIC	Quasi-likelihood	Estimates
< 12 months	Topi	Null		1241.3	-618.00	in. = 0.698 ± 0.111
		Linear		948.0	-468.64	in. = -0.866 ± 0.184 β = 0.059 ± 0.007
		Piecewise - slope/plateau	60	964.6	-477.23	in. = -0.987 ± 0.191 β1 = 0.069 ± 0.007 μ2 = 0.958 [0.926; 0.977]
		Piecewise - slope/slope	**30**	**946.5**	**-464.45**	**in. = -3.202 ± 0.624** **β1 = 0.031 ± 0.017** **β2 = 0.090 ± 0.022**
	Kongoni	Null		4992.3	-2493.63	in. = 0.609 ± 0.054
		Linear		3726.5	-1858.95	in. = -1.139 ± 0.108 β = 0.089 ± 0.006
		Piecewise - slope/plateau	90	3726.6	-1859.03	in. = -1.140 ± 0.108 β1 = 0.089 ± 0.006 μ2 = 0.999 [0.997; 1]
		Piecewise - slope/slope	**12**	**3684.8**	**-1835.45**	**in. = -3.041 ± 0.271** **β1 = 0.213 ± 0.029** **β2 = 0.066 ± 0.006**
	Grant's gazelle	Null		3127.4	-1561.20	in. = -0.154 ± 0.067
		Linear		2940.5	-1463.22	in. = -0.837 ± 0.140 β = 0.049 ± 0.010
		Piecewise - slope/plateau	30	2866.2	-1428.27	in. = -1.285 ± 0.132 β1 = 0.091 ± 0.009 μ2 = 0.809 [0.748; 0.859]
		Piecewise - slope/slope	**41**	**2866.4**	**-1425.59**	**in. = -0.009 ± 0.506** **β1 = 0.083 ± 0.010** **β2 = -0.029 ± 0.013**

Discussion

Our study reveals the strength and weaknesses of using citizen-based assessment of age classes on camera trap pictures. Clearly, citizen involvement through an online platform has been critical for the classification of the millions of photographs collected by the Snapshot Serengeti initiative. Also, despite leaving it to the volunteers to decide what a juvenile looks like, volunteers' classification allows a rough, moderately accurate, but quick sorting of sequences with/without juveniles.

Our study makes clear that, for the species studied and given the minimal guidelines given to volunteers, the 'absence' of very young (< 1 month) individuals on pictures can be reliably assumed when no volunteer reports a presence. The sequences almost never labelled by volunteers as containing 'young' were very unlikely to contain young under one month of age according to the trained observers. This suggests that volunteers rarely miss very young juveniles. This likely occurs because very young juveniles are distinctively smaller than adults, and possibly also because very young mammals share some physical characteristics such as relatively large eyes, long legs, short and rounded nose, all belonging to 'Kindchenschema', known to be very attractive stimuli for humans (Brosch *et al.* 2007, Golle *et al.* 2013). By contrast, the 'presence' of very young individuals appears more difficult to ascertain from volunteers' data, and this apparently comes from the lack of guidelines given to volunteers. Indeed, consistent with the idea that volunteers easily identify very young individuals, a large consensus among volunteers around the presence of a very young juvenile could be a reliable indication of actual presence, but only when no older juveniles are present (compare Fig. 3a–c and Supporting information 5 – Fig. A). Unfortunately, the absence or presence of older juveniles cannot currently be known without a reassessment of the pictures because volunteers were not asked to differentiate between juvenile age classes. Therefore, the presence of very young juveniles remains difficult to ascertain. On the other hand, the 'presence' of juveniles, irrespectively of their age, can be reliably assumed when all volunteers agree about a presence (Fig. 3a–c), especially for topi and kongoni: the model predicted that when all the volunteers reported the presence of juveniles, the probability that there was juveniles < 12 months was indeed at least 99.8%. This time, the 'absence' of juveniles regardless of their age is less accurate, meaning that they are missed quite often. As they grow, juveniles become increasingly similar to adults, and are more likely to be mistaken for the latter by volunteers. Anyhow, we emphasize that detectability of juveniles is not equal between species (Fig. 3).

Among the three trained observers, we found the best agreement in the detection of age classes for a given sequence for topi and kongoni, suggesting that they are the easiest species to classify, and Grant's gazelle the hardest. The combination of small body size and gregariousness could explain why the determination of age was more difficult and heterogeneous for Grant's gazelle than for the two other species. Topi and kongoni are fairly large, and the small body size of Grant's gazelle makes the detection of some inconspicuous age criteria challenging (*e.g.,* presence or absence of very small horn buds on the forehead of the individuals). On the contrary, it is certainly easier to discriminate between adults and juveniles in the largest herbivores, such as giraffe *Giraffa camelopardalis* or elephant *Loxodonta africana* because of the marked size difference between them. Discrimination between several juvenile age classes will certainly be difficult still as individuals are often only partially spotted by camera traps and subtle aging criteria are not visible. More generally, in species forming large herds such as wildebeest, young might be particularly difficult to spot and are likely missed frequently. In large groups, the body of many individuals overlaps, hampering our ability to see aging criteria correctly, and to age them accurately. This could explain why in our study for instance, Grant's gazelle frequently occurring in large herds reaching more than 30 individuals in some sequences, is also the one with the lowest identification success of juveniles. Finally, a pronounced sexual dimorphism in horn growth in Grant's gazelle likely led to confusions between the first two age classes as male horns grow faster, a young male can look like an older female when using the length of the horns as an aging criteria. This would also be the case for species with a sexual dimorphism in which only males grow horns like impala Aepy*ceros melampus* or waterbuck *Kobus defassa*. Clearly, a description of the morphological changes that occur throughout the development of young herbivores (Spinage 1976 in our species, Cunningham *et al.* 2011, Dezeure *et al.* 2020 in other species) is of great value and substantially helps at reaching consistent results among different observers.

Another limitation of camera trapping in the context of reproductive studies is the level of effort required to obtain a sufficient sample size. Here, working with data from one of the world's largest and long-running camera trap studies, we ended up with a small number of sequences with juveniles < 1 month old after appropriate data selection. We identified four main explanations for this important reduction in exploitable sequences. First and foremost, our ability to determine an individual's age class depends strongly on the photograph quality and particularly its framing and exposure. In many cases, individuals were located too far from the camera or were only partly visible, or photographs were too blurry, dark or overexposed to be

scrutinized, leading to potentially significant loss of reproductive data and a high number of individuals of unknown or over-estimated age. Another potential source of information loss was species misidentification by volunteers. In our study, about 30% of the sequences labelled with Grant's gazelle were misidentified because it greatly resembles species such as impala and Thomson's gazelle which are also present in the study site. Species abundance obviously directly impacts the number of sequences collected. The abundance of the three studied species is low compared to other ungulates in the Serengeti system. Sinclair and Norton-Griffiths (1995) reported 55 500 individuals topi, 20 700 individuals kongoni and 6000 individuals Grant's gazelle in the 1970s, whereas the numbers of wildebeest and zebra were 720 000 and 240 000 individuals respectively. Finally, the anti-predator strategy of juvenile large herbivores, known as the hider-follower gradient (Lent 1974, Rutberg 1987), could influence the number of sequences containing very young individuals. While followers become active and stick with their mother just a few hours after birth, hiders stay concealed in dense vegetation during their first weeks of life. The detection probability of hiders from camera traps should then be much lower than of followers, consistent with our observation of very young topi seen in a greater proportion than kongoni and Grant's gazelle.

Volunteers' classification provides information that can reliably be used to infer the 'presence' of juveniles < 12 months or the 'absence' of juveniles < 1 month, as these annotations appear robust. However, because volunteers seem able to discriminate between individuals of less than one month old and the rest of the juveniles even in the absence of any stated criteria, more precise results could be achieved by asking them to differentiate between two age classes of juveniles, such as 'juvenile' and 'newborn'. The level of agreement between trained observers in the classification of age classes according to species is also a good indication of what kind of tasks could be successfully conducted by volunteers. When this agreement is low (*e.g.,* in the identification of topi and Grant's gazelle yearlings), one could not expect volunteers to properly identify such an age class. We advise to limit the number of classes the volunteers are asked to identify, and to focus on the most recognisable ones. Another way to improve results generated via citizen science platforms could be the inclusion of detailed information, as for species identification (Swanson *et al.* 2015). When a volunteer detects a young on his/her photograph, he or she could be prompted with comprehensive keys to age juvenile from its morphology along with a set of reference pictures or drawings. In general, however, we would recommend to ask citizen scientists to identify newborn, *i.e.,* individuals under one month of age versus other juveniles. To identify newborn of bovid species with horns like in our study, volunteers would have to look for the smallest individuals, with no evidence of bud horns, with

specific coat colour (*e.g.,* darker coat colour in Grant's gazelle in our study, or lighter coat colour in wildebeest) or even with umbilical cord remnants. One difficulty is to adapt the different criteria to every species studied.

We finally suggest evaluating volunteers' classification skills by presenting them with images of individuals of known age (captive or tagged animals for instance) and assessing their accuracy compared to labels provided by experts. Volunteers could then be assigned classification tasks adapted to their skills (*e.g.,* species identification would belong to the easiest tasks, whereas age classification would belong to the hardest). Snapshot Safari and Zooniverse continue to create new modes of annotation that best leverage the public's interest in contributing to research, and this is a logical next step for the Snapshot Safari initiative. Overall, we find that by closely investigating the data already collected by volunteer-based programs, data collection procedures can be adjusted to enhance the contributions of citizen scientists to scientific research and conservation efforts.

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Supporting information

Supporting information 1

Number of sequences per species and per year, according to the classifiers: Zooniverse volunteers and trained observers as LT, LK and MC (pictures from Snapshot Serengeti program, Tanzania, between July 2010 and April 2013). Here is reported the number of sequences only for sequences gathering at least one volunteer identifying at least one juvenile on the sequence. Note that years go from July of the year *n* to June of the following year *n+1*.

Species	**Year**	**Total number of sequences assessed by the volunteers**	**Total number of sequences assessed by the trained observers after reclassification of the right species**
Topi	Total	281	324
	July 2010 - June 2011	101	105
	July 2011 - June 2012	78	98
	July 2012 - June 2013	102	121
Kongoni	Total	1 290	1 281
	July 2010 - June 2011	412	433
	July 2011 - June 2012	501	489
	July 2012 - June 2013	377	359
Grant's gazelle	Total	1 095	754
	July 2010 - June 2011	491	358
	July 2011 - June 2012	368	221
	July 2012 - June 2013	236	175

Supporting information 2

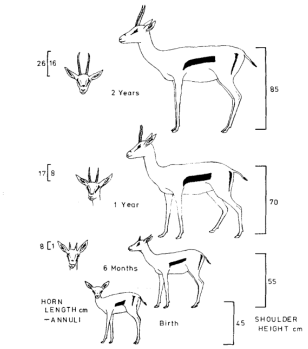
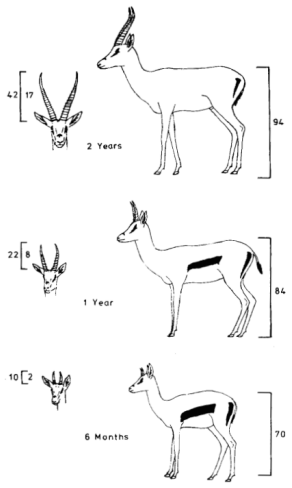
Selection criteria to decide on the studied species (see text for details). Pictures from Serengeti Snapshot Program, Tanzania, between July 2010 and April 2013. "+" corresponds to a satisfied criterion, "-" corresponds to an unsatisfied criterion, the choice is based on informal criteria. The species studied here, which fulfilled the most criteria, are in bold.

Species	**Nb of sequences available**	**Presence of horns in males and females**	**Large size of the young**	**Small group size**
African Buffalo	+	+	+	-
Blue Wildebeest	-	+	+	-
Bushbuck	-	-	-	+
Dik-dik	+	-	-	+
Eland	-	+	+	+
Elephant	+	- (but tusks)	+	+
Giraffe	+	-	+	+
Grant's gazelle	**+**	**+**	**+**	**+**
Hippopotamus	-	-	+	+
Impala	+	-	+	-
Kongoni	**+**	**+**	**+**	**+**
Reedbuck	+	-	+	+
Rhinoceros	-	+	+	+
Thomson's gazelle	-	+	-	-
Topi	**+**	**+**	**+**	**+**
Warthog	+	- (but tusks)	-	+
Waterbuck	-	-	+	+
Zebra	-	-	+	-

Supporting information 3

Criteria for age classification of topi, kongoni and Grant's gazelle.

Species	Category	Criterion	Age	Reference
Topi	*Horns*	Absence of horns	newborn	Ogutu *et al.* 2010
		Horns visible but shorter than the ear	less than 6 months	Ogutu *et al.* 2008
		Presence of "bud" horns	6 months	Jewell 1972
		Horns still straight; less than twice the length of the ear	less than 10 months	Ogutu *et al.* 2008
		7 to 9 ridges on the horns	more than 12 months	Jewell 1972
	Coat colour	Pale fawn coat	6 months	Jewell 1972
	Body size	Half adult size	6 months	Jewell 1972
Kongoni	*Horns*	Absence of horns	newborn to 1 month	Gosling 1969
		Horns straight, approximately 10 cm	2 or 3 months	Ansell 1960
		Horns visible but shorter than the ear	less than 6 months	Ogutu *et al.* 2008
		Horns straight, less than twice the length of the ear	less than 10 months	Ogutu *et al.* 2008
		Horns distinctly curved in toward each other	11 to 18 months	Ogutu *et al.* 2008
		Horns lyre-shape but not full size	19 to 24 months	Ogutu *et al.* 2008
Grant's gazelle	*Horns*	In males and females: top of the horns visible	5 to 6 months	Walther 1972
		In males: horns are ⅓ of ear length, clearly more massive than adult female's one, forehead at the basis of the horns swollen (corresponding to the eruption of the first ring(s))	7 to 12 months	Walther 1972
		In males: horns as long as in adult females or longer, with pronounced rings, but thicker than in adult females. No backward curvature yet, but rather concavely and a little inward curved at the top	12 to 24 months	Walther 1972

Species	Category	Criterion	Age	Reference
Grant's gazelle	*Horns*	In females: length of the horns slightly below those of an adolescent male, and much thinner	7 to 12 months	Walther 1972
		In females: horns longer than the ear but by far not as long as in a fully adult female	less than 24 months	Walther 1972
	Coat colour	darker in colour	newborn to 2 weeks	Walther 1972
	Body size	In males and females: half the size of an adult female, or a little more	5 to 6 months	Walther 1972
		In males: size about ¾ of that of adult male, body still weaker than adult female's one	7 to 12 months	Walther 1972
		In males: size and body strength of an adult female	12 to 24 months	Walther 1972
		In females: approximately, although not yet completely, reached the size of an adult female, body still slimmer	12 to 24 months	Walther 1972
	General			Spinage 1976
	General			Spinage 1976

For all the species: persistence of the umbilical cord denotes very recent birth (*e.g.,* Ogutu *et al.* 2010).

Supporting information 4

Evaluation of the significance of the difference between the Fleiss' κ values by the method of the bootstraps.

To check for the significance of the difference between the Fleiss' κ values between species for a given age class and between ages classes for a given species, we used the bootstraps methods described in Vanbelle and Albert (2008). We describe here the estimation of the difference between species for a given age class, but the procedure is the same for the estimation of the difference between ages classes for a given species.

We generated 9,999 batch (the 10,000^{ths} corresponding to the Fleiss' κ calculated from the original dataset) by sampling with replacement n=324, 1,281 and 754 sequences for the topi, the kongoni and he Grant's gazelle respectively, corresponding to the number of sequences with at least one individual of known age. We calculated the difference in Fleiss' κ values between species, two by two for a given age class. We then applied a one sample Student's test on the distribution of the 10,000 differences with α level = 5% to check if it is significantly different from 0.

The results of the comparison of the Fleiss' κ values between species for a given age class are reported here (significant p values are in bold type):

Species compared	**Age class**	**p value**	**CI lower boundary**	**CI upper boundary**	**t statistic**
Topi - Kongoni	< 1 month	**< 0.001**	0.08754	0.08936	189.89
	1 - 6 months	**< 0.001**	0.04046	0.04183	117.28
	6 - 12 months	**< 0.001**	0.13225	0.13500	190.24
	1 - 12 months	**< 0.001**	0.03029	0.03156	94.89
	< 12 months	**< 0.001**	0.06714	0.06832	226.57
	> 12 months	**< 0.001**	-0.37617	-0.37418	-737.73
	adults	**< 0.001**	-0.02906	-0.02641	-41.06
Topi - Grant's gazelle	< 1 month	**< 0.001**	0.17390	0.17617	302.23
	1 - 6 months	**< 0.001**	0.15953	0.16111	397.07
	6 - 12 months	**< 0.001**	0.18003	0.18283	253.83
	1 - 12 months	**< 0.001**	0.08313	0.08453	234.12

	< 12 months	**< 0.001**	0.09347	0.09473	292.15
	> 12 months	**< 0.001**	-0.07374	-0.0719	-155.15
	adults	**< 0.001**	-0.07205	-0.0693	-100.80
Kongoni - Grant's gazelle	< 1 month	**< 0.001**	0.08557	0.08759	168.13
	1 - 6 months	**< 0.001**	0.11858	0.11977	393.43
	6 - 12 months	**< 0.001**	0.04689	0.04871	103.03
	1 - 12 months	**< 0.001**	0.05239	0.05342	199.75
	< 12 months	**< 0.001**	0.02589	0.02685	108.39
	> 12 months	**< 0.001**	0.30152	0.30320	706.03
	adults	**< 0.001**	-0.04361	-0.04227	-125.74

The results of the comparison of the Fleiss' κ values between age classes for a given species are reported here (significant p values are in bold type):

Age classes compared	**Species**	**p value**	**CI lower boundary**	**CI upper boundary**	**t statistic**
< 1 month / 1-6 months	Topi	**< 0.001**	0.06109	0.06301	127.16
	Kongoni	**< 0.001**	0.01413	0.01536	46.93
	Grant's gazelle	**< 0.001**	0.04635	0.04833	93.74
< 1 month / 6-12 months	Topi	**< 0.001**	0.25694	0.25980	354.08
	Kongoni	**< 0.001**	0.30272	0.30437	721.38
	Grant's gazelle	**< 0.001**	0.26369	0.26583	484.89
< 1 month / 1-12 months	Topi	**< 0.001**	0.01931	0.02117	42.63
	Kongoni	**< 0.001**	-0.0379	-0.03667	-118.61
	Grant's gazelle	**< 0.001**	-0.07192	-0.07000	-144.77
< 1 month / < 12 months	Topi	**< 0.001**	-0.06178	-0.05999	-133.34
	Kongoni	**< 0.001**	-0.08221	-0.08099	-262.32
	Grant's gazelle	**< 0.001**	-0.14276	-0.14087	-294.92

< 1 month / > 12 months	Topi	**< 0.001**	0.70058	0.70267	1317.59
	Kongoni	**< 0.001**	0.23715	0.23886	546.53
	Grant's gazelle	**< 0.001**	0.45276	0.45479	877.02
< 1 month / adults	Topi	**< 0.001**	0.19596	0.19887	265.28
	Kongoni	**< 0.001**	0.08056	0.08189	238.15
	Grant's gazelle	**< 0.001**	-0.04931	-0.04728	-93.38
1-6 months / 6-12 months	Topi	**< 0.001**	0.19494	0.19770	279.00
	Kongoni	**< 0.001**	0.28809	0.28950	802.83
	Grant's gazelle	**< 0.001**	0.21660	0.21825	515.13
1-6 months / 1-12 months	Topi	**< 0.001**	-0.04264	-0.04098	-98.36
	Kongoni	**< 0.001**	-0.05246	-0.0516	-235.71
	Grant's gazelle	**< 0.001**	-0.11895	-0.11764	-354.23
1-6 months / < 12 months	Topi	**< 0.001**	-0.12373	-0.12214	-303.89
	Kongoni	**< 0.001**	-0.09678	-0.09592	-440.62
	Grant's gazelle	**< 0.001**	-0.18978	-0.18852	-589.71
1-6 months / > 12 months	Topi	**< 0.001**	0.63861	0.64055	1291.37
	Kongoni	**< 0.001**	0.22254	0.22398	607.57
	Grant's gazelle	**< 0.001**	0.40572	0.40716	1102.75
1-6 months / adults	Topi	**< 0.001**	0.13396	0.13677	188.26
	Kongoni	**< 0.001**	0.06596	0.06700	251.53
	Grant's gazelle	**< 0.001**	-0.09636	-0.0949	-257.31
6-12 months / 1-12 months	Topi	**< 0.001**	-0.23947	-0.23678	-346.80
	Kongoni	**< 0.001**	-0.34152	-0.34014	-968.91
	Grant's gazelle	**< 0.001**	-0.33651	-0.33494	-840.16
6-12 months / < 12 months	Topi	**< 0.001**	-0.32057	-0.31793	-475.15

	Kongoni	**< 0.001**	-0.38584	-0.38446	-1094.11
	Grant's gazelle	**< 0.001**	-0.40734	-0.40582	-1047.05
6-12 months / > 12 months	Topi	**< 0.001**	0.44182	0.44469	605.49
	Kongoni	**< 0.001**	-0.06645	-0.06463	-141.54
	Grant's gazelle	**< 0.001**	0.18816	0.18987	435.70
6-12 months / adults	Topi	**< 0.001**	-0.06273	-0.05917	-67.15
	Kongoni	**< 0.001**	-0.22307	-0.22156	-577.94
	Grant's gazelle	**< 0.001**	-0.31390	-0.31221	-728.07
1-12 months / < 12 months	Topi	**< 0.001**	-0.08188	-0.08037	-210.52
	Kongoni	**< 0.001**	-0.04473	-0.0439	-208.96
	Grant's gazelle	**< 0.001**	-0.07142	-0.07028	-244.31
1-12 months / > 12 months	Topi	**< 0.001**	0.68045	0.68232	1425.68
	Kongoni	**< 0.001**	0.27457	0.27601	747.80
	Grant's gazelle	**< 0.001**	0.52407	0.52541	1531.10
1-12 months / adults	Topi	**< 0.001**	0.17579	0.17857	249.87
	Kongoni	**< 0.001**	0.11801	0.11902	459.96
	Grant's gazelle	**< 0.001**	0.02200	0.02334	66.05
< 12 months / > 12 months	Topi	**< 0.001**	0.76161	0.76341	1653.02
	Kongoni	**< 0.001**	0.31889	0.32032	873.98
	Grant's gazelle	**< 0.001**	0.59494	0.59624	1792.69
< 12 months / adults	Topi	**< 0.001**	0.25694	0.25966	371.90
	Kongoni	**< 0.001**	0.16233	0.16333	641.84
	Grant's gazelle	**< 0.001**	0.09287	0.09417	281.00
> 12 months / adults	Topi	**< 0.001**	-0.50568	-0.50275	-673.85
	Kongoni	**< 0.001**	-0.15755	-0.15601	-399.09
	Grant's gazelle	**< 0.001**	-0.50281	-0.50133	-1322.38

Supporting information 5

Detection of juveniles < 1 month when no other juveniles are present.

Concerning juveniles < 1 month, we developed two kinds of models: one with the complete dataset (see "Material and methods" and "Results"), and another one exclusively with sequences characterized by 1) a perfect agreement between the three trained observers concerning the presence or absence of the juveniles < 1 month, 2) a perfect agreement between the three trained observers concerning the absence of other categories of juveniles. This second model was developed to make sure that the other juvenile age classes did not interfere with our definition of "no juvenile in the sequence" as it is not necessarily the same for trained observers (it means the absence of juveniles < 1 month old) and for the volunteers (it means the absence of "young"). So we could analyse both the extent to which volunteers classification can be used to infer on the presence of juveniles < 1 month on the one hand (model on the complete dataset presented in "Results"), and the ability of the volunteers to detect juveniles < 1 month on the other hand (model on selected dataset presented here, sequences containing juveniles older than one month removed). We fitted the same models as presented in "Material and methods" (Table A).

Table A: Statistics of models investigating the relationship between the proportion of volunteers identifying at least one "young" and the probability of presence of at least one individual < 1 month, assessed by the trained observers on a given sequence for the three species of interest: topi, kongoni and Grant's gazelle (on a selected dataset, see text for details). Best models are in bold. θ = estimated threshold (% of volunteers), QIC = Quasi-likelihood under the Independence model Criterion, in. = intercept, estimates ± standard error and [95% confidence interval].

Age class	Species	Model type	θ	QIC	Quasi-likelihood	Estimates
< 1 month gold	Topi	Null		163.2	-80.61	μ = -0.822 ± 0.190
		Linear		**44.1**	**-18.43**	**μ = -5.378 ± 0.816** **β = 0.116 ± 0.022**
		Piecewise - slope/plateau	80	44.0	-18.78	μ = -5.589 ± 0.844 $\beta 1$ = 0.124 ± 0.020 $\mu 2$ = 0.987 [0.907; 0.998]
		Piecewise - slope/slope	22	44.2	-17.80	μ = -10.768 ± 1.585 $\beta 1$ = 0.288 ± 0.067 $\beta 2$ = 0.097 ± 0.021

Table A: continued.

Age class	Species	Model type	θ	QIC	Quasi-likelihood	Estimates
< 1 month gold	Kongoni	Null		376.5	-187.26	μ = -1.621 ± 0.132
		Linear		100.6	-47.64	μ = -5.370 ± 0.474 β = 0.139 ± 0.016
		Piecewise - slope/plateau	77	100.6	-47.81	μ = -5.440 ± 0.467 $\beta 1$ = 0.142 ± 0.014 $\mu 2$ = 0.996 [0.980; 0.999]
		Piecewise - slope/slope	**14**	**98.1**	**-45.71**	**μ = -10.042 ± 1.889** **$\beta 1$ = 0.415 ± 0.149** **$\beta 2$ = 0.108 ± 0.015**
	Grant's gazelle	Null		166.8	-82.42	μ = -2.714 ± 0.220
		Linear		116.2	-52.88	μ = -4.271 ± 0.389 β = 0.071 ± 0.018
		Piecewise – slope/ plateau	**39**	**88.3**	**-41.58**	**μ = -6.032 ± 0.669** **$\beta 1$ = 0.173 ± 0.022** **$\mu 2$ = 0.670 [0.480; 0.816]**
		Piecewise - slope/slope	39	90.2	-41.33	μ = -5.695 ± 0.852 $\beta 1$ = 0.185 ± 0.027 $\beta 2$ = -0.013 ± 0.017

In the absence of any other juvenile, volunteers are able to detect very precisely the presence or absence of juveniles < 1 month in topi and kongoni (Fig. A). This ability is less clear for Grant's gazelle, as the probability to effectively observe juveniles < 1 month when all the volunteers agree about the presence of juveniles is only 0.670. It seems reasonable to think that one could achieve precise estimation of the presence of very young individuals by asking volunteers to identify two juvenile age classes, such as "juvenile" and "newborn".

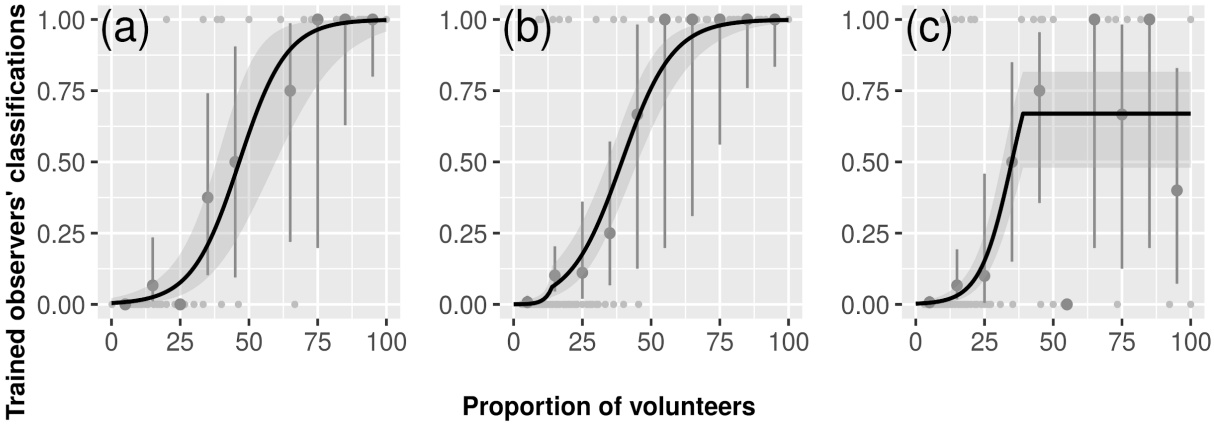


Figure A: relationship, as predicted from the best model (see text for details), between the proportion of volunteers identifying the presence of "young" and the probability of presence of at least one individual < 1 month assessed by the trained observers in a given sequence on a selected dataset (0 < proportion of volunteers identifying "young" ≤ 1, sequences containing juveniles older than one month removed), for the three species of interest: a) topi, b) kongoni and c) Grant's gazelle. Light grey dots represent the probability of presence of at least one individual < 1 month in each sequence assessed by the three trained observers, dark grey dots represent the mean of those probabilities for each 10% volunteers interval, vertical bars represent 95% confidence intervals. Solid line represents predicted values from the best model. Shaded areas represent 95% confidence intervals.

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Chapter 2

How to describe and measure phenology? An investigation on the diversity of metrics using phenology of births in large herbivores

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Abstract

Proposed in 1849 by Charles Morren to depict periodical phenomena governed by seasons, the term "phenology" has spread in many fields of biology, from evolutionary to molecular biology. The wide adoption of the concept of phenology has been associated with the publication of a large number of metrics, with sometimes confusion about what they measure. Here, we aimed to link these metrics to four characteristics of phenology: timing, synchrony, rhythmicity and regularity. From 52 published metrics previously used to quantify phenology of births in large herbivores, we conducted a quantitative analysis based on simulations of normal and non-normal distributions of births (both intra and inter-annual variations). We first compared and classified the metrics using a correlation matrix. Then, we evaluated the ability of each metric to capture the variation of the four phenology characteristics via a sensitivity analysis. We finally scored each metric according to eight criteria we thought were important to describe phenology correctly. The high correlation we found among the metrics corresponding to each of the four characteristics of phenology suggests that such diversity of metrics is all but useful. Additionally, we show that the best metrics are not necessarily the most commonly used, and that simpler is often better. Circular statistics seem particularly suitable to describe the timing and synchrony of births in a wide range of distribution patterns. The level of repeatability of both timing and synchrony is still poorly described, but general non-parametric tests such as Mood and Kolmogorov tests allow a first and easy quantification of this variability across the years. We provide some guidelines and advice to facilitate repeatability and comparison of phenology between studies. We trust our study can facilitate the use of well-defined and robust concepts and metrics in studies of phenology, in the context of climate change for instance.

Keywords: regularity, rhythmicity, seasonality, synchrony, timing, ungulate

Introduction

In 1849, Charles Morren coined the term "phenology" to describe how periodical phenomena such as plant growth and reproduction are governed by the course of seasons (Morren 1849, see also Demarée 2011). With his observations, he opened a new field of research, and almost two centuries later the concept of phenology has become a cornerstone of ecology (Begon *et al.* 1986), used in plant and animal ecology indifferently (Forrest and Miller-Rushing 2010). By describing when particular life-history events (*e.g.,* flowering, parturition) occur in relation to the characteristics or states of the individual (*e.g.,* size, age) as well as to external factors (*e.g.,* photoperiod, predation risk) the concept of phenology is key to understanding the temporal cycles in the life cycle of species (Forrest and Miller-Rushing 2010). Nowadays the term phenology is commonly employed to describe the temporal occurrence of many aspects of a species' biology (*e.g.,* moulting, migration, diapause in animals), but the phenology of reproduction (*e.g.,* Sinclair et la. 2000, Rubenstein and Wikelski 2003, van den Hoff 2020) has attracted most interest. Reproductive phenology is an integral part of life history theory as it is at the heart of inter-generational trade-offs (*i.e.,* between parents and offspring) and is a key factor of the reproductive success and fitness of the individuals (Stearns 1989, Forrest and Miller-Rushing 2010). On the one hand, the time of the year when most births occur is often linked to seasonal variations in food resources so that the flush of food resources matches the energetic needs of breeding, which ultimately improves the reproductive success of parents and the fitness of offspring (Plard *et al.* 2015). On the other hand, the spread of birth dates in a year is supposed to reflect anti-predator strategies to reduce the mortality associated with predation (Darling 1938, Gosling 1969), but also many other social and biological mechanisms (Ims 1990), such as the avoidance of male harassment undergone by the females (Boness *et al.* 1995) or intra-specific competition between offspring (Hodge *et al.* 2011).

In most ecological study cases, measurements and observations of phenology are frequently performed at the population level by characterizing the temporal distribution of biological events (Visser *et al.* 2010). Those rather complex and variable patterns are then reduced to two main components: "timing", which is the date at which the event of interest occurs, and "synchrony", which is the spread of the dates at which the event occurs, *i.e.,* the variability between individuals (Fig. 1). Besides, stimulated by research on the effects of climate change on biodiversity (*e.g.,* Crick and Sparks 1999, Parmesan 2007, Sarkar *et al.* 2019), the question of whether phenology is consistent or varies in time both at individual and population levels has received increased interest in recent years (*e.g.,* Renaud *et al.* 2019). We

therefore need to quantify underappreciated properties of phenology: the consistencies of the timing and synchrony (at the population scale) of the events from one reproductive season to the next. As those characteristics of phenology are not described by specific words yet, we suggest to use "rhythmicity" and "regularity" to describe the consistency of timing and synchrony respectively (Fig. 1), in line with Newstrom's terminology coined for tropical plants (Newstrom *et al.* 1994).

Even if it is simple to grasp at first sight, the concept of phenology nevertheless carries a lot of confusion in literature, both from a semantic and a descriptive point of view (Visser *et al.* 2010). Past studies have explored phenology through the analysis of a huge diversity of mathematical descriptors, many of which remaining specific to one single study. This is problematic because well-defined, comparable and reliable descriptors of the temporal distribution of biological events are key to achieving meaningful comparisons of phenology patterns within or across species. For instance, English and colleagues reassessed the most influential factors of reproductive synchrony in large herbivores from the existing literature, but they had to narrow their original data set because there was no standardized way of measuring and comparing synchrony across the studies (English *et al.* 2012). This large diversity of metrics is further associated with a lack of generally accepted definitions of them or even divergent definitions of the same word (see "seasonality" *sensu* Skinner *et al.* 2002 and Heideman and Utzurrum 2003), which really hampers our ability to make meaningful comparisons (*e.g.,* Ryan *et al.* 2007, Heldstab *et al.* 2018). Because experimental works are logistically challenging or virtually impossible to conduct with large species, the comparison of phenology patterns within a species living in contrasting environments, or across species (Clauss *et al.* 2020) is of major importance to assess the role of explanatory factors accounting for the often marked variability in phenology reported in empirical studies (Rutberg 1987). Such comparative approaches (*sensu* Felsenstein 1985) shed light on the ecological and evolutionary causes shaping the main stages of the life cycle of organisms (Bronson 1989).

In spite of the diversity of approaches to describe phenology, we found only a few attempts comparing phenology metrics to provide advice on which one should be used preferentially according to the context of the study (Moussus *et al.* 2010, Landler *et al.* 2018). Those initiatives are rare, and we currently lack a comprehensive comparison of metrics previously used to characterize phenology and assess the extent to which the different metrics actually capture the desired characteristics of the temporal distribution of events, nor do we have a proper assessment of the sensitivity of those metrics to actual changes in phenology. Here, we propose such a comparison of metrics based on a literature survey of reproductive

phenology in large herbivore species. We focus our overview on the taxonomic group of the large herbivores because it has been studied in many species and at many locations (Rutberg 1987). As a consequence, we expect to find a wide variety of patterns of births, and a wide diversity of metrics associated to describe them in literature. As hinted above, we first clarified and formally defined four main terms describing phenology, built on our knowledge of the literature: timing, synchrony, rhythmicity and regularity. We then conducted a comparative analysis of 52 metrics that have been used to quantify the different characteristics of phenology of births in large herbivores, highlighting their strengths and weaknesses, and offering some guidance on which ones to use preferentially.

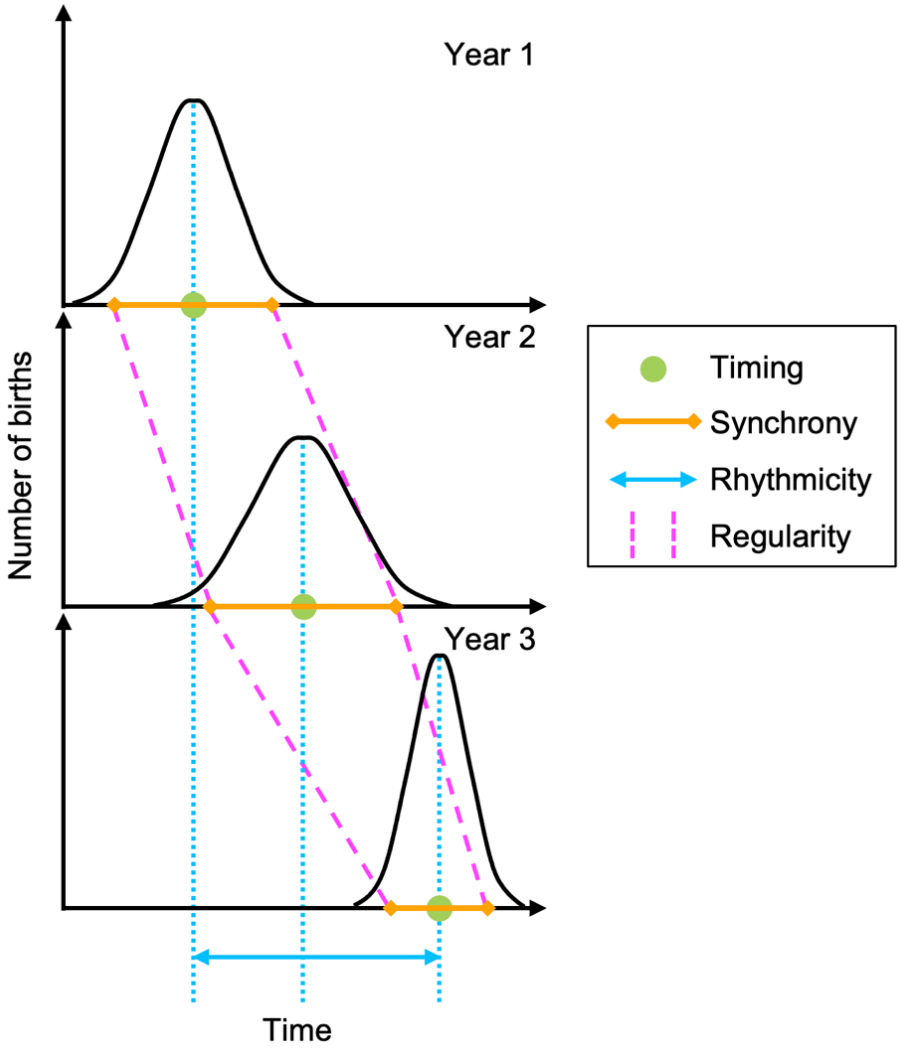

Figure 1: Four characteristics of phenology of births can be explored to fully describe phenology at the population scale: timing, synchrony, rhythmicity and regularity. Timing describes when within the year most births occur, synchrony illustrates whether females tend to give birth at the same time in a population in a given year, rhythmicity defines the consistency of timing between years, regularity refers to the consistency of synchrony between years. Green = timing, orange = synchrony, blue = rhythmicity, pink = regularity.

Materials and methods

We achieved a quantitative comparison of a wide range of metrics used to analyse phenology in six steps. In Step 1, we recorded all metrics employed to measure phenology in a selection of papers that we considered representative of the study of phenology of births in large herbivores. In Step 2, we simulated contrasting phenology by varying independently the four parameters that determine timing, synchrony, rhythmicity and regularity of phenology of births (see details below). In Step 3, we calculated all metrics on the simulated phenology to understand how they compare and what characteristics of phenology they actually measure. In Step 4, we explored the similarities between metrics from a correlation matrix, and identified categories of metrics capturing the same characteristic of phenology. In Step 5, we evaluated the sensitivity of each metric to changes in the estimated parameter. In Step 6, we ranked each metric based on eight criteria that we considered important to identify robust and efficient metrics, but also meaningful from an ecological point of view (see Table 1 for a description of each criterion).

Step 1: Retrieving and coding the different phenology metrics

We opportunistically searched the literature for articles focusing on the distribution of births in large herbivores using keywords such as “phenology”, “timing”, “synchrony”, “seasonality”, “period” or “season”, and using various sources such as search engines and the references in previously found articles. From these articles, published between 1966 and 2019, we recorded the metrics used to describe phenology of births at the population level. We stopped our search once the rate at which we discovered new metrics with additional papers became negligible.

We *a priori* classified each metric into one out of four categories, based on our understanding of the original description and formula of the metric (Fig. 1): (1) *timing* metrics, defining when within the year most births occur, (2) *synchrony* metrics, defining whether females tend to give birth at the same time in a population in a given year, (3) *rhythmicity* metrics, defining the consistency of timing between years, (4) *regularity* metrics, defining the consistency of synchrony between years. In the literature, the term “seasonality” can be used to describe the position of births in the year (*i.e.,* timing, *e.g.,* in Sinclair *et al.* 2000), the duration of birth period (*i.e.,* synchrony, *e.g.,* in Zerbe *et al.* 2012), and even the fact that births occur at the same period of the year every year (*i.e.,* rhythmicity and/or regularity, *e.g.,* in Heideman and Utzurrum 2003). However, this term is initially used to describe the cyclical nature of the environment in a wider range than the study of birth phenology (Visser *et al.* 2010). Thus, it

should be used to describe organisms' phenology only when a direct relationship between periodic environmental phenomena and the cycle of the organism at stake has been demonstrated, which is not always the case in phenology studies. That is why we suggest using the term "seasonality" only to describe the cyclicity of the environment and to prefer neutral terms such as those we introduced in this paper to describe phenology of births: rhythmicity and regularity.

Forty-seven articles (Supporting information 1) presented at least one mathematically-defined phenology metric yielding overall 52 different metrics. We could code all of them in R software (R Core Development Team 2019; except one in Perl, www.perl.org). In order to compare metrics quantitatively, we had to slightly tweak some of them (Supporting information 2).

Step 2: Simulating phenology of births

We simulated phenology of births from statistical distributions with known parameters (Supporting information 3) to assess what characteristic of phenology (timing, synchrony, rhythmicity, regularity) each metric would capture, their sensitivity to changes into these four key characteristics of interest, and the correlation between the 52 metrics. We simulated the distributions of births over a year as most large herbivores breed once a year. This choice does not limit the generality of our results: for species breeding more than once per year (*e.g.,* small species with short gestation length such as dikdik *Rynchotragus (Madoqua) kirki*, Sinclair *et al.* 2000), the same metrics may be applied on sub-periods of time, each displaying only one peak of births.

Each simulated phenology was generated by randomly distributing births in time, following a normal distribution. We distributed n = 1,000 births within a year of 365 days, repeated over 10 years (see why in Material and Methods - Step 3). We changed four parameters independently to modify the distribution of births: the mean day of birth for a given year (*mean*), the standard deviation of the distribution of births for a given year (*sd*), the range over which the mean birth date can vary across years (*Δmean*), and the range over which the standard deviation can vary across years (*Δsd*). Each parameter varied in a range from a minimum to a maximum value and was incremented with a constant step (Supporting information 3). By choosing the value of these parameters, we could simulate changes in the timing, synchrony, rhythmicity and regularity of the phenology of births respectively, and independently. Because the simulated phenology of births relied on random draws, the actual values of parameters in

the simulated distribution of births could differ from the theoretical values used in the simulation algorithm. We used the realized values of the distribution parameters in the following analyses. Note that we replicated the same analyses using non-normal distributions of births (*i.e.,* skewed normal, bimodal, Cauchy, and random distribution) to cover the variety of empirical distributions of births observed in *natura* (Supporting information 4). We performed all simulations using the R software and made the code available on GitHub (see Data availability statement).

Step 3: Computing the phenology metrics from simulated patterns of births

Among the 52 phenology metrics we coded, most applied to a single year, but others required two or more years of data to be computed (see the complete list in Supporting information 2). Because we wanted to compute all 52 metrics, we chose to simulate annual distributions of births over 10 consecutive years by default. For each simulation, we used data from the first year to compute metrics requiring only one year of data (n = 33 metrics), data from the first two years for metrics requiring two years of data (n = 9 metrics), and data from the whole simulation for the other metrics (n = 10 metrics).

Step 4: Comparing the metrics

From the results of Step 3, we computed the global correlation matrix between all pairs of metrics using Pearson correlations. We then identified groups of strongly correlated metrics from the pairwise correlation coefficients and assigned each metrics to one or several of the four characteristics of phenology it was best related. We compared this categorization with our *a priori* classification of the metrics. This step enabled us to check our intuitive classification of the metrics in addition to reveal whether some metrics could incidentally capture several aspects of the distribution of births at once.

Step 5: Estimating the sensitivity of the metrics

For each metric, we performed a sensitivity analysis by quantifying the observed variation of each metric with a fixed variation in the characteristic of phenology it was previously associated with in Step 4. We did so by computing, for each possible pair of simulations within the set of all simulations performed, the proportional difference between the realized values of the phenology parameter of interest of the two simulations, and the proportional difference between the values of the metric of interest of the same two simulations. In each case the proportional

difference was calculated as $[(Value_{max} - Value_{min}) / Value_{min}] * 100$. This formulation allowed us to work with positive values only, as we were interested in the amplitude but not in the direction of the differences. We represented the scaled proportions of variation by centring and scaling the proportions. We standardized the sensitivity of each metric individually to prevent the representation of highly varying metrics from flattening the representation of sparsely varying ones in the heat map representation.

Step 6: Scoring metrics

Finally, because there were too many different metrics, we could not discuss the pros and cons for all of them. We chose instead to provide guidance about the usefulness of the different metrics by scoring them according to a set of eight criteria that we considered as important behaviour for a metric to be relevant (Table 1). We ranked the metrics from 0 (not advised) to 8 (strongly advised) according to the number of criteria they fulfilled. Each criterion could be evaluated independently from the others, except from the first four that should all be met to consider that the metric describes the phenology characteristic *a minima*. The proposed criteria (Table 1) consisted in verifying if 1) the metric varied according to the phenology characteristic it was supposed to measure, 2) the variation of the metric according to the phenology characteristic was monotonous, 3) the relationship with the characteristic of phenology was strong (we evaluated the correlation visually as numerous relationships were not linear), 4) the metric did not saturate within a biologically realistic range of distributions of births. If those four criteria were satisfied, we then evaluated an additional set of four criteria (see Table 1 for details). We considered that suitable metrics were characterized by scores > 6, meaning the first four essential criteria are validated and at least two additional criteria are satisfied. Conversely metrics with scores ≤ 4 (for which the first four essential criteria are not validated) should not be advised.

Table 1: Ordered list of the criteria used to evaluate the relevance of each metric describing phenology of births. Each criterion can be individually fully (score of 1) or partially (score of 0.5) validated or no (score of 0) by each metric. The value for the first four criteria (in bold type) should be > 0 to consider a metric to be possibly worthwhile and evaluate the remaining criteria. The sum of the value obtained for each criterion gives the relevance index of the metric (range between 0 and 8 points).

Criterion	Description	Score
goodness	Actually measures the parameter it is expected to measure	true = 1 false = 0
monotony	Varies monotonically with the value of the phenology parameter it is expected to measure, *i.e.,* the sign of the slope coefficient is constant	true = 1 false = 0
saturation	Does not saturate at the upper or lower boundary in a biological range of values (*e.g.,* if a synchrony metric returned the same value when all births occurred during a period of either one, two or three months for instance, it was considered to saturate within a biologically realistic range of birth distributions because such distributions of births can be found in the wild)	true = 1 false = 0
strength[1]	Is characterized by a strong relationship with the parameter it is expected to measure, *i.e.,* is the scatter plot not too dispersed around the general trend of the relationship between the metric and the phenology characteristic, as an empirical approach of the predictive power	strong relationship = 1 noisy relationship = 0.5 very noisy relationship = 0
normality[2]	Is not based on normality hypothesis	true = 1 better = 0.5 false = 0
origin	Does not depend on the temporal origin set by the investigator	true = 1 false = 0
linearity[3]	Is characterized by a linear relationship with the parameter it is expected to measure	type 1 = 1 type 2 and 3 = 0.5 type 4 = 0
unicity	Gives a unique result	true = 1 false = 0

1 a strong relationship has a very small dispersion of points, a noisy relationship has a small dispersion of points that does not prevent from detecting a trend, a very noisy relationship has a dispersion of points large enough to prevent from detecting any trend, whatever the shape of the relationship (linear, but also logistic or quadratic for instance). 2 better for metrics that does not explicitly need normal distribution but more efficient if satisfied. 3 type 1 is a linear relationship, type 2 is a relationship with two inflexion points (i.e., sigmoid like function), type 3 is a relationship with one inflexion point (e.g., quadratic function), type 4 is a binary relationship.

Results

The mean number of metrics used in each paper was 3.8 ± 2.1 sd (*range* = 1-8). Eleven metrics were *a priori* associated with timing, 25 with synchrony, 10 with rhythmicity and five with regularity (we did not classify one metric because it could be a rhythmicity or regularity metric *a priori*). Those metrics were based on descriptive statistics, circular statistics, statistical tests or statistical modelling such as general linear models. The metrics were either date or duration, count information (*e.g.,* a number of births), binary classification (*i.e.,* if a given condition was satisfied or not), or unitless indices (Supporting information 2). We identified 48 metrics linked to the parameter they were supposed to measure according to our *a priori* classification. Among them, 8 metrics had a detectable relationship with at least one of the three remaining phenology characteristics in addition to the relationship with the nominal phenology characteristic they were supposed to quantify (Supporting information 2 and 5).

The correlation matrix (Step 4) revealed obvious groups of metrics that were highly correlated and thus reflected the same characteristic of phenology (Fig. 2). Five groups were clearly identifiable, representing timing metrics (box 1), synchrony metrics (boxes 2 and 5), rhythmicity metrics (box 3), and regularity metrics (box 4). The two groups of metrics measuring synchrony (boxes 2 and 5) had highly but negatively correlated values (box 6). This was indicative that all metrics of the two groups captured synchrony correctly, but in an opposite way. Three metrics had a particular behaviour and were isolated from the five groups, *i.e.,* they were not clearly associated with any other metric. One metric, "*splcomp*" seemed misclassified *a priori* as it correlated better with synchrony than with regularity metrics. Another metric correlated well both with rhythmicity and regularity metrics ("*diffbgper*").

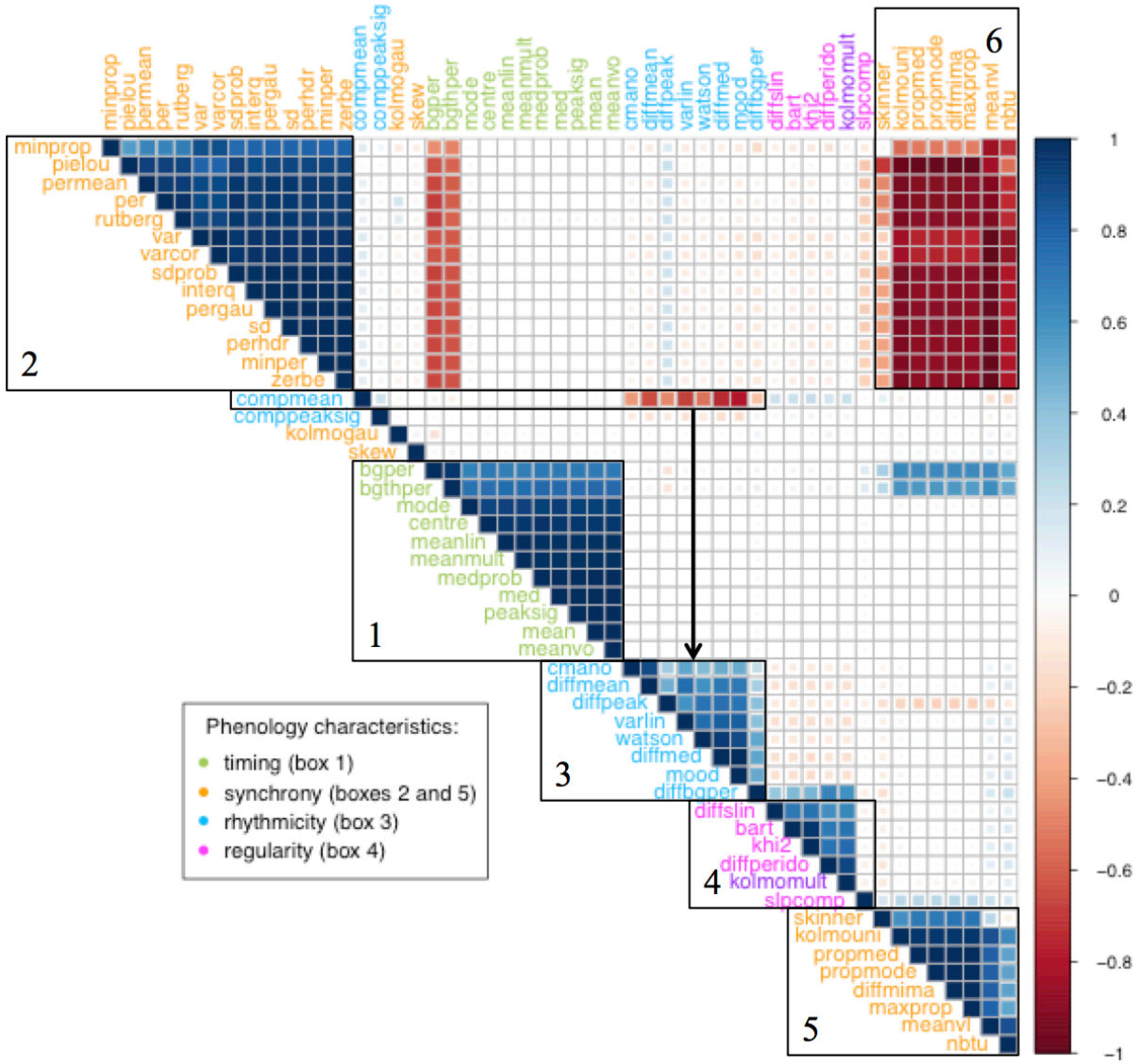

Figure 2: Correlation matrix between all pairs of metrics, using Pearson correlations (n = 51, "rayleigh" removed because no variation observed). It was not possible to classify "kolmomult" a priori in rhythmicity or regularity metrics, as it compares the complete distribution of births between two years. Box 6 highlights the high but negative correlation between the two groups of metrics measuring synchrony (boxes 2 and 5). Green = timing metrics, orange = synchrony metrics, blue = rhythmicity metrics, pink = regularity metrics.

The sensitivity of the metrics to the simulated variation of the phenology characteristics (Step 5) differed markedly between metrics, especially in synchrony and regularity metrics (Fig. 3 and Supporting information 5). The scaled proportion of variation of the metrics according to the proportion of variation of the associated parameters ranged from -1.73 to 3.79 for timing metrics, from -3.81 to 2.01 for synchrony metrics, from -1.62 to 2.01 for rhythmicity metrics and from -1.60 to 1.91 for regularity metrics. The variation of almost all timing, rhythmicity and regularity metrics according to variations of their associated parameter was

highly homogeneous. Synchrony metrics were less homogeneous, certainly due to the fact that those metrics were the most numerous and based on more diverse methods (proportion of variation, integrative indexes or moments of the distribution of births, for instance). The metrics that were isolated in the correlation matrix were clearly visible in the heat maps, characterized by erratic or non-existent variations (*e.g.,* "*skew*", "*compmean*").

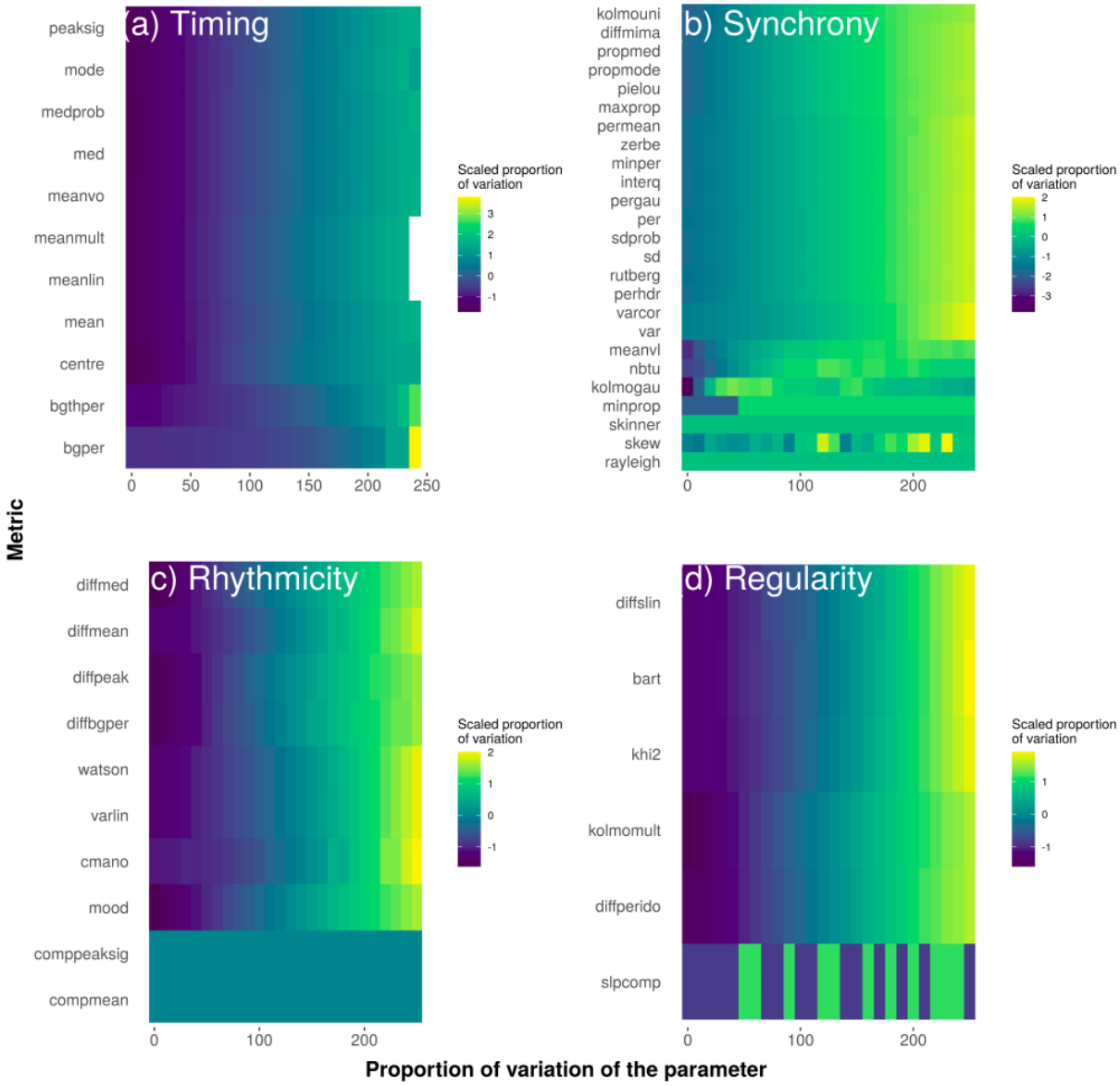

Figure 3: Heat maps representing the (scaled) proportion of variation of the metric in relation to the proportion of variation of the parameter of phenology associated: a) timing metrics according to the mean birth date for a given year (mean, n = 11), b) synchrony metrics according to the standard deviation of the distribution of births for a given year (sd, n = 25), c) rhythmicity metrics according to the range over which the mean birth date can vary across years (Δmean, n = 10), d) regularity metrics according to the range over which the standard deviation of the distribution of births can vary across years (Δsd, n = 6). Colours in the heat maps reflect the amplitude of variation of each metric, scaled within metric. This scaling was done to prevent the large variation of some metrics to obscure the smaller but meaningful variations of other metrics to be visible.

The same analyses conducted on the basis of non-normal distributions led to similar observations in the case of asymmetric distributions (skewed normal, bimodal and Cauchy distributions). The correlation matrices showed similar patterns of correlations between the metrics, and the metrics varied analogously according to the variation of the *mean*, *sd*, *Δmean* and *Δsd* of the distributions for normal and asymmetric distributions either (see Supporting information 4 for a detailed analysis). Nevertheless, it is worth noting that a very limited number of metrics depending on the skewness of the distribution did not perform as well with the normal distribution than with asymmetric distributions. On the opposite, metrics depending on the presence of a period without any birth did not perform as well with non-normal distribution than with a normal distribution. In the case of a random distribution, no clear correlations between metrics nor relationships between the metrics and the four parameters of the distribution were detectable, except for some rare synchrony and timing metrics (Supporting information 4).

The relevance score of the metrics (Step 6) varied between 0 and 7.5, while the possible range of variation was 0-8 (Supporting information 6). The best metrics to quantify timing *via* the analysis of several years reached a score of 7 and were based on the evaluation of the mean: "*meanlin*" which finds the mean birth date thank to a linear model with random effects, and "*meanmult*" which calculates the mean of the mean birth dates (Table 2). The metrics "*bgper*", "*bgthper*" (based on the detection of the beginning of the birth period), "*centre*", "*mean*", "*med*" and "*meanvo*" (respectively based on the estimation of the centre, mean, median and mean vector orientation of the distribution of births) were equally good to quantify timing of births when only one year of data was available, scoring 7 too (Table 2). All metrics used in the description of timing got a score of at least 6, meaning that they were all satisfying. Three metrics stood out from the others to measure synchrony from one year of data only, all of them getting a score of 7.5. Those metrics were "*pielou*" (corresponds to the evenness index), "*meanvl*" (which calculates the mean vector length), and "*kolmouni*" (which compares the distribution of births to a uniform distribution). The metrics "*interq*" (which evaluates the period length gathering a certain percentage of births), "*sd*", "*var*", "*varcor*" (based on the calculation of the variance of the distribution of births) and "*rutberg*" (which evaluates the period length gathering a certain percentage of births from first birth) were also successfully measuring synchrony with a score of at least 6.5 (Table 2). The best metric to quantify rhythmicity was "*diffmed*", evaluating the period length between the median birth dates of two years (*score* = 7). The metrics "*diffbgper*" (which evaluates the period length between the first birth dates of two years), "*mood*" (which compares the median birth dates between two years)

and "*varlin*" (which calculates the variance of the distribution of births of several years thanks to a linear model with random effects) also successfully measured rhythmicity with a score of at least 6.5 (Table 2). There was a very good metric quantifying regularity according to our criteria: "*kolmomult*", which compares two birth distributions (*score* = 7.5). The metric "*diffperiod*" (which evaluates the period length between two birth period durations), also successfully measured regularity with a score of 6.5 (Table 2). Our classification revealed what could be considered as ineffective (*score* = 0, *n* = 5) and poor metrics (*score* ≤ 4, *n* = 13). All criteria were attributed visually by one of us (LT) to each metric. However, the subjectivity was reduced by the use of systematic criteria described at length in Table 1. We invite the reader to consult Supporting information 2 and 5 to make his/her own opinion on the relevance of each metric for his/her own work.

Table 2: List of the best metrics (according to the criteria defined in Table 1) to describe each characteristic of phenology of births (timing, synchrony, rhythmicity, regularity). The preferred metric for each characteristic of phenology for comparative purpose is reported in bold type.

	Best metrics (when one year available)	**Best metrics (when several years available)**
Timing	"*bgper*": first birth date "*bgthper*": first birth date when at least a certain percentage of births have occurred "*centre*": central date between first and last birth dates "*mean*": mean birth date "*med*": median birth date "***meanvo***": mean vector orientation for circular data	"*meanlin*": mean birth date *via* linear model with random effects "*meanmult*": mean of mean birth dates
Synchrony	"*pielou*": evenness index of distribution of births "***meanvl***": mean vector length for circular data "*kolmouni*": compare birth distribution to a uniform distribution "*interq*": period gathering a certain percentage of births based on quantiles "*sd*": standard deviation of distribution of births "*var*": variance of distribution of births "*varcor*": variance of distribution of births corrected by the Sheppard method "*rutberg*": shortest period gathering at least a certain percentage of births since first birth	/

Table 2: Continued.

	Best metrics (when one year available)	**Best metrics (when several years available)**
Rhythmicity	Not applicable	"*diffmed*": period length between median birth dates of two years "*diffbgper*": period length between first birth dates of two years "***mood***": compare median birth dates of two years "*varlin*": variance between years *via* a linear model with random effects
Regularity	Not applicable	"***kolmomult***": compare distributions of births of two years "*diffperiod*": period length between birth period durations (between first and last birth dates) of two years

Discussion

With more than fifty metrics used to describe and analyse the distribution of births in large herbivores since 1966, our survey of the literature clearly illustrates the diversity of approaches, even when focusing on a specific taxonomic group. Although the choice of a metric is most of the time justified to answer a specific ecological question or on statistical grounds, the lack of consensual methods to quantify phenology makes comparisons across species or populations difficult at best, if possible at all. Our simulation study suggests that such a diversity of metrics might be confusing and unnecessary because we could identify a reduced set of simple metrics that work well to measure the different characteristics of phenology.

Many of the metrics we retrieved can be organised into four main categories, each one capturing a particular characteristic of phenology: timing, synchrony, rhythmicity and regularity. Of course, metrics belonging to the same category are not perfectly equivalent and interchangeable (Fig. 2, see also a discussion comparing "*zerbe*" and "*rutberg*" metrics in Zerbe *et al.* 2012). For instance, the correlations between timing metrics range between 0.68 and 1.00. The difference among metrics is more pronounced in the synchrony category with correlations ranging from 0.05 to 1.00 (excluding "*kolmogau*" and "*skew*" metrics that appear as singularities in the correlation matrix, Fig. 2). The way the different characteristics of phenology are measured can lead to dependency between one another, and this could explain

the confusions noticed in literature between timing and synchrony through terms such as "period" or "season" of births. Indeed, several metrics we tested vary not only according to the phenology characteristic they were supposed to measure, but also according to other characteristics of the phenology (n = 8 metrics). For instance, we show a strong correlation between "*bgper*" and "*bgthper*" metrics, which evaluate the start of the birth period (*i.e.,* timing metrics), and the synchrony metrics. This unexpected association between different kinds of metrics arises because the standard deviation of the distribution of births increases, all other parameters being equal, the first births occur earlier (Fig. 2).

We attempted to identify what metrics could be the most suitable for measuring timing, synchrony, regularity and rhythmicity by scoring them according to what we subjectively considered as the main suitable properties. We considered for instance that a good metric should not be restricted to one kind of pattern (*e.g.,* unimodal), and we actually found that less than 25% of the metrics (based on the metrics for which this criterion was evaluated, Supporting information 2) theoretically require unimodal distribution to work well. A workaround for multimodal distributions of births is to separate each reproductive period and conduct independent analyses (*e.g.,* Heideman and Utzurrum 2003 in bats). Besides, we illustrated that only a limited number of metrics really changed their behaviour when applied to non-normal distributions (Supporting information 4). The metric should also not be sensitive to the temporal origin set by the investigator, as each species (and even each population) has different favourable periods for its reproduction cycle (*e.g.,* mountain sheep from desert and alpine habitat, Bunnell 1982). Using the calendar year would be biologically meaningless and might create artificial patterns of births by splitting the distribution at the end of the year. Metrics that do not take into account the temporal origin of the data prevent such limitations and allow an objective comparison. To our knowledge, only five metrics ("*pielou*", "*mode*", "*meanvl*", "*kolmouni*" and "*kolmomult*") meet this assumption. Circular statistics could be prioritized to answer the difficulties linked to the selection of temporal origin, as it is frequently done in primate literature (*e.g.,* Di Bitetti and Janson 2000, see also MacKay *et al.* 2018 in Eastern grey kangaroo *Macropus giganteus*). Notwithstanding such limitations, we could find several metrics that meet our expectations of a good metric for each phenology characteristic (Table 2). Conversely, a few metrics should not be recommended to describe phenology of births like "*diffmean*" (which evaluates the slope of the linear regression describing the evolution of the mean dates of births of several years) or "*nbtu*" (which identifies the duration of the period gathering at least a certain percent of births). Those latter metrics do not capture the changes in the phenology parameter that they are supposed to measure, or present undesirable statistical

properties. For instance, "*nbtu*" varied non-monotonously with the level of synchrony of the birth phenology. Another one like "*per*" (which identifies the duration between first and last birth) plateaued for a range of biologically realistic values limiting its use in a wide range of ecological conditions (Supporting information 5).

Overall, some phenology characteristics have been more consistently evaluated across studies, a fact illustrated by the number of metrics of each category used in more than two papers (Supporting information 7). If timing and synchrony of births are the easiest and most frequent characteristics of phenology estimated and compared, only a handful of metrics evaluates rhythmicity and regularity of the phenology of births across the years, and even less are used more than twice ($n = 2$ and 0 metrics respectively). This gap might reflect the difficulty in acquiring the adequate data. Indeed, robust analysis of rhythmicity and regularity requires many years of data, which may not be available as phenology data collection is costly and time-consuming (Kharouba and Wolkovich 2020). Moreover, scientists are less interested in timing and synchrony consistency *per se* than in the relationship between timing and synchrony, and ecological or environmental factors. Instead of measuring the consistency of timing and synchrony *per se* across the years, they assess how the timing and synchrony changes with temperature, rainfall or spring snow cover for instance (Paoli *et al.* 2018). In any case, our study makes it clear that the currently available metrics are seldom and only moderately correlated, particularly in the context on non-normal distributions of births (Supporting information 4). Capturing the temporal variation of phenology across years appears difficult and requires thoughtful selection and interpretation of the used metric. In the context of climate change, there is an urgent need to develop statistical tools for measuring regularity and rhythmicity, to test the hypothetical responses of phenology to changing climate and predation regimes, for instance. Cosinor and Fourier analyses can help detecting long-term trends and the phenology departure from such trends for example, but require a large amount of data (Cancho-Candela *et al.* 2007).

The past development of so many metrics to quantify phenology likely arose from the need to describe the large diversity of birth distribution documented across species and populations (Bronson 1989). For instance, the wildebeest *Connochaetes taurinus* have very synchronous and normal-like distribution of births (Estes 1976). At the other extreme, the distribution of births of giraffe *Giraffa camelopardalis* is quite unpredictable and spread out over the course of the year (Sinclair *et al.* 2000). Offspring's survival depends on numerous environmental, biotic and even social factors, and so does the shape of the distribution of births at the population scale (Festa-Bianchet 1988). Besides, reproductive females face their own

constraints, such as failure to conceive during the first oestrous because of a degraded body condition (Guinness *et al.* 1978). Conception failure may then disrupt the general trend of the population, and contributes to the diversity of phenology of births encountered in the wild.

We show that the assumption of a normal distribution or another bell-shaped (asymmetric or not) distribution mimicking those found in *natura* (*e.g.,* skewed normal, bimodal or Cauchy distribution) has little consequences on our conclusions (Supporting information 4). The conclusion differs, however, when no clear structure in the timing of births, as often encountered in some populations of large herbivores living in the southern hemisphere (Sinclair *et al.* 2000). In this case most metrics give inconsistent and unreliable results (Supporting information 4) because beyond the heterogeneity of results provided by metrics measuring the same phenology characteristic for such patterns, describing them using common metrics is simply not appropriate. When births occur year round, the timing and rhythmicity are meaningless as they cannot reduce to one or two summarizing statistics. Using evenness indexes such as "*pielou*" could provide a quantification of at least the heterogeneity of such phenology. In the context of a comparative study with mainly non-random distributions, we recommend using "*meanvo*" to describe timing and "*meanvl*" synchrony respectively, because both are among the best metrics of their category, and are not influenced by temporal origin. Finally, we recommend using the underused "*mood*" (which compares the median birth dates, a better descriptor than the first birth) to describe rhythmicity and "*kolmomult*" to describe regularity (see Table 2 and Supporting information 2 for a description of those metrics). Being non-parametric tests, they are applicable in wide range of distributions as frequently observed in large herbivores populations.

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Supporting Information

Supporting information 1

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Supporting information 2

Detailed description of the metrics extracted from phenology of births in large herbivore literature. The description of each metric (*e.g.,* characteristic of phenology associated, number of years it requires to be implemented, null hypothesis tested if this is the case) are provided. The details of the score obtained by each metric for each criterion listed in Table 1 are provided too.

Column "Mat&Met ms - Adjustments":

(*i*) when more than one value was possibly returned by the function, we retained only one value according to a predefined rule. For instance, for metrics returning the dates of the peaks in the distribution of births (n = 2 metrics), we only kept the date of the first peak if more than one peak was detected; (*ii*) when the metric was a boolean (true/false) variable based on the significance of a statistical test (n = 9 metrics), we used the value of the test statistics as output metric, thereby allowing us to investigate how the statistics was influenced by the value of phenological parameters; (*iii*) when the metric was boolean but not based on a statistical test (n = 4 metrics), we coded its value as binary variable taking a "1" when the test was significant or "0" when not significant at the alpha = 0.05 level; (*iv*) when the metric could take both positive and negative values representing the direction of a deviation such as the skewness (n = 2 metrics), we used the absolute value as we were interested in the amplitude and not in the direction of the deviation. One metric ("*khi2*" metric) could not be used for some simulations (1.5 % of the simulations) because the range of birth dates was sometimes too small to run the function associated to this metric.

Metric	Theoretical phenology characteristic associated	Observed phenology characteristic associated	Application period	Vary according to more than one characteristic	Unit	Lower bound	Upper bound
bart	regularity	regularity	several cycles	F	T/F + coef	F	T
bgper	timing	timing+	one cycle	T	date	1	365
bgthper	timing	timing+	one cycle	T	date	1	365
centre	timing	timing	one cycle	F	date	1	365
cmano	rhythmicity	rhythmicity	several cycles	F	T/F + coef	F	T
compmean	rhythmicity	rhythmicity	two cycles	F	T/F	F	T
comppeaksig	rhythmicity	none	two cycles	F	T/F	F	T
diffbgper	rhythmicity	rhythmicity+	two cycles	T	duration	0	364
diffmean	rhythmicity	rhythmicity	several cycles	F	duration	"-Inf"	"+Inf"
diffmed	rhythmicity	rhythmicity+	two cycles	T	duration	0	364
diffmima	synchrony	synchrony	one cycle	F	count	0	100
diffpeak	rhythmicity	rhythmicity+	two cycles	T	duration	0	364
diffperiod	regularity	regularity	two cycles	F	duration	0	364
diffslin	regularity	regularity+	several cycles	T	duration	"-Inf"	"+Inf"
interq	synchrony	synchrony	one cycle	F	duration	1	365
khi2	regularity	regularity	several cycles	F	T/F + coef	F	T
kolmogau	synchrony	synchrony	one cycle	F	T/F + coef	F	T
kolmomult	rhythmicity - regularity	regularity+	two cycles	T	T/F + coef	F	T
kolmouni	synchrony	synchrony	one cycle	F	T/F + coef	F	T
maxprop	synchrony	synchrony	one cycle	F	count	>0	100
mean	timing	timing	one cycle	F	date	1	365
meanlin	timing	timing	several cycles	F	date	1	365
meanmult	timing	timing	several cycles	F	date	1	365
meanvl	synchrony	synchrony	one cycle	F	unitless	0	1
meanvo	timing	timing	one cycle	F	date_radian	0	6,28
med	timing	timing	one cycle	F	date	1	365
medprob	timing	timing	one cycle	F	date	1	365
minper	synchrony	synchrony	one cycle	F	duration	1	365
minprop	synchrony	synchrony	one cycle	F	count	>0	100
mode	timing	timing	one cycle	F	date	1	365
mood	rhythmicity	rhythmicity	two cycles	F	T/F + coef	F	T
nbtu	synchrony	synchrony	one cycle	F	duration	1	365
peaksig	timing	timing	one cycle	F	date	1	365
per	synchrony	synchrony	one cycle	F	duration	1	365
pergau	synchrony	synchrony	one cycle	F	duration	1	365
perhdr	synchrony	synchrony	one cycle	F	duration	1	365
permean	synchrony	synchrony	several cycles	F	duration	1	365
pielou	synchrony	synchrony	one cycle	F	unitless	0	1
propmed	synchrony	synchrony	one cycle	F	count	>0	100
propmode	synchrony	synchrony	one cycle	F	count	>0	100
rayleigh	synchrony	none	one cycle	F	T/F + coef	F	T
rutberg	synchrony	synchrony	one cycle	F	duration	1	365
varlin	rhythmicity	rhythmicity+	several cycles	T	duration	0	"+Inf"
skew	synchrony	none	one cycle	F	unitless	"-Inf"	"+Inf"
skinner	synchrony	synchrony	one cycle	F	T/F	F	T
slpcomp	regularity	synchrony	several cycles	F	T/F	F	T
sd	synchrony	synchrony	one cycle	F	duration	0	"+Inf"
sdprob	synchrony	synchrony	one cycle	F	duration	0	"+Inf"
var	synchrony	synchrony	one cycle	F	duration	0	"+Inf"
varcor	synchrony	synchrony	one cycle	F	duration	0	"+Inf"
watson	rhythmicity	rhythmicity	two cycles	F	T/F + coef	F	T
zerbe	synchrony	synchrony	one cycle	F	duration	1	365

Metric	Description
bart	compare variances of birth distributions
bgper	find first birth date
bgthper	find first birth date when at least x percent of births have occurred
centre	find central date between first and last birth dates
cmano	compare mean birth dates between several reproductive cycles thanks to one way anova
compmean	compare mean birth dates between two reproductive cycles
comppeaksig	compare date of inflection point of birth distribution between two reproductive cycles
diffbgper	evaluate duration between first birth dates of two reproductive cycles
diffmean	evaluate slope coefficient of linear model describing distribution of mean birth dates of several reproductive cycles
diffmed	evaluate duration between median birth dates of two reproductive cycles
diffmima	evaluate difference between "maxprop" and "minprop" metrics
diffpeak	evaluate duration between mode birth dates of two reproductive cycles
diffperiod	evaluate difference of duration between birth period duration (period between first and last birth dates) of two reproductive cycles
diffslin	evaluate slope coefficient of linear model describing distribution of "pergau" metric of several reproductive cycles
interq	find period gathering x percent of births based on quantiles
khi2	compare distribution of proportion of births around median birth date of several reproductive cycles to a uniform distribution
kolmogau	compare birth distribution to a gaussian distribution
kolmomult	compare birth distribution between two reproductive cycles
kolmouni	compare birth distribution to a uniform distribution
maxprop	evaluate maximum proportion of births for a given duration
mean	find mean birth date
meanlin	find mean birth date thanks to linear model with random effects
meanmult	calculate mean of mean birth dates
meanvl	evaluate mean vector length (circular statistics)
meanvo	evaluate mean vector orientation (circular statistics)
med	find median birth date
medprob	evaluate median birth date thanks to probit analysis
minper	evaluate shortest period gathering x percent of births
minprop	evaluate proportion of births occurring during the consecutive period gathering the less births
mode	find mode birth date
mood	compare median birth dates between two reproductive cycles
nbtu	find duration gathering at least x percent of the births
peaksig	find inflection point based on logistic regression describing cumulative births
per	calculate duration between first and last birth
pergau	calculate 2*2*standard deviation of birth distribution
perhdr	evaluate duration gathering x percent of births thanks to high density regions
permean	evaluate mean duration between first and last births
pielou	evaluate evenness index
propmed	evaluate proportion of births occurring around median birth date
propmode	evaluate proportion of births occurring around mode birth date
rayleigh	compare birth distribution to a uniform distribution (alternative hypothesis: unimodal distribution)
rutberg	evaluate shortest period gathering at least x percent of births since first birth
varlin	calculate inter-reproductive cycles variance thanks to linear model with random effects
skew	evaluate skewness of birth distribution
skinner	evaluate presence or absence of a period of a given duration gathering x percent of births
slpcomp	compare slope coefficients of linear models describing birth distributions after transformation
sd	calculate standard deviation of birth distribution
sdprob	calculate standard deviation of birth distribution based on probit analysis
var	calculate variance of birth distribution
varcor	calculate variance of birth distribution corrected by the Sheppard method
watson	compare mean birth dates between two reproductive cycles
zerbe	find shortest period gathering x percent of births around mode birth date

Metric	Tested hypothesis
bart	Variances of the birth distributions are similar
bgper	
bgthper	
centre	
cmano	Median birth dates are similar
compmean	Confidence intervals of mean birth dates overlap
comppeaksig	Confidence intervals of inflection points overlap
diffbgper	
diffmean	
diffmed	
diffmima	
diffpeak	
diffperiod	
diffslin	
interq	
khi2	Distribution of birth proportions around median birth date follows a uniform distribution
kolmogau	Birth distribution follows a normal distribution
kolmomult	Birth distribution similar for both reproduction cycles
kolmouni	Birth distribution follows a uniform distribution
maxprop	
mean	
meanlin	
meanmult	
meanvl	
meanvo	
med	
medprob	
minper	
minprop	
mode	
mood	Median birth dates are similar
nbtu	
peaksig	
per	
pergau	
perhdr	
permean	
pielou	
propmed	
propmode	
rayleigh	Birth distribution follows a random distribution
rutberg	
varlin	
skew	
skinner	At least one period of x days gathering y percents of births
slpcomp	Slopes of the linear regressions of the number of births according to time are similar
sd	
sdprob	
var	
varcor	
watson	Mean birth dates are similar
zerbe	

	1-Goodness	2-Monotony	3-Saturation	4-Strength	5-Normality	6-Origin	7-Linearity	8-Unicity
Metric	Good characteristic	Monotony	Saturate	Relation strength	Based on normal like distribution	Temporal origin importance	Relation shape	Nb of output
bart	T	T	F	noisy	T	T	Type 2	one
bgper	T	T	F	clear	F	T	Type 1	one
bgthper	T	T	F	clear	F	T	Type 1	one
centre	T	T	F	clear	F	T	Type 1	one
cmano	T	T	T					
compmean	T	T	T					
comppeaksig	F							
diffbgper	T	T	F	noisy	F	T	Type 1	one
diffmean	T	T	T					
diffmed	T	T	F	clear	F	T	Type 1	one
diffmima	T	T	T					
diffpeak	T	T	F	noisy	better	T	Type 1	several
diffperiod	T	T	F	noisy	F	T	Type1	one
diffslin	T	T	T					
interq	T	T	F	clear	F	T	Type 1	one
khi2	T	T	F	noisy	F	T	Type 3	one
kolmogau	T	T	T					
kolmomult	T	T	F	noisy	F	F	Type 1	one
kolmouni	T	T	F	clear	F	F	Type 3	one
maxprop	T	T	T					
mean	T	T	F	clear	F	T	Type 1	one
meanlin	T	T	F	clear	F	T	Type 1	one
meanmult	T	T	F	clear	F	T	Type 1	one
meanvl	T	T	F	clear	F	F	Type 3	one
meanvo	T	T	F	clear	F	T	Type 1	one
med	T	T	F	clear	F	T	Type 1	one
medprob	T	T	F	clear	T	T	Type 1	one
minper	T	T	F	clear	F	T	Type 1	several
minprop	T	T	T					
mode	T	T	F	noisy	better	F	Type 1	several
mood	T	T	F	clear	F	T	Type 3	one
nbtu	T	F						
peaksig	T	T	F	clear	T	T	Type 1	one
per	T	T	T					
pergau	T	T	F	clear	T	T	Type 1	one
perhdr	T	T	F	clear	better	T	Type 1	several
permean	T	T	T					
pielou	T	T	F	clear	F	F	Type 3	one
propmed	T	T	T					
propmode	T	T	T					
rayleigh	F							
rutberg	T	T	F	noisy	F	T	Type 1	one
varlin	T	T	F	clear	F	T	Type 3	one
skew	F							
skinner	T	T	T					
slpcomp	F							
sd	T	T	F	clear	F	T	Type 1	one
sdprob	T	T	F	clear	T	T	Type 1	one
var	T	T	F	clear	F	T	Type 3	one
varcor	T	T	F	clear	F	T	Type 3	one
watson	T	T	F	clear	T	T	Type 3	one
zerbe	T	T	F	clear	F	T	Type 1	several

	Discu	Mat&Met	Mat&Met	Wrong metrics	Not advisable metrics	Other metrics	Highly advised metrics
Metric	Score	Adjustments	NA output	score =0	score >0 & <=4	score >4 & <=6	score >6
bart	5	ii	F			1	
bgper	7		F				1
bgthper	7		F				1
centre	7		F				1
cmano	2	ii	F		1		
compmean	2	iii	F		1		
comppeaksig	0	iii	F	1			
diffbgper	6,5		F				1
diffmean	2		F		1		
diffmed	7		F				1
diffmima	2		F		1		
diffpeak	5		F			1	
diffperiod	6,5		F				1
diffslin	2		F		1		
interq	7		F				1
khi2	6	ii	T			1	
kolmogau	2	ii	F	1			
kolmomult	7,5	ii	F				1
kolmouni	7,5	ii	F				1
maxprop	2		F		1		
mean	7		F				1
meanlin	7		F				1
meanmult	7		F				1
meanvl	7,5		F				1
meanvo	7		F				1
med	7		F				1
medprob	6		F			1	
minper	6		F			1	
minprop	2		F		1		
mode	6	i	F			1	
mood	6,5	ii - iv	F				1
nbtu	1		F		1		
peaksig	6		F			1	
per	2		F		1		
pergau	6		F			1	
perhdr	5,5		F			1	
permean	2		F		1		
pielou	7,5		F				1
propmed	2		F		1		
propmode	2	i	F		1		
rayleigh	0	ii	F	1			
rutberg	6,5		F				1
varlin	6,5		F				1
skew	0	iv	F	1			
skinner	2	iii	F		1		
slpcomp	0	iii	F	1			
sd	7		F				1
sdprob	6		F			1	
var	6,5		F				1
varcor	6,5		F				1
watson	5,5	ii	F			1	
zerbe	6		T			1	

Supporting information 3

Parameters used in the simulation of phenology of births and default parameters used to implement the phenological metrics.

Table S3-1: Ranges of the four parameters varying in the simulated phenology of births: mean birth date for a given year, standard deviation of the birth distribution for a given year, range over which the mean birth date can vary across years, range over which the standard deviation can vary across years.

Characteristic of phenology	**Observed parameter**	**Minimum value**	**Maximum value**	**Increment**	**Nb of values**	**Nb of repetitions**	**Total nb of simulations**
Timing	mean	85	283	4	50	50	2500
Synchrony	standard deviation (sd)	1	75	1.5	50	50	2500
Rhythmicity	Δmean	10	100	10	10	250	2500
Regularity	Δsd	3	40	4	10	250	2500

Table S3-2: Default parameters for the metrics, selected according to the most common practice in the literature of phenology of births in large herbivores.

Parameter	**Value selected**	**Reference**
Minimum percentage of births to consider that births are synchronous	80%	Rutberg 1987
First quantile of the distribution of births (to evaluate births synchrony)	25%	Gaillard *et al.* 1993
Last quantile of the distribution of births (to evaluate births synchrony)	75%	Gaillard *et al.* 1993
Minimum percentage of births to consider that births are synchronous ("*nbtu*" metric)	1%	Moe *et al.* 2007
Birth should be accounted for only if they are distributed in consecutive days	FALSE	/
Number of boots for simulation procedures	1000	/
Transformation of the data	NONE	/
Confidence intervals	95%	/
Period to consider that births are synchronous	Mean theoretical standard deviation of all the 2500 patterns simulated for which standard deviation varies	/

Because the implementation of a few metrics relied on the validation or invalidation of *a priori* condition (*e.g.,* "at least a certain percentage of births occurs during a given period" to determine whether or not births are synchronous), we selected the most commonly used setting for that particular metric according to what we encountered in the literature or settings as general as possible to suit a large range of phenology of births.

Supporting information 4

Evaluation of phenology metrics in scenarios of non-normal distribution of births.

Introduction

In the main text, we chose to base our simulations on a normal distribution of births for biological and methodological considerations (see Materials and Methods section). Normally distributed dates of birth were reported for roe deer *Capreolus capreolus* (Gaillard *et al.* 1993) and wildebeest *Connochaetes taurinus* for instance (Sinclair *et al.* 2000). However, the distribution of births of some species is not necessarily normal. Here, we replicated our analyses on the metrics with additional distributions of births previously reported in the literature. We identified four scenarios (Fig. S4-1):

1) a **skewed normal distribution**, which would better approximate distributions of births characterized by numerous early births and fewer late births. Such asymmetric distributions of dates of birth were documented for warthog *Phacochoerus aethiopicus* (Sinclair *et al.* 2000), or bighorn sheep *Ovis canadensis* (Festa-Bianchet 1988) for instance;

2) a **bimodal distribution with two close peaks**, which would better approximate distributions of births characterized by a main peak closely followed by a second one, often smaller. Such distributions could arise from second attempts to breed for females whose first attempt failed (*e.g.,* because fertilization failed at the first oestrus). Examples of species displaying such a bimodal distribution of dates of birth are the impala *Aepyceros melampus* (Anderson 1975) or the red deer *Cervus elaphus* (Guinness *et al.* 1978);

3) a **Cauchy distribution**, which represents a bell-shape distribution of births with fat tails. Even if such distribution looks like a normal distribution at first glance, it is however characterized by the existence of few births occurring all year long in addition to the main delimited peak. The distribution of births of zebra *Equus burchelli böhmi* (Leuthold and Leuthold 1975) or Grant's gazelle *Gazella granti* (Sinclair *et al.* 2000) match with this theoretical distribution;

4) a **random distribution** whereby births can occur anytime in the year, because conditions are always favourable, for instance. Giraffe *Giraffa camelopardalis* (Sinclair *et al.* 2000) and waterbuck *Kobus ellipsiprymnus* (Leuthold and Leuthold 1975) can give birth all year round.

Materials and Methods

Here, we evaluated the behaviour of each metric presented in the main text and in Supporting information 2, according to the four characteristics of phenology (timing, synchrony, rhythmicity and regularity). We replicated the methodology described in Materials and Methods section of the main text, Steps 2 to 4. Each simulated phenology of births was generated following one of the four distributions presented above by distributing approx. 1,000 births within a year of 365 days, replicated over 10 years (Step 2). According to the distribution, we fixed specific parameters and we changed our four parameters of interest independently (Table S4-1) to illustrate variations of: *i*) the timing (*i.e.,* mean day of birth for a given year), *ii*) the synchrony (*i.e.,* standard deviation of the distribution of births for a given year), *iii*) the rhythmicity (*i.e.,* size of the range over which the mean birth date can vary across years), and *iv*) the regularity (*i.e.,* size of the range over which the standard deviation can vary across years). Each of those parameters varied in a range from a minimum to a maximum value and was incremented with a constant step. We then computed the metrics from each simulated phenology following Step 3. We finally produced the global correlation matrix between all pairs of metrics, using Pearson correlations, for each distribution (Step 4).

We compared the results obtained using the above-described distributions with those obtained when using a normal distribution. To do so, for each metric, we (1) extracted the correlation coefficients between this metric and the others while using a normal distribution, (2) did the same with correlation values obtained when using other distributions, and (3) fitted a linear model between values obtained in (2) and those obtained in (1), thereby testing to what extent values obtained using non-normal distributions could be predicted from those obtained using normal distributions. We used the coefficient of determination R^2 as measure of the fit. A high R^2 indicated that the correlation between metrics was not greatly affected by the choice of the distribution of births.

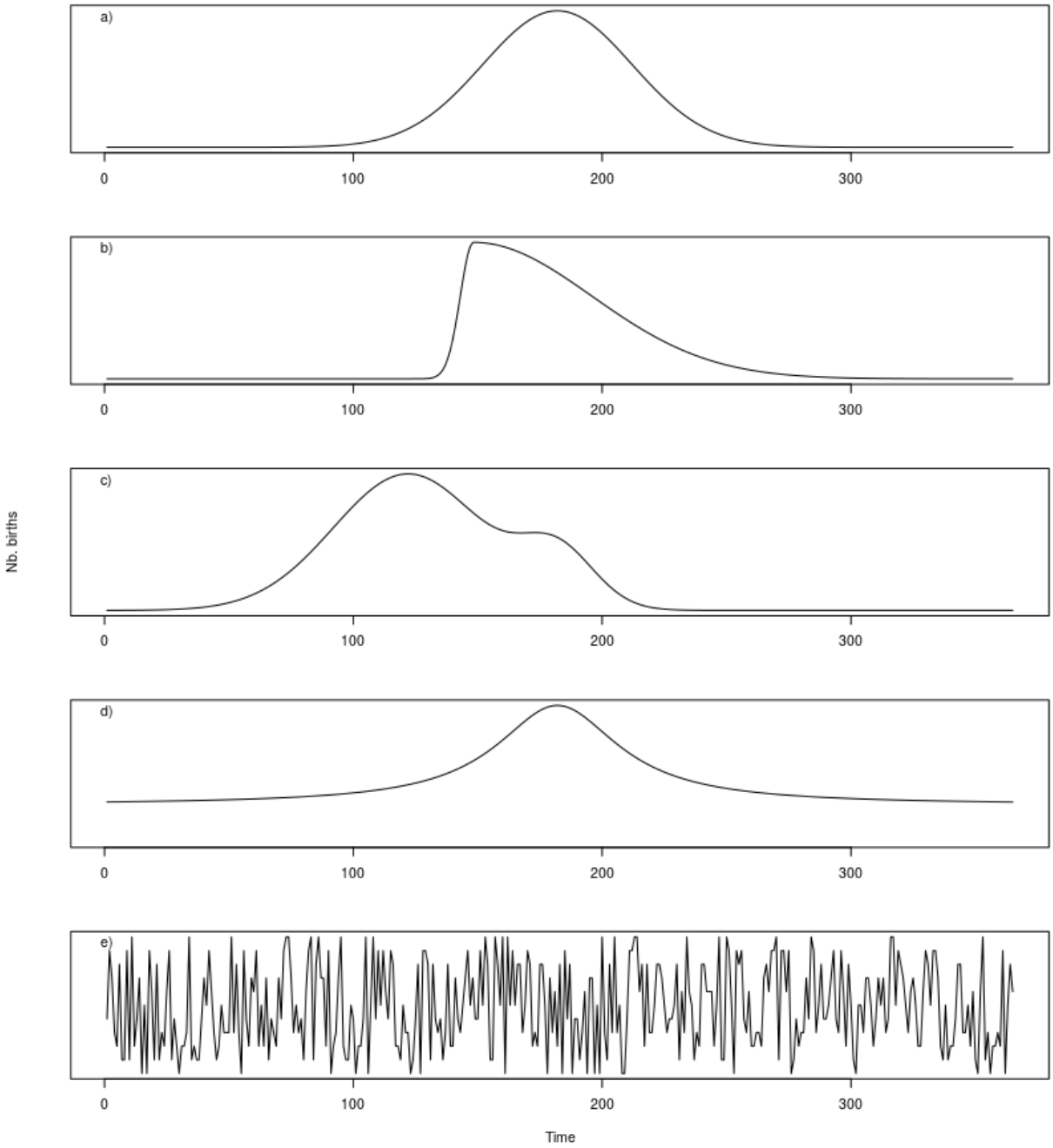


Figure S4-1: theoretical distributions that could illustrate phenology of births of large herbivore species in natura: a) normal distribution, b) skewed normal distribution, c) bimodal distribution with two close peaks, d) Cauchy distribution, e) random distribution.

Table S4-1: Values of the parameters used in the simulated phenology of births following the four scenarios (skew normal distribution, bimodal distribution with two closed peaks, Cauchy distribution, random distribution). For the variable parameters (mean, standard deviation, range of variation of both parameters), 10 different values were used, with 10 repetitions each time, leading to 100 simulations per unique combination of parameters.

Distribution	Characteristic of phenology	Observed parameter	Default value	Minimum value	Maximum value	Incre-ment
Skewed normal	Timing	mean	182	90	270	20
	Synchrony	standard deviation (sd)	30	2	74	8
	Rhythmicity	Δmean	0	10	100	10
	Regularity	Δsd	0	5	41	4
	Skewness	skew	3.5			
Bimodal	Timing	mean	122	90	225	15
	Synchrony	sd	30	10	37	3
	Rhythmicity	Δmean	0	5	50	5
	Regularity	Δsd	0	3	30	3
	Distance between main and second peak	Δmean/mean2	60			
	Synchrony second peak	sd2	15			
	Proportion of births in main peak	pb1	0.75			
Cauchy	Timing	mean	182	90	270	20
	Synchrony	sd	30	2	74	8
	Rhythmicity	Δmean	0	10	100	10
	Regularity	Δsd	0	5	41	4
Random	Maximum number of births per day	max_{nb}	5			

Results

Most of the relationships between the correlation coefficients based on the skewed normal, bimodal or Cauchy distributions and the correlation coefficients based on the normal distribution showed a $R^2 > 0.75$ (96 %, 71 % and 80 % of the metrics for the skewed normal, bimodal and Cauchy distributions respectively, Table S4-2). Similarly, less than 6 % of the relationships showed a $R^2 < 0.25$ for those three distributions. Although the results were generally congruent with those we reported when using the normal distribution as the baseline distribution of births (compare Fig. 2 in the main text and Fig. S4-2, a), b) and c)), some metrics measuring the same characteristic of phenology in the context of a normal distribution were

less correlated when applied to non-normal distribution of dates of birth. For instance, "*diffpeak*" evaluates the duration between the mode birth dates of two years. Depending on whether the mode is located in the first or the second peak in each year, the difference returned by "*diffpeak*" can vary in the bimodal distribution. Also, "*rutberg*", "*diffperiod*", "*bgper*" and "*bgthper*" suffered from the absence of real break in the Cauchy distribution. All these metrics rely on the detection of the beginning of a definite period of births so the absence of any period with no birth limits their relevance. To the contrary, some metrics do better when applied to the three asymmetrical patterns of births. This is the case for "*skew*", which measures the skewness of the distribution, and "*kolmogau*", which compares the distribution of births to a normal distribution. The two metrics correlate with the other synchrony metrics for those three distributions better than for the normal distribution. Indeed, "*skew*" detects the skewness of a distribution, a feature existing in the three distributions but not in the normal one. "*kolmogau*" detects patterns departing from the normal distribution in the three other scenarios.

To the contrary, the random distribution of births produced very different results from all the other distributions (Fig. S4-2, d)). None of the relationships between the correlation coefficients for the random distribution and the correlation coefficients based on the normal distribution had a $R^2 > 0.75$, and 67 % had a $R^2 < 0.50$ (Table S4-2). Some synchrony and timing metrics remains highly correlated, mainly because births are quite consistent through the year, such as the mean date of births ("*mean*") or the variance of the distribution of births ("*var*"), but it is statistically and biologically meaningless to characterize such distribution by its mean or variance though.

Figure S4-2: Correlation matrices between all pairs of metrics using Pearson correlations based on four scenarios: a) skewed normal distribution, b) bimodal distribution with two close peaks, c) Cauchy distribution, d) random distribution. It was not possible to classify "kolmomult" a priori in rhythmicity or regularity metrics, as it compares the complete distribution of births between two years. Green = timing metrics, orange = synchrony metrics, blue = rhythmicity metrics, pink = regularity metrics. When the value of a given metric was constant for a given distributions, it was not possible to assess the coefficients of correlation (reported in grey in the matrices).

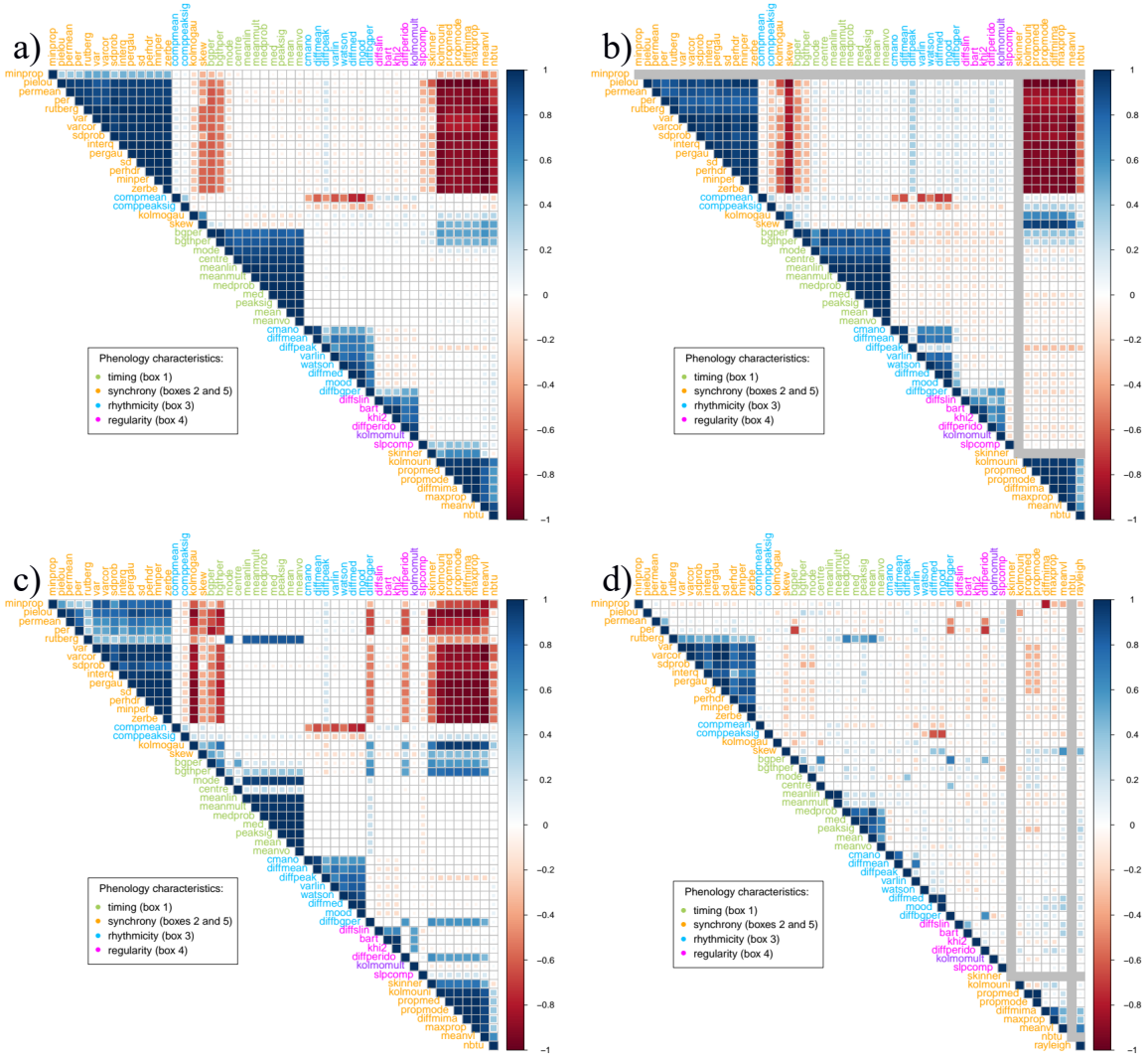


Table S4-2: Comparison of the coefficients of correlation between all pairs of metrics based on the normal distribution and those based on the other distributions (skew normal distribution, distribution with two closed peaks, Cauchy distribution and random distribution), using the coefficient of determination of the linear relationship. When the value of a given metric was constant either for the normal or the non-normal distributions, it was not possible to assess the coefficients of correlation, so the linear relationship was not explored (reported as "not applicable" in the table).

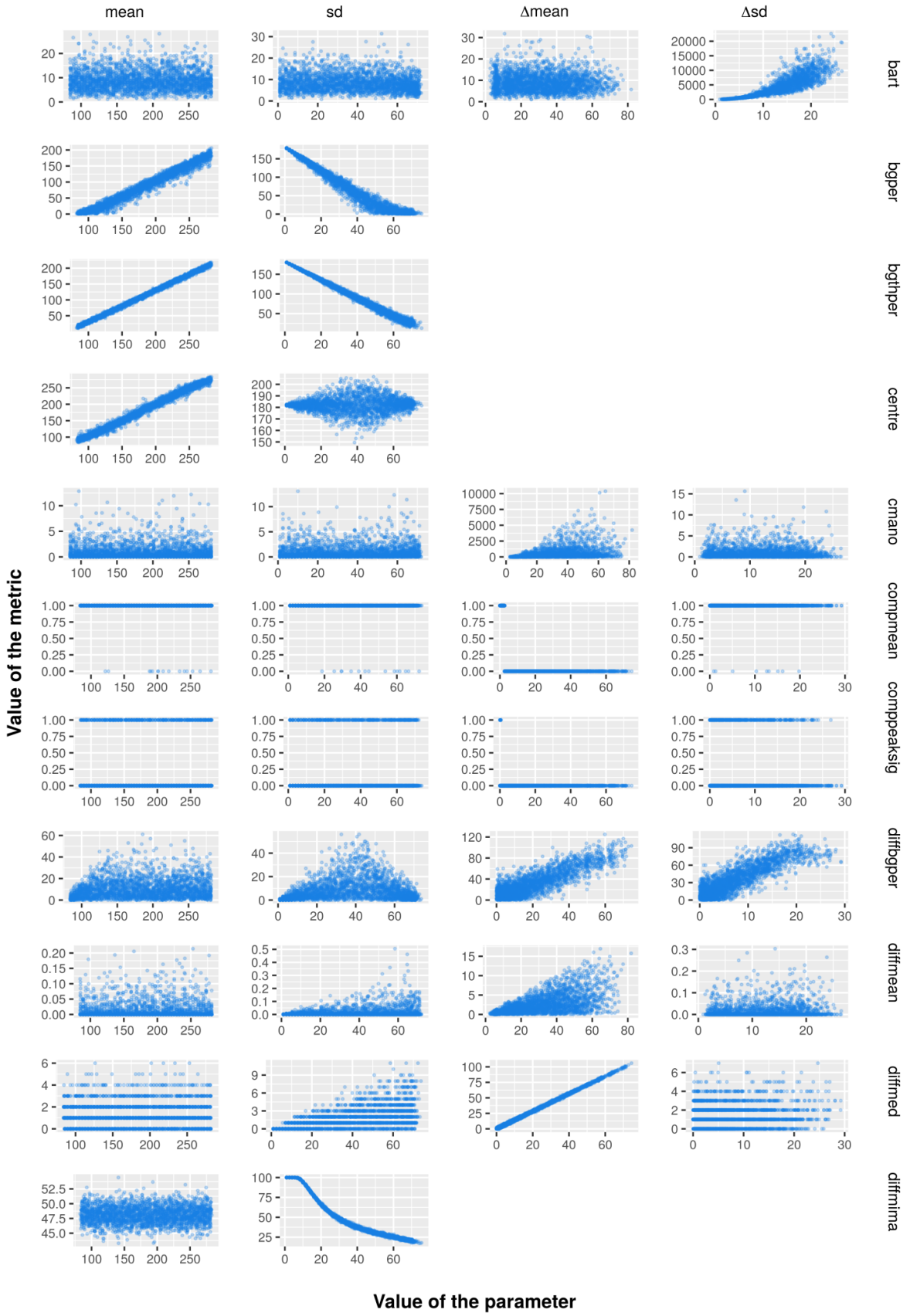
Metric	Skewed normal	Bimodal	Cauchy	Random
bart	0.98	0.7	0.82	0.42
bgper	0.98	0.85	0.7	0.24
bgthper	0.98	0.8	0.74	0.37
centre	0.99	0.9	0.56	0.09
cmano	0.99	0.85	0.94	0.56
compmean	0.98	0.67	0.9	0.45
comppeaksig	0.79	0.26	0.36	0.68
diffbgper	0.89	0.46	0.11	0.16
diffmean	0.98	0.8	0.93	0.56
diffmed	0.98	0.72	0.9	0.48
diffmima	0.98	0.89	0.89	0.34
diffpeak	0.97	0.59	0.92	0.19
diffperido	0.96	0.57	0.12	0.29
diffslin	0.98	0.71	0.78	0.37
interq	0.98	0.88	0.92	0.54
khi2	0.97	0.72	0.76	0.26
kolmogau	0.46	0.2	0.1	0.64
kolmomult	0.97	0.73	0.59	0.16
kolmouni	0.98	0.89	0.9	0.11
maxprop	0.98	0.89	0.89	0.48
mean	0.99	0.95	0.78	0.51
meanlin	0.99	0.95	0.78	0.28
meanmult	0.99	0.95	0.78	0.28
meanvl	0.97	0.89	0.91	0.38
meanvo	0.97	0.94	0.78	0.47
med	0.98	0.91	0.78	0.54
medprob	0.99	0.97	0.79	0.49
minper	0.98	0.89	0.91	0.59
minprop	0.93	Not applicable	0.92	0.15
mode	0.94	0.87	0.78	0.2
mood	0.98	0.68	0.9	0.46
nbtu	0.97	0.86	0.79	Not applicable
peaksig	0.98	0.93	0.78	0.39
per	0.98	0.9	0.78	0.26
pergau	0.98	0.9	0.91	0.59
perhdr	0.98	0.88	0.91	0.57
permean	0.98	0.89	0.81	0.19
pielou	0.98	0.89	0.88	0.09
propmed	0.98	0.89	0.89	0.37
propmode	0.98	0.89	0.89	0.37
rayleigh	Not applicable	Not applicable	Not applicable	Not applicable
rutberg	0.97	0.89	0.41	0.29

Table S4-2: Continued.

Metric	Skewed normal	Bimodal	Cauchy	Random
varlin	0.99	0.77	0.92	0.54
skew	0.34	0.23	0.35	0.48
skinner	0.98	Not applicable	0.76	Not applicable
slpcomp	0.95	0.22	0.83	0.22
sd	0.98	0.9	0.91	0.59
sdprob	0.98	0.9	0.9	0.56
var	0.97	0.89	0.92	0.61
varcor	0.97	0.89	0.92	0.61
watson	0.98	0.82	0.91	0.29
zerbe	0.98	0.89	0.91	0.59

Supporting information 5

Variation of each phenological metric according to the variation of the four parameters of phenology, within and between years, in the simulations of phenology of births. *mean*: variation of each metric according to the variation of the mean birth date in a given year; *sd*: variation of each metric according to the variation of the standard deviation of the distribution of births for a given year; *Δmean*: variation of each metric according to the variation of the size of the range over which the mean birth date can vary across years; *Δsd*: variation of each metric according to the variation of the size of the range over which the standard deviation of the distribution of births can vary across years.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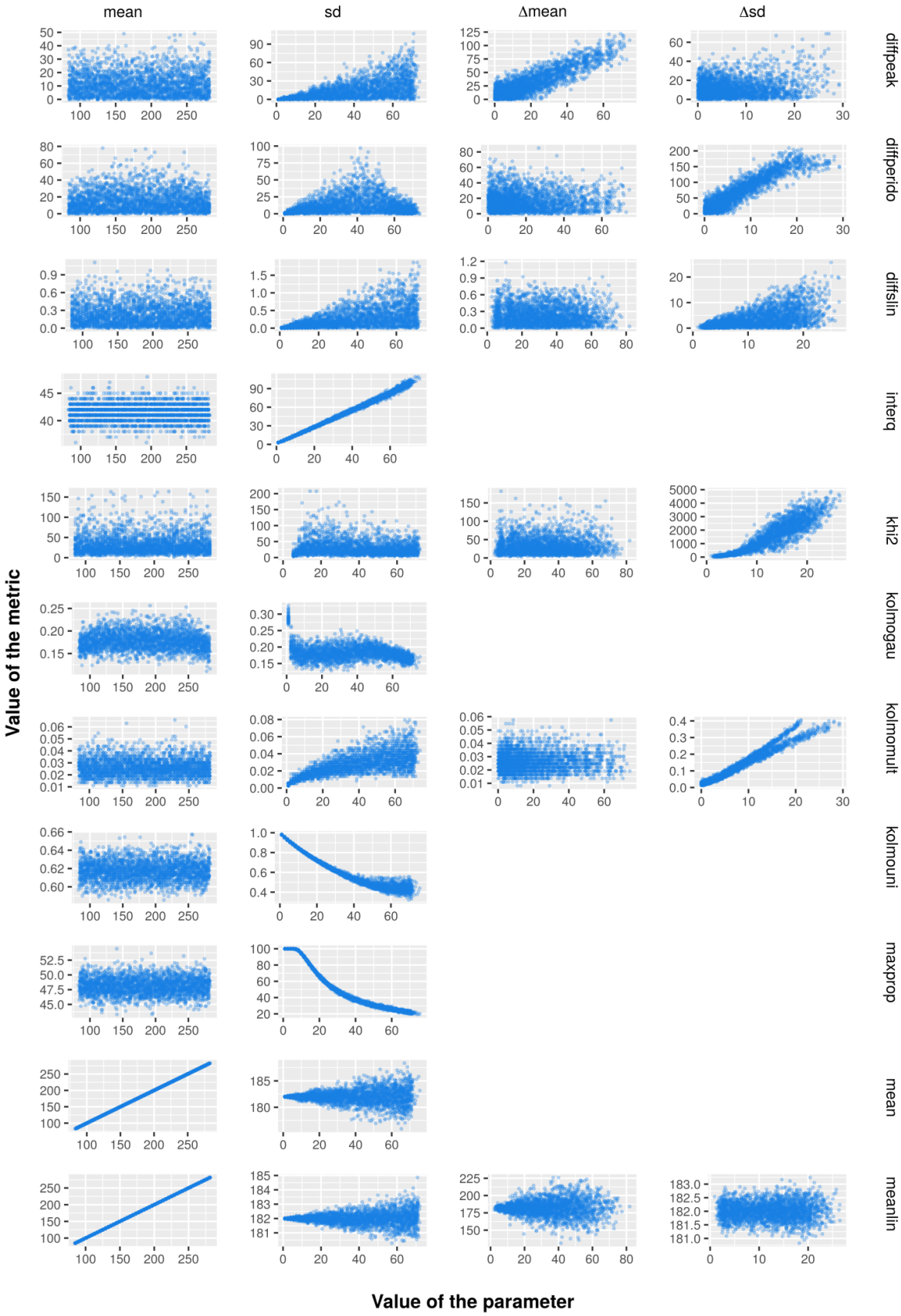
Value of the parameter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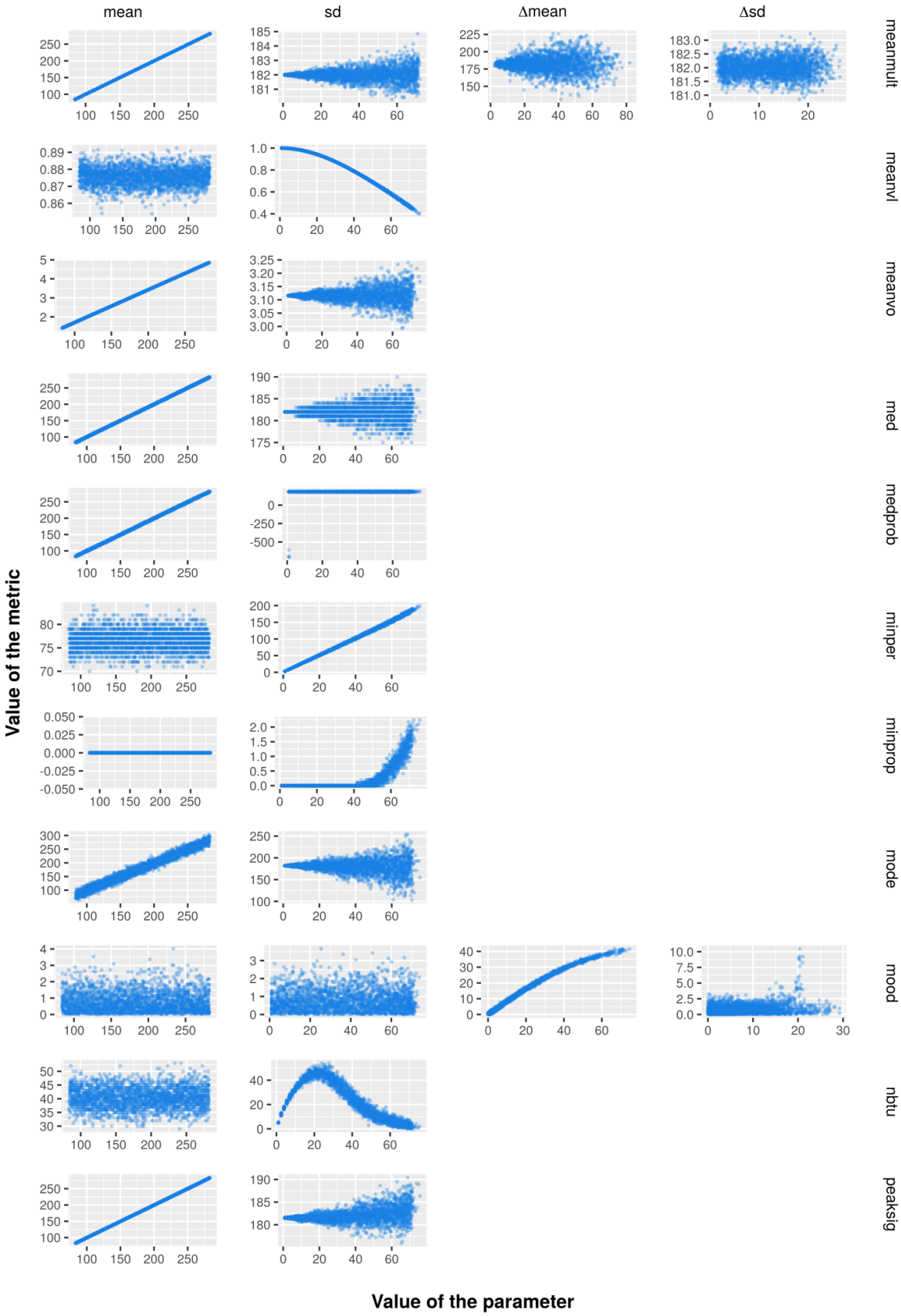
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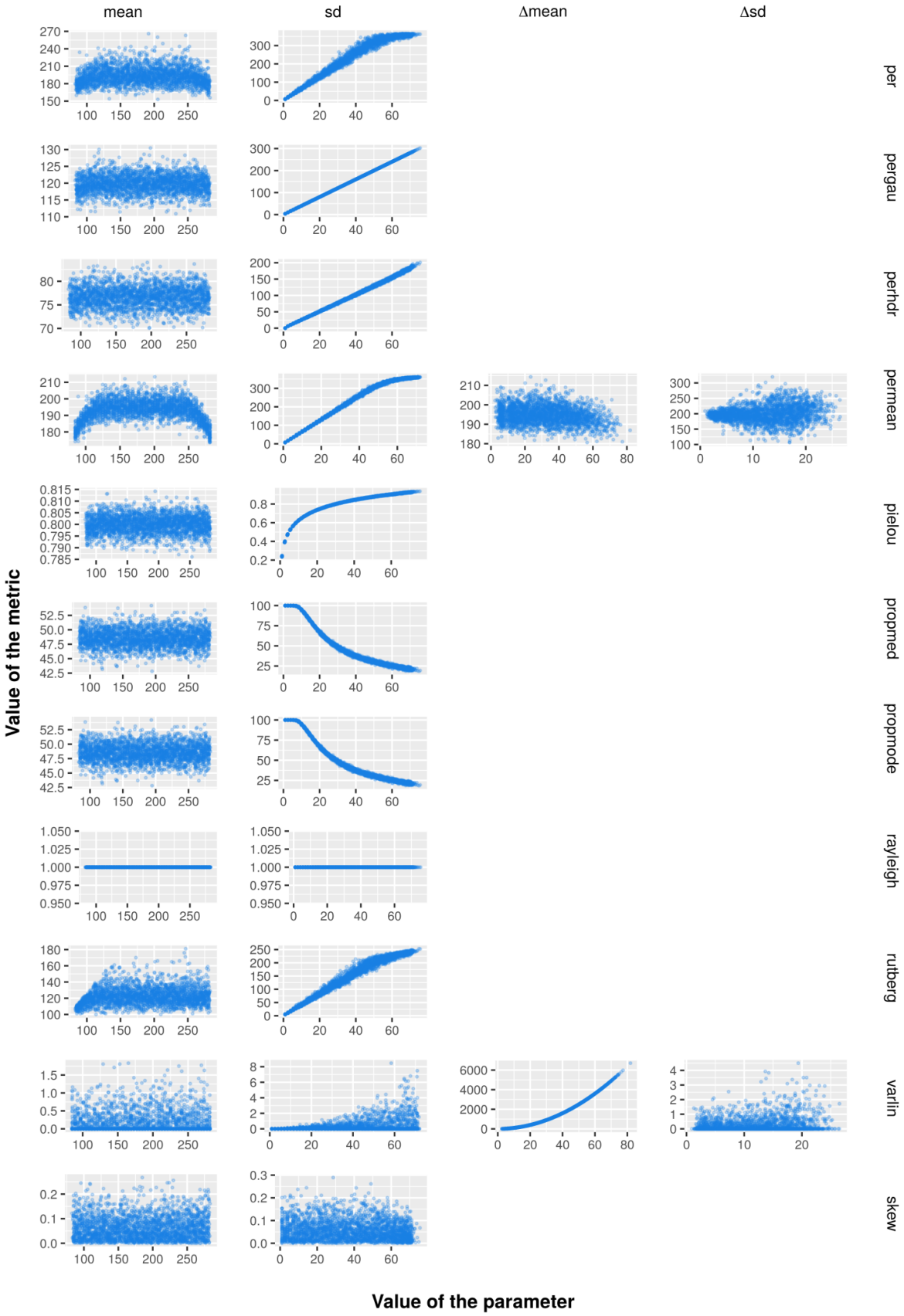
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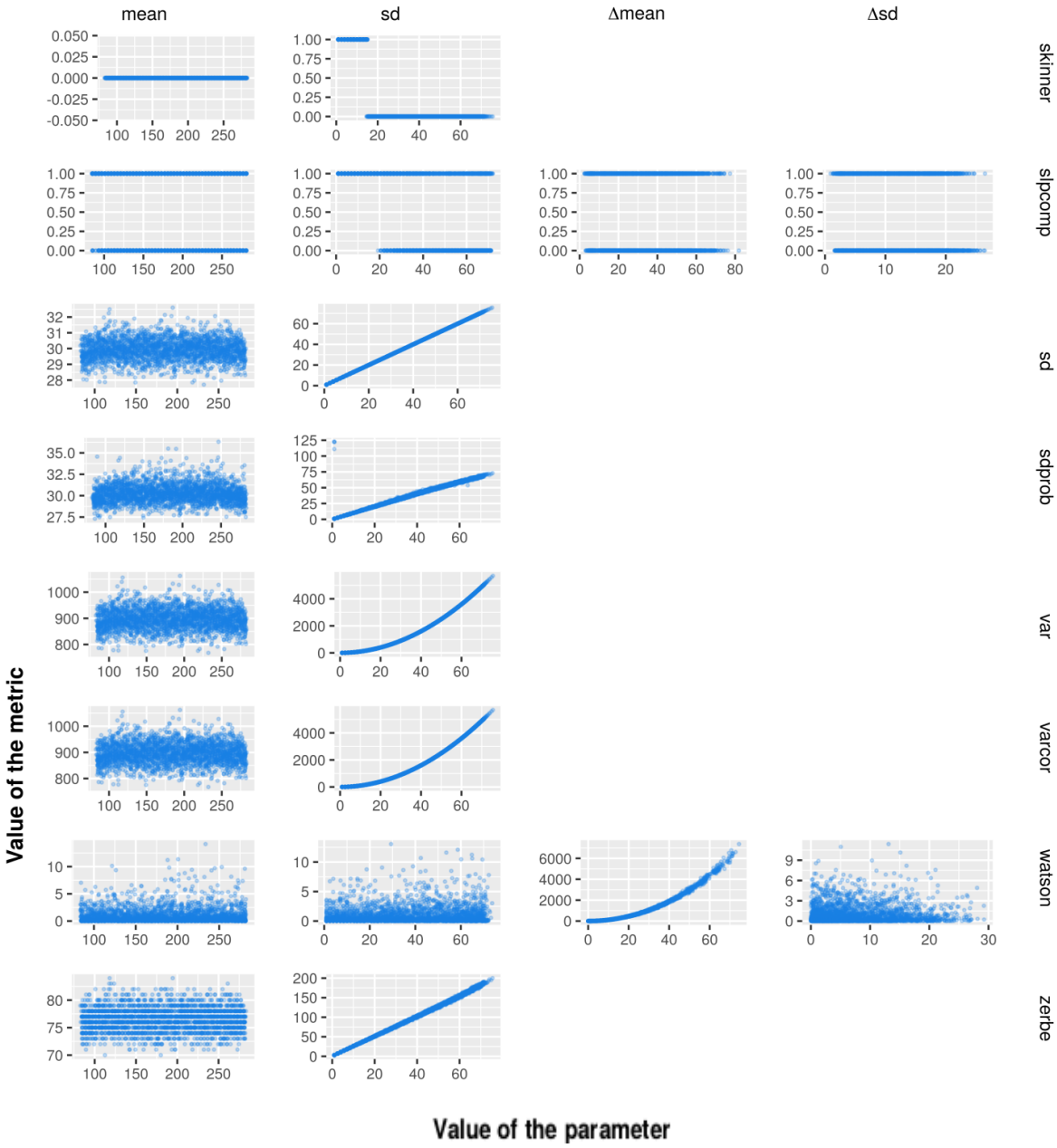
mean
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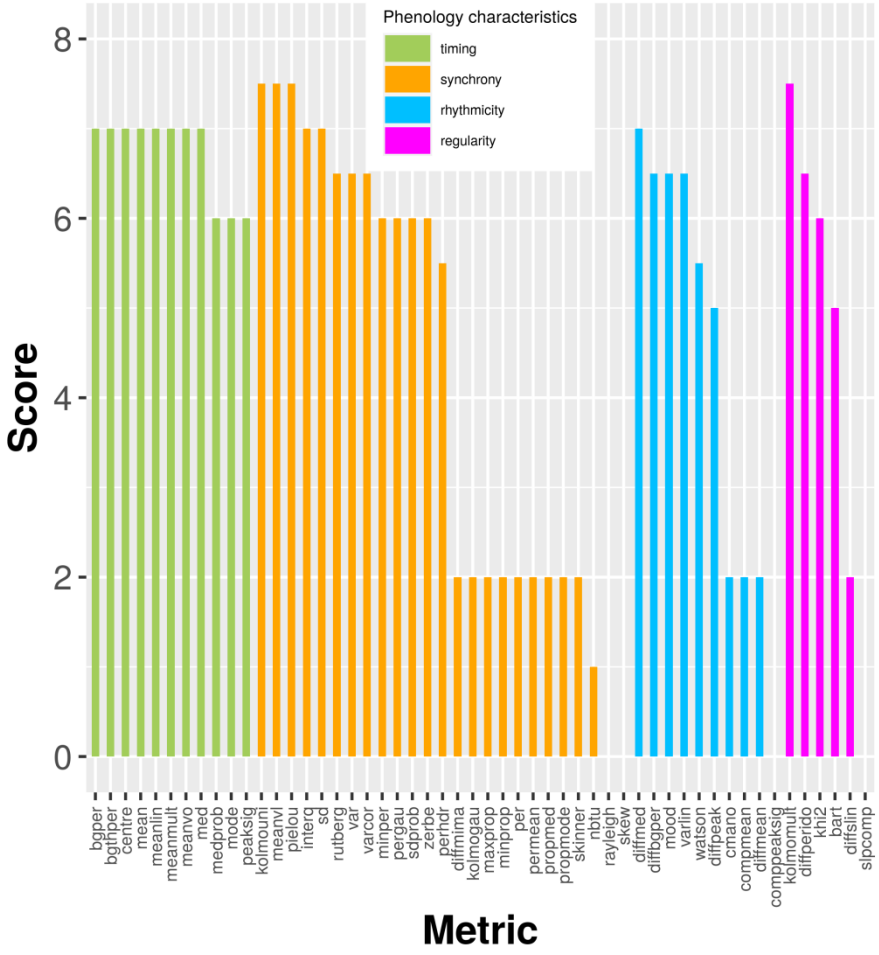
Δmean
Δsd
skinner
slpcomp
sd
sdprob
var
varcor
watson
zerbe
Value of the metric
Value of the parameter

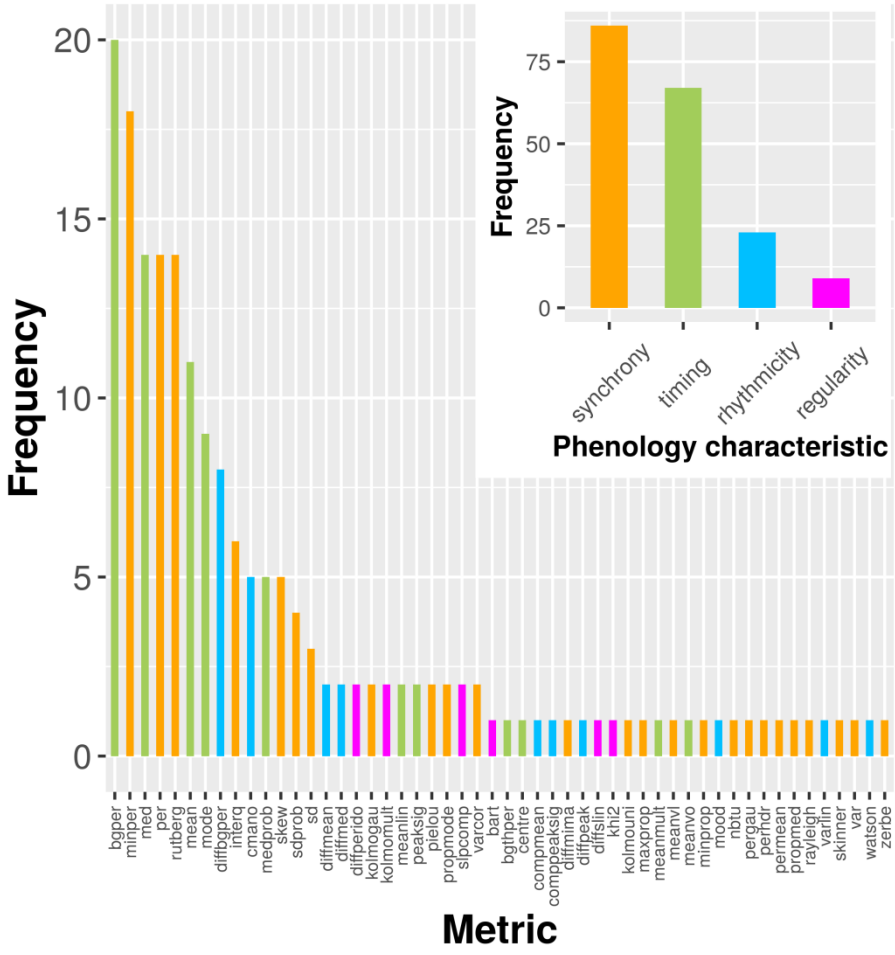
Supporting information 6

Score obtained by each phenological metric (n = 52) according to the eight criteria used to assess the quality of the metrics (goodness, monotony, saturation, strength, normality, origin, linearity and unicity, defined in Table 1). Green = timing metrics, orange = synchrony metrics, blue = rhythmicity metrics, pink = regularity metrics.



Supporting information 7

Number of times each metric was used in the reviewed articles ($n = 47$). Inset: number of times each characteristic of phenology was studied in the reviewed articles, based on our *a priori* classification of each metric into one of the four characteristics we defined (see text for details: Materials and methods, Step 1). Green = timing metrics, orange = synchrony metrics, blue = rhythmicity metrics, pink = regularity metrics.



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Axis 2

Ecological and evolutionary approach of the phenology of births

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Chapter 3

Does timing of birth affect juvenile and mare survival in wild plains zebra?

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Article *in prep.*

Abstract

In large herbivores, the timing of births is mainly driven by the seasonal availability of their food resource. Population dynamics is strongly influenced by juvenile survival and recruitment, which highly depend on whether individuals are born during a favourable period or not. If births often occur during the most suitable season in northern cyclical environments for many large herbivore species, zebra give birth year-round at Hwange National Park, Zimbabwe, a tropical bushland characterized by the succession of a favourable wet season and a less favourable dry season. We used capture-recapture models for analysing long term observation data collected between 2008 and 2019 in this zebra population. We investigated the effect of the season (as a categorical variable) and the time spent in dry season on three categories of juveniles (younger foals of less than six months old, older foals between six and twelve months old, and yearlings between one and two years old) and mares survival, according to their reproductive state. The season had no effect on any survival. Younger foals annual survival was not affected by the time spent in dry season, whereas older foals and yearlings annual survival decreased with an increasing exposure to the dry season. Mares annual survival also decreased with an increasing time spent in dry season, whatever the reproductive status, but to a large extend when non-reproducing. The timing of birth, by determining the external conditions experienced by the offspring and their mothers during critical phases of their life cycle, plays a determinant role in their survival. As climate change is expected to lead to more frequent droughts, longer and harsher dry seasons in tropical ecosystems, we hypothesize a detrimental effect on zebra population dynamics in the future.

Keywords: capture-mark-recapture, environmental seasonality, Equus quagga, Hwange National Park, reproduction, tropical ecosystem.

Introduction

The timing of births, determined by environmental, biotic and internal factors, is a major life history trait of the organisms, involved in the determination of individual fitness and survival (Plard *et al.* 2015). Although the demographic role of the phenology of reproduction, *i.e.,* the distribution of a reproductive event such as births across the year in a given population, has been illustrated theoretically (*e.g.,* Calabrese and Fagan 2004 in plants and insects), its empirical support is less clear (*e.g.,* Franks *et al.* 2018 in birds). This is particularly true for large herbivores (Plard *et al.* 2014), where it has been only marginally explored because of various limitations (*e.g.,* need for detailed long-term individual-based datasets, Clutton-Brock and Sheldon 2010).

The timing of birth and the following months are associated with a critical period for the newborn and its mother in terms of energetic demand: early growth for the former and lactation for the latter (Bronson 1989). In large herbivores, juvenile survival is regulated by various factors such as population size *via* density-dependent effects (Gaillard *et al.* 1998) and predation (Severud *et al.* 2019), but above all, environmental conditions. Juvenile survival depend on the environmental seasonality (*sensu* Heldstab *et al.* 2018), *i.e.,* the succession of the seasons defined by an ensemble of environmental and climatic characteristics, with a reduced survival during the harshest season. For instance, calves survival is lower during the dry season than during the wet season in Serengeti wildebeest *Connochaetes taurinus* (Mduma *et al.* 1999). Hence, by determining the environmental conditions experienced by the new individual during its first months of life, the timing of birth has indirect consequences on newborn survival, through the modification of its growth rate for instance (*e.g.,* Feder *et al.* 2008).

Thus, the phenology of birth is generally supposed to be adjusted to maximize offspring survival. In large herbivores, this mainly goes through the synchronization of parturition with food resource availability and quality (Post *et al.* 2003). Bighorn sheep *Ovis canadensis* for instance, give birth during a restricted period of time, just before the forage quality peak, to provide sufficient milk and high-quality vegetation access to their growing lambs (Festa-Bianchet 1988). Nevertheless, numerous species are characterized by highly variable dates of birth inside their population, even when living in seasonal environments (*e.g.,* Sinclair *et al.* 2000). Why such a variability, and what are the demographic consequences of this variability? Still few studies have explored the consequences of the timing of birth on early life-stages survival in tropical ungulates, and most of them did not correct for imperfect detection (Gaillard

et al. 2000, Grange *et al.* 2015), leading to less reliable conclusions. Thus, this field of research remains poorly known and needs further explorations (Lee *et al.* 2017).

In addition, the period around parturition is also critical for reproductive females themselves, as they endure their offspring needs in addition to their own. Lactation costs are particularly high in mammals (Clutton-Brock *et al.* 1989), and could turn reproductive females more susceptible to environmental conditions. Therefore, lactating females have to adjust their foraging behaviour to meet the extra energetic requirements. In zebra *Equus burchellii*, lactating mares do not increase their feeding time to keep matching the activity budget of the rest of their harem, but increase their bite frequency when feeding (Neuhaus and Ruckstuhl 2002). They also lead their harem more frequently than non-lactating mares to initiate movements to waterholes due to their increased water demand (Fischhoff *et al.* 2007). However, if a higher mortality rate could have been observed in females undergoing nursing energetic costs than in those who did not raise an offspring during the same year (Clutton-Brock *et al.* 1983), this does not appear to be the rule. A large literature, mainly based on northern hemisphere species, found no or positive correlation between the reproductive state and survival in mammal females, depending on their age class, social status or overall quality for instance (*e.g.,* Weladji *et al.* 2008, Descamps *et al.* 2009, Morano *et al.* 2013). The absence of clear pattern and the low representation of species from the southern hemisphere spurs further investigations.

Here we investigated the effect of the phenology of births on juvenile and mother annual survival in relation to environmental conditions in wild plains zebra *Equus quagga*. We explored the impact of the time spent in dry season, defined by the timing of birth and the duration of the associated dry season, on the survival of two juvenile stages, yearlings and adult females. We took advantage of a population of individually known animals living in Hwange National Park (HNP), Zimbabwe and followed since 2004. Even if their environment is seasonal (*i.e.,* characterized by the succession of a wet and a dry season, Chamaillé-Jammes *et al.* 2006), zebras breed year round in this study site. Coupled with a high inter-annual variability in the starting date of the seasons, this constitutes the adequate framework to study the impact of variable environmental conditions related to seasonality on juveniles and females survival during the reproductive period, in a tropical herbivore.

As a large-bodied species living in a seasonal environment, the plains zebra is supposed to belong to the capital end of the capital-income breeder continuum (Jonsson 1997, Ogutu *et al.* 2014). Once the mother is engaged in reproduction, she will provide the energetic effort to bring her foal to weaning age mainly using previously stored resources. Moreover, newborn almost exclusively rely on its mother for food provisioning through lactation and nursing

(Jackson *et al.* 2021), and is not exposed to thermo-regulation issues in our tropical study site. Thus, we hypothesized foals survival should not be sensitive to environmental conditions until weaning (*i.e.,* during the first six months of life) (i). Then, the foal becoming progressively independent from its mother during the following six months (*i.e.,* between six and 12 months of age, Smuts 1976), it should experience a subsequent decrease in its survival probability (ii). We expected a similar trend in yearling (*i.e.,* between one and two years old) survival (Gaillard *et al.* 2000) because at this stage, it is fully independent from its mother but not fully grown yet (iii). To the contrary, the period immediately following parturition should be critical for the mother, which could experience lower survival than a non-breeding female (iv-1) and a stronger negative response to harsh environmental conditions (v-1). Besides, regarding the variability in the findings associated with the literature focusing on reproductive females survival and the possible confounding effect of mares quality, we also considered the alternative hypothesis that a reproductive female could instead experience higher survival than a non-reproductive one (iv-2) and show less sensitivity to harsh environmental conditions (v-2).

Materials and methods

Context of the study

Study site

Hwange National Park (19°00’ S, 26°30’ E), Zimbabwe, covers 14,651 km^2 of bushlands, woodlands and scrublands interspersed with grassland (Arraut *et al.* 2018), at between 900 and 1,100 m a.s.l.. Average annual rainfall is c. 600 mm, with high inter-annual variations (Chamaillé-Jammes *et al.* 2006). Most, if not all, rainfall events occur during the wet season from October to April. The start of the wet season is characterised by a high inter-annual variability, leading to variable duration of the dry season. The study took place in the north-east of the park where artificial waterholes retain water year round and where areas > 8 km from a waterhole are rare, even in the dry season (Chamaillé-Jammes *et al.* 2007). There is no hunting in the park, but the densities of the two main zebra predators, lion *Panthera leo*, and spotted hyena *Crocuta crocuta* are high (Loveridge *et al.* 2007, Drouet-Hoguet 2007).

Study species

Plains zebras live in harems composed of a stallion, several mares and their foals under two years old (Klingel 1969). They give birth year-round in most of their range, including Zimbabwe (Dasmann and Mossman 1962), even if a births peak can be observed around

January to March in this area. Foals are weaned around 11 months of age (Smuts 1976), and are considered as "followers" on the hider-follower gradient (Lent 1974), as they stand and follow their mother soon after birth (Sinclair *et al.* 2000). Zebras are grazers, feeding virtually only on grasses. Their food resource is thus mainly driven by rainfall (DuPlessis 2001). In HNP, the population of zebras is mostly resident (unpublished GPS data).

Zebra demographic data

Following the protocol presented in Grange *et al.* (2015), we recorded the presence of individually identified zebras between 2008 and 2019 using visual identification of their unique stripe pattern. Censuses were conducted twice a year, around March and August, during field sessions (hereafter called "sessions") at the transition between wet and dry seasons (n = 24 sessions, *mean session duration* = 45 ± 25 days, *range* = 13 - 88 days). When first sighted, individuals were classified according to three age classes: foal (from birth to 12 months old), yearling (12 to 24 months old) and adults (more than 24 months old). When possible, the precise age of foals and yearlings was determined using the criteria of Smuts 1975 and Penzhorn 1984, and photographs of individuals of known age (see details in Grange *et al.* 2015). For those individuals, we estimated a date of birth and its accuracy.

Season delineation

For each year, we identified the transition date between wet and dry season using 500 m resolution bi-monthly Normalized Difference Vegetation Index (NDVI) records from the NASA website (MOD13A1 product, https://modis.gsfc.nasa.gov) and daily rainfall records from the Climate Hazards Center website (Rainfall Estimates from Rain Gauge and Satellite Observations, https://www.chc.ucsb.edu)(Supporting information 1). During the study period and according to our estimations, the wet season in HNP started between the 1st of November and the 19th of December, and the dry season started between the 9th of May and the 29th of July.

Statistical analysis

General purpose

We ran Capture-Mark-Recapture (CMR) analyses (Lebreton *et al.* 1992) on two distinct datasets: a first one for individual of known date of birth with an accuracy ranging from 0 to ± 90 days (n = 310) to estimate the annual probability of survival of the two foal age classes (*i.e.,*

"younger foals" of less than six months old and "older foals" between six and 12 months old) and yearling (*i.e.,* between one and two years old). We used a second dataset composed of adult females (n = 205) to estimate the annual probability of survival of mares according to their reproductive state using multi-states models (Lebreton *et al.* 2009). We tested the effect of the time spent in dry season since births for younger foals and mothers, and the subsequent time spent in dry season between two successive seasons for older foals, yearlings and non-reproductive mares (detailed below). We performed CMR analyses using the program MARK (www.phidot.org/software/mark) and R (R statistical software, www.r-project.org), with the R package *RMark* (Laake 2013). The Goodness Of Fit tests (GOF) were assessed using the R package *R2ucare* (Gimenez *et al.* 2017).

For both datasets, we considered each session as punctual, summarized by its starting date. As it was variable, we accounted for the time interval between two successive sessions in the model specification. We calculated the proportion of time elapsed between two successive sessions pertaining a year as follows: $\Delta t_{s2\text{-}s1} = (Start\ date_{s2} - Start\ date_{s1}) / 365$.

Juvenile survival

As in previous works of demographic analyses performed on these data (Grange *et al.* 2015, Vitet *et al.* 2020, Vitet *et al.* 2021), we ran the analyses on individuals observed at least once in the field (n = 290), but also on individuals which were never observed but whose mother was detected to be pregnant thanks to opportunistic faecal sampling and subsequent hormone (20-oxopregnanes and oestrogens, Ncube *et al.* 2011) dosage (n = 20, Supporting information 2). We recorded those foals as being identified at birth only and never seen again. For both categories (*i.e.,* seen and unseen individuals), we retained individuals whose date of birth was estimated (n = 310). We attributed a session and a season of birth to each individual based on the date of birth nearest session. So, all the foals born during the same session constituted a cohort, experimenting similar environmental conditions. We defined three age classes: "younger foals" of less than six months old, "older foals" between six and 12 months old and "yearlings" between one and two years old. Individuals remained in the dataset even after becoming adults (*i.e.,* > 2 years old) to get better estimations of yearling survival, but adult survival was not considered in this analysis. We estimated the time spent in dry season between two successive sessions. The variable *tids* was defined as the proportion of days of dry season between the first day of the session s and the first day of the following session $s+1$. We used the scaled value of *tids* in the models to ease model convergence. We summarized observations data in a life history dataset, with one observation per known individual per session: 0

corresponding to "no sighting of the individual during the session *s*", and 1 corresponding to "at least one sighting of the individual during the session *s*".

The GOF tests of the fully time-dependent model (Gimenez *et al.* 2018) denoted problems of overdispersion (Test 2.CL: $\chi^2 = 40.79$, $df = 16$, $P < 0.01$; Test 3.Sm: $\chi^2 = 11.05$, $df = 19$, $P = 0.92$), trap-dependence ($\chi^2 = 139.35$, $df = 17$, $P < 0.01$) and transience ($\chi^2 = 70.47$, $df = 22$, $P < 0.01$). After examination of Test 2.CL, we noticed that overdispersion was mainly caused by three sessions in the dataset. So, we considered it as marginal and ignored overdispersion in the analyses. We took into account trap-dependence by adding a default trap-dependence (*td*) effect in each recapture model tested. Transience was likely due to the age structure as young individuals often have low survival in large herbivores (Gaillard *et al.* 2000). Thus, we fitted all survival models tested with a default age class effect. We explored the effect of the season and *tids* on recapture and survival probabilities, for the two age classes of foals and the yearlings, and on several groupings of those age classes (Supporting information 3). We also fitted the null models and models including solely a time effect. We conducted a similar analysis on the two foal age classes using a Generalized Linear Model (GLM) approach, presented in Supporting information 4.

Mare survival

We ran the analyses on all the adult females observed at least once during the sessions ($n = 322$). The season and *tids* variables were defined in the same way than for juveniles (see above). We summarized observations data in a life history dataset, with one observation per known individual per session: 0 corresponding to "no sighting of the mare during the session *s*", 1 corresponding to "at least one sighting of the mare alone during the session *s*" and 2 corresponding to "at least one sighting of the mare with a dependent foal during the session *s*". We considered a dependent foal as an individual that is still suckled, so under 6 months of age. Even if weaning generally occurs around 11 months of age in zebras, foals can survive without their mother from 9 months old upwards (Smut 1976). We chose 6 months to exclude such possibility and match our sessions frequency.

As there were too few repetitions to conduct the GOF tests of the multi-states model, we conducted the GOF tests on the one-state model instead. The tests denoted overdispersion (Test 2.CL: $\chi^2 = 49.02$, $df = 19$, $P < 0.01$; Test 3.Sm: $\chi^2 = 72.10$, $df = 20$, $P < 0.01$), trap-dependence ($\chi^2 = 112.13$, $df = 21$, $P < 0.01$) and transience ($\chi^2 = 62.23$, $df = 21$, $P < 0.01$). After examination of Test 2.CL and 3.Sm, we noticed that overdispersion was mainly caused by five and three sessions in the dataset respectively. So overdispersion could be ignored because

considered as marginal. We took into account trap-dependence by adding a default trap-dependence effect in each recapture model tested. To take into account transience, we added a categorical covariable *sight* in all survival models to differentiate between mares captured for the first time during the survey and mares already captured at least once during the survey, following the method described by Pradel *et al.* 1997. We evaluated the effect of the reproductive state (*i.e.,* with or without a dependent foal), the season and *tids* on recapture, survival and transition probabilities. Unfortunately, age was not known for a large number of females, so we were not able to include it in the models. We also fitted null models and models including solely a time effect.

Model selection

Because of the huge number of combinations possible between recapture and survival (and transition for mares) models, we conducted a two-step selection model using the lowest Akaike Information Criterion adjusted for small sample sizes (AICc) and the number of parameters (principle of parsimony) (Burnham 2002). We conducted a first model selection step on recapture and survival (and transition for mares) models independently. When proceeding to model selection on a given demographic parameter (*i.e.,* recapture, survival or transition), we set the other models to depend exclusively on the covariables related to GOF corrections (*e.g., w*hen selecting recapture models in foals, we set survival model as depending on the age class, see Supporting information 3). We considered all the models within ΔAICc < 2 from the best model for the next model selection step. When there was only one competing model emerging from this model selection step for a given demographic parameter, we also included the second best model in terms of AICc to allow a real model selection for each of the demographic parameters based on at least two different models (see model selection for data on mares in Supporting information 3).

In the second selection step, we ran all the combinations possible between the best recapture and survival (and transition for mares) models resulting from the first model selection step to identify the best complete models. We retained the complete models (recapture and survival, and transition for mares) within ΔAICc < 2 from the best model as competing models, and we retained the models with the lowest number of parameters as the best models. Following Arnold 2010, we set the confidence intervals at 85%, in accordance with our AICc model selection procedure.

Results

Juvenile survival

We found four competing models (*AICc* ∈ [1718.922; 1720.291], *deviance* ∈ [1658.641; 1660.011]) to estimate the survival and recapture of juveniles, three of them correspond to the most parsimonious models (k = 29, see Table 1 and Supporting information 3). In all three models, the probability of recapture included an additive effect of trap-dependence and time, and the probability of survival increased with age and decreased with the proportion of time spent in dry season. The difference between them lied in the effect of *tids*, which was found to act in addition with the age class, or exclusively on older foals, or on older foals and yearlings grouped together in a unique age category. The season was not retained in the competing models.

Table 1: Statistics of the four competing models investigating the relationship between annual survival and the proportion of time spent in dry season according to the age class in plains zebra juveniles (Hwange National Park, Zimbabwe, 2008-2019).

Model	Explanatory variables	Nb. of para-meters (k)	AICc	Deviance	ΔAICc
1	Survival ~ foal_old + yearl + adult + tids * fo_ye Recapture ~ td + time	29	1718.922	1658.641	0
2	Survival ~ foal_old + yearl + adult + tids * fo_ye Recapture ~ td + age_class + time	32	1719.827	1653.049	0.906
3	Survival ~ foal_old + yearl + adult + tids * foal_old Recapture ~ td + time	29	1720.134	1659.853	1.212
4	Survival ~ age_class + tids Recapture ~ td + time	29	1720.291	1660.011	1.37

tids = proportion of time spent in dry season; foal_old = older foals; yearl = yearlings; fo_ye = older foals and yearlings gathered.

The following stated results are from Table 1, model 1: the variable *tids* had a significant negative effect on both older foals and yearlings (β = -0.637 ± 0.367 SE, 85% CI [-1.167; -0.108]). The probability of survival of older foals ranged from 0.840 ± 0.108 SE, 85% CI [0.624; 0.944] when the proportion of time spent in dry season was the shortest (*i.e.,* 9 % of the time) to 0.378 ± 0.144 SE, 85% CI [0.201; 0.595] when the proportion of time spent in dry season was the longest (*i.e.,* 80 % of the time, Fig. 1). Similarly, the probability of survival of yearlings ranged from 0.891 ± 0.085 SE, 85% CI [0.699; 0.967] to 0.486 ± 0.123 SE, 85% CI [0.318; 0.657]. The survival of younger foals was not significantly affected by *tids*, and was of 0.431 ± 0.042 SE, 85% CI [0.371; 0.492] on average. Besides, the supplementary analyses on

the two foal age classes using a GLM approach provided similar results (Supporting information 4). Therefore, hypotheses (i) stating that younger foals survival should not be sensitive to environmental conditions, (ii) and (iii) stating that older foals and yearlings *resp*. survival should be lower, were validated by our results. The effect of trap-dependence on the probability of recapture was significant (β = 1.756 ± 0.182 SE, 85% CI [1.494; 2.018]). The probability of recapture varied from 0.123 ± 0.069 SE, 85% CI [0.053; 0.259] to 0.634 ± 0.151 SE, 85% CI [0.404; 0.815].

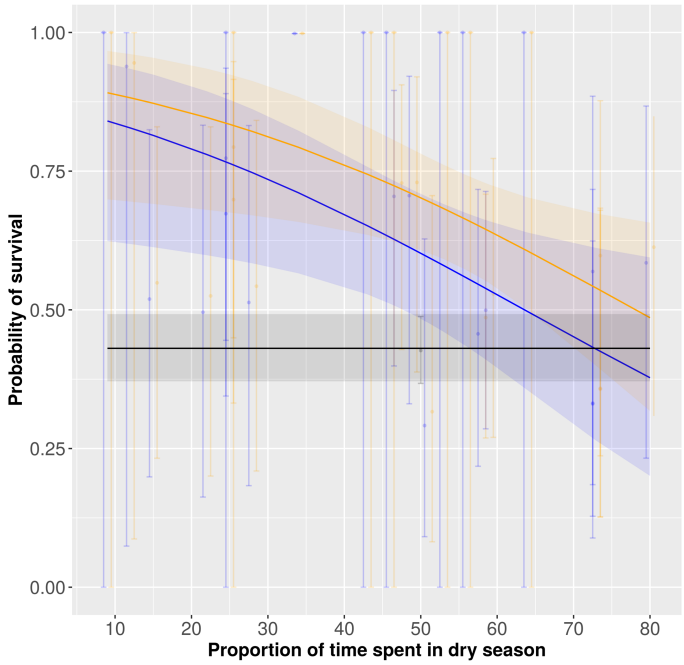

Figure 1: Probability of annual survival of plains zebras juveniles in Hwange Nation Park, Zimbabwe (2008-2019), according to the proportion of time spent in dry season. Black: younger foals (between birth and six months old), blue: older foals (between six and 12 months old), orange: yearlings (between one and two years old). Solid lines represent predicted values from the best model. Shaded areas represent 85% confidence intervals of these predicted values. Dots represent survival predicted by the time model, vertical bars represent 85% confidence intervals. Scaled proportion of time spent in dry season converted back to the proportion of time spent in dry season.

Mare survival

We found two competing models (*AICc* ∈ [3294.197; 3295.161], *deviance* ∈ [3226.108; 3224.943]) to estimate the survival, transition between reproductive states and recapture of mares, one of them being the most parsimonious model (k = 33, see Table 2 and Supporting information 3). In both models, the probability of recapture included an additive effect of the

trap-dependence, reproductive state and time. The probability of survival was higher for reproductive than for non-reproductive mares, and the proportion of time spent in dry season decreased the probability of survival. The probability of transition between reproductive states varied according to the season (see details below). The only difference between the two models came from the fact that *tids* acted either in addition or in interaction with the reproductive state to predict mares survival.

Table 2: Statistics of the two competing models investigating the relationship between annual survival and the proportion of time spent in dry season according to the reproductive state in plains zebra mares (Hwange National Park, Zimbabwe, 2008-2019).

Model	Explanatory variables	Nb. of para-meters (k)	AICc	Deviance	ΔAICc
1	Survival ~ sight + repro_status + tids Recpature ~ td + repro_status + time Transition ~ season * from_repro_status * to_repro_status	33	3294.197	3226.108	0
2	Survival ~ sight + repro_status * tids Recapture ~ td + repro_status + time Transition ~ season * from_repro_status * to_repro_status	34	3295.161	3224.943	0.964

tids = proportion of time spent in dry season; sight = first capture or not for a given female; repro_status = reproductive state; from_repro_status = reproductive state of departure for the transition models; to_repro_status = reproductive state of arrival for the transition models; td = trap-dependence.

The best-supported model included a significant effect of *sight* on the survival probability (β = 1.075 ± 0.272 SE, 85% CI [0.683; 1.467]). Here we present results for mares in their second and following observations only, results relying on a single first observation being less informative. The best-supported model also included a significant negative effect of *tids* on both reproductive and non-reproductive females (β = -0.729 ± 0.221 SE, 85% CI [-1.047; -0.410], Fig. 2a). The probability of survival of non-reproductive females varied from 0.963 ± 0.020 SE, 85% CI [0.921; 0.984] when the proportion of time spent in dry season was the shortest to 0.690 ± 0.060 SE, 85% CI [0.600; 0.769] when the proportion of time spent in dry season was the longest. Similarly, the probability of survival of reproductive females varied from 0.989 ± 0.008 SE, 85% CI [0.969; 0.996] to 0.883 ± 0.054 SE, 85% CI [0.779; 0.941]. Therefore, hypothesis (iv-1) was not validated by our results in favour of hypothesis (iv-2) stating that mothers could experience higher survival than non-breeding females. Similarly, we did not validate hypothesis (v-1) in favour of hypothesis (v-2) stating that mothers could experience a lower negative response to harsh environmental conditions. The probability for a

mare to move from the reproductive to the non-reproductive state was significantly higher (at least 0.713 ± 0.044 SE, 85% CI [0.646; 0.772]) than the probability to stay in the reproductive state (at most 0.287 ± 0.044 SE, 85% CI [0.228; 0.354]) whatever the season (Fig. 2b). The probability to stay in the non-reproductive state was similar to the probability to move from the non-reproductive to the reproductive state in the dry season (0.486 ± 0.039 SE, 85% CI [0.431; 0.542] and 0.514 ± 0.039 SE, 85% CI [0.458; 0.569] respectively), but it was significantly higher in the wet season (0.688 ± 0.058 SE, 85% CI [0.600; 0.765] against 0.312 ± 0.058 SE, 85% CI [0.235; 0.400] respectively). The effect of trap-dependence on the probability of recapture was significant (β = 1.034 ± 0.174 SE, 85% CI [0.784; 1.284]). The probability of recapture was higher for non-reproductive than for reproductive females. It varied from 0.411 ± 0.072 SE, 85% CI [0.313; 0.517] to 0.908 ± 0.049 SE, 85% CI [0.808; 0.959] for non-reproductive females, and from 0.129 ± 0.041 SE, 85% CI [0.080; 0.200] to 0.676 ± 0.106 SE, 85% CI [0.511; 0.807] for reproductive females.

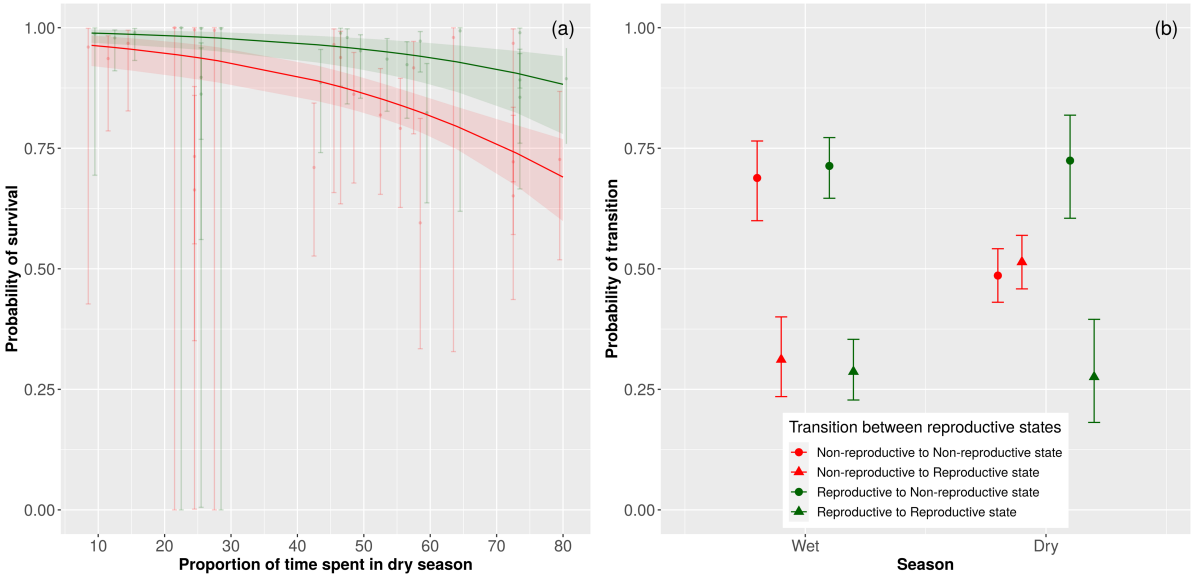

Figure 2: a) Probability of annual survival of plains zebra mares according to the proportion of time spent in dry season and their reproductive state (for mares in their second and subsequent observations only, see text for details). Solid lines represent predicted values from the best model (red: non-reproductive females, green: reproductive females). Shaded areas represent 85% confidence intervals of these predicted values. Dots represent females survival predicted by the time model respectively, vertical bars represent 85% confidence intervals. Scaled proportion of time spent in dry season converted back to the proportion of time spent in dry season. b) Probability of transition between reproductive and non-reproductive states for plains zebra mares according to the season. Dots represent predicted values from the best model. Vertical bars represent 85% confidence intervals of these predicted values. For both graphs: data from Hwange Nation Park, Zimbabwe (2008-2019).

Discussion

The phenology of births, by determining the environmental conditions experienced by newborn at birth and during the following months, has major effects on their survival. Although the annual cohort survival of younger foals (between birth and six months old) is stable around 0.431, the one of older foals (between six and twelve months old) and even yearlings (between one and two years old) significantly decreases with increasing time spent in dry season. The decline observed, from approx. 0.8 to 0.4 for both age classes, is of a factor two between the shortest and the longest exposure to dry season experienced by juveniles in this study. Mares annual survival is also altered by an increasing time spent in dry season weather they are in a reproductive state (*i.e.,* with a dependent foal) or not, but in a lower extent. However, this effect is all the more strong for non-reproductive females.

The timing of birth is intrinsically related to the timing of conception because of a slight flexibility in the duration of gestation (Kiltie 1982). As the reproductive cycle of zebra mares lasts slightly more than one year (Ncube *et al.* 2011), even if they experience post-partum oestrus (Klingel 1969), one can expect their parturition date should progressively be shifted from the optimal period, unless they delay their reproductive cycle to wait for the next favourable birthing period. But a consequence of this is that their inter-birth interval (mean inter-birth interval of 480 ± 116 days in the study site, Barnier *et al.* 2012) would be significantly increased and their lifetime reproductive success decreased (as observed in giraffe *Giraffa camelopardalis,* Lee *et al.* 2017). In addition, we found only a small negative effect of the time spent in dry season on reproductive mares annual survival and no effect on annual survival of younger foals, demonstrating that the timing of birth seems not to be crucial for them. Moreover, females can engage reproduction only when they reach a certain threshold in body condition (Grimsdell 1973), which can be delayed in case of adverse environmental conditions during the year preceding parturition, such as drought years (Ogutu *et al.* 2014). This is thus a supplementary factor acting as a constraint on the determination of the timing of birth. Altogether, these observations argue in favour of breeding year-round in our zebra population in the interest of the mare fitness, as observed in our population.

However, older foals and yearlings annual survival suffered from a date of birth exposing them to a long period of time in dry season while they are gaining independence from their mother. The date of birth can be the result of a trade-off between the mother and the offspring, with the most adequate period being not necessarily the same for the mother than for the offspring (Dezeure *et al.* 2021). In our study, one can hypothesize that the optimal timing

of birth for the offspring is situated at the beginning of the dry season: the harsh conditions during early life are buffered by the mother at this time, and the offspring starts to become independent while conditions are improving through the following wet season. Moreover, the foal benefits from higher quality reserves stored by the mother during the previous wet season, as suggested in African large herbivores (Ogutu *et al.* 2014). To the contrary, the optimal timing of parturition for the mare could be more variable, in order to minimize the inter-birth interval as they are only slightly affected by environmental conditions.

Although the timing of birth defines the environmental conditions experienced at birth, it also determines susceptibility to predation, which is a major factor of mortality in zebra foals (Mills and Shenk 1992) and probably in adults too (Grange *et al.* 2015). On the one hand, the dry season implies higher water demand (which shall be added to the already increased demand of lactating mares) while its availability is reduced. As water holes are hot spots of predation (zebras use movement strategies to minimize risk such as diel migration, Courbin *et al.* 2018), one can expect a higher predation risk on foals and mares during this season. This could explain their higher mortality as the time spent in dry season increases. On the other hand, they could also benefit from an interaction between environmental conditions and predation during the dry season: the reduced vegetation cover could improve predator detectability and reduce the exposure of zebras to predation (Lee *et al.* 2017). It is necessary to explore the interactive effect of environmental conditions and predation as defined by the timing of birth to understand their concurrent effect on juvenile survival in tropical ecosystems.

We did not have information about the quality of the mares of our population, whereas it is known to influence reproductive success in other large herbivore species, as illustrated by a lower offspring survival or a lower probability to breed in lower quality females (Hamel *et al.* 2009). These observations are nevertheless indirectly supported by our data too, as non-reproductive females were more sensitive to the time spent in dry season with a survival decreasing more rapidly than reproductive females. This suggests that they were of lower quality or at least in poorer body condition than breeding females, and were unable to engage reproduction or lost their foal at an early stage.

Due to data collection happening only every six months, our ability to precisely estimate the age of the foals was variable, depending on the distance between its date of birth and its date of first observation (but the same limitations are often encountered in similar studies conducted *in natura*, Lee *et al.* 2017). Foals born during the field sessions were more likely to be assigned a precise date of birth. This variability in the precision of the estimation of the dates of birth (ranging from ± 0 to 90 days) together with the gathering of foals in discrete periods of

births could have limited the robustness of our analyses. However, the same analysis conducted on individuals with a date of birth twice as accurate (*i.e.,* ranging from ± 0 to 45 days) provided very similar results, with an analogous negative effect of the time spent in dry season on older foals and yearlings survival (β = -0.571 ± 0.430 SE, 85% CI [-1.191; 0.048], results not shown). In addition, the low detectability of early dead foals limits the ability to spot them in the field. However, the opportunistic faecal samples coupled with the hormone dosage conferred a major strength to this study by allowing the detection of a consistent number of probable early dead foals (n = 20) and their inclusion in the foals survival estimations, even if the cause and age of death remained unknown.

In large ungulates, juvenile survival and then recruitment have long term consequences on the population dynamics (Gaillard *et al.* 2000, Raithel *et al.* 2007). The phenology of births, by determining the external conditions experience at birth and then the timing of the first critical phases of the life cycle of the individuals (*e.g.,* early growth, age at sexual maturity), plays a determinant role in the quality of the cohort produced, affecting in turn the population growth rate. In the southern hemisphere, climate change is expected to lead to an increasing frequency of droughts and of their unpredictability, but also to longer and harsher dry seasons in general (Zhao and Dai 2015, Dunning *et al.* 2018). The latter, associated with a lower survival of older foals and yearlings as the time spent in dry season increases, could affect the population dynamics of zebras. However, as southern species already live in unpredictable environments to a certain extent (Owen-Smith and Ogutu 2013), one could expect phenotypic adjustments in the timing of birth could occur in response to the changing climate, as it is already observed in drought years in topi or warthog (Ogutu *et al.* 2010). Phenotypic adjustments are more likely than evolutionary processes, which seems overall less frequently observed in response to climate change (Hoffmann and Sgrò 2011), in particular in species with a long generation time.

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Supporting information

Supporting information 1

Determination of the transition dates between wet and dry seasons in Hwange National Park during the study period (2008-2019) using NDVI and rainfall records.

We extracted the mean NDVI and rainfall values for the study area using Google Earth Engine facilities (earthengine.google.com/). We used 500 m resolution bi-monthly Normalized Difference Vegetation Index (NDVI) raster from the NASA website (MOD13A1 product, https://modis.gsfc.nasa.gov) and daily rainfall raster from the Climate Hazards Center website (Rainfall Estimates from Rain Gauge and Satellite Observations, https://www.chc.ucsb.edu) between 2007 and 2020.

Based on the work of Chamaillé-Jammes and colleagues (2006) and field observations, we considered that January, February and March generally fall during wet season, and that August, September and October generally falls during dry season. We used those periods as reference periods to calculate the mean NDVI during wet and dry season ($mean_{NDVI\ Wet}$ = 0.68 ± 0.05 SD, $mean_{NDVI\ Dry}$ = 0.34 ± 0.03 SD). We calculated the mean of both values ($mean_{NDVI\ Wet\ \&\ Dry}$ = 0.51) to obtain the threshold between dry and wet season. We also evaluated the maximum NDVI that occurs during dry seasons during our study period ($max_{NDVI\ Dry}$ = 0.42) to use it as threshold between dry and wet season.

We used the fact that NDVI peaks around August and drops around February every year during our study period to narrow our searching window as follows: i) we searched for the first NDVI record after the month of August above $max_{NDVI\ Dry}$ to determine the transition date between wet and dry season every year; ii) we search for the first NDVI record after the month of February bellow $mean_{NDVI\ Wet\ -\ Dry}$ to determine the transition date between dry and wet season every year. Finally, we visually checked the consistency of our estimations based on NDVI with rainfall records (Fig. S1-1). We noticed that rainfalls occur slightly earlier than our estimations of the beginning of the wet season every year, consistent with the expected latency period before vegetation growth in response to the increase of water availability.

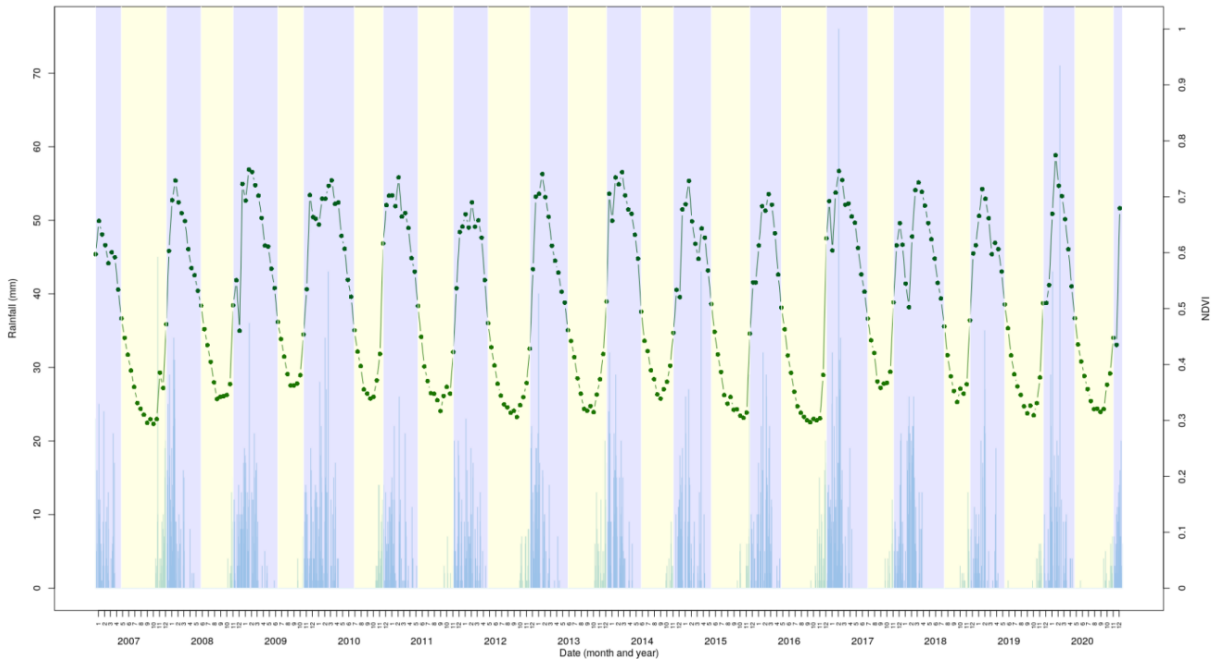

Figure S1-1: mean NDVI and rainfall records in the area of Main Camp, in Hwange National Park, Zimbabwe, between 2007 and 2020 used to estimate the transition dates between wet and dry season (see text for details). Green dots: NDVI bi-monthly records; blue bars: daily rainfall (in mm); blue shade: estimated period of the wet season; yellow shade: estimated period of the dry season.

Supporting information 2

Identification of the date of birth of unseen foals using hormonal samples in the mares.

Opportunistic faecal samples (n = 556) from female zebras collected during sessions between 2007 and 2017 were used in this study. We assessed the gestation stage of each mare based on each hormones sample available according to the level of 20-oxopregnanes (fpm) and oestrogens (fem) and using the following decision table (Table S2-1, see also Ncube *et al.* 2011):

Table S2-1: decision table to assess gestation according to the level of 20-oxopregnanes (fpm) and oestrogens (fem).

Gestation stage	**Detailed gestation stage**	**Level of fpm (ng/g)**	**Level of fem (ng/g)**
No or early pregnancy	Not informative about parturition date	<30	<100
Mid pregnancy	9 to 3 months prior to parturition	<30	>100
		>30	>140
Late pregnancy	≤ 3 months prior to parturition	>30	<140

We estimated all potential periods of parturition according to the samples identifying "late" or "mid" pregnancy (n = 264). We estimated the periods when parturition seemed really unlikely using the samples identifying "no or early" pregnancy for females for whom at least one potential period of parturition could be estimated (n = 192). We considered gestation period lasts 375 days (Ncube *et al.* 2011), and we added 15 days uncertainty around our periods estimations.

Then, on the one hand, we searched for overlaps between the potential periods of parturition predicted; on the other hand, we searched for overlaps between the periods during which parturition seemed very unlikely. We only kept periods supported by at least two different samples (n = 65 and 50 for potential periods of parturition and periods during which parturition seemed very unlikely, respectively).

We finally removed the very unlikely periods of parturition from overlapping potential periods of parturition. We took the middle of the estimated period as date of birth (*DOB*), and the range of the potential period of birth divided by 2 as uncertainty (*Acc*) around the date of birth (n = 64).

We checked for redundancy between periods of parturition estimated via the hormones samples and foals observed in the field by looking for overlaps between the potential periods

of births of those two categories of individuals. For foals observed in the field, we defined the potential period of birth as the period spanning the time interval [*DOB-Acc; DOB+Acc*]. We found $n = 28$ individuals estimated thanks to hormones samples that were effectively observed in the field and removed them from our dataset of foals identified thanks to hormones samples. We finally checked for estimated periods of birth (*via* hormones samples) not overlapping any known potential period of birth (*via* field observations), but happening too close to another date of birth, *i.e.,* in a time interval <375 days (*i.e.,* one gestation length) ($n = 9$). We removed them too from our dataset of foals identified thanks to hormones samples. We finally added $n = 27$ unseen foals estimated via hormones samples to our final dataset.

Supporting information 3

Model selection.

Foals

1. Recapture p (with survival fixed as Phi~age_class):

Model	Number of parameters	AICc	Deviance	ΔAICc
Phi(~age_class)p(~td + time)	**28**	**1720.978**	**1662.852**	**0**
Phi(~age_class)p(~td + age_class + time)	**31**	**1721.953**	**1657.345**	**0.975**
Phi(~age_class)p(~td + tids)	7	1732.806	1718.663	11.828
Phi(~age_class)p(~td + age_class + tids)	10	1733.479	1713.197	12.501
Phi(~age_class)p(~td + season)	7	1735.142	1720.999	14.164
Phi(~age_class)p(~td + age_class + season)	10	1736.166	1715.885	15.188
Phi(~age_class)p(~td + age_class * tids)	13	1738.033	1711.566	17.055
Phi(~age_class)p(~td)	6	1739.86	1727.754	18.882
Phi(~age_class)p(~td + age_class)	9	1740.152	1721.922	19.174
Phi(~age_class)p(~td + age_class * season)	13	1740.792	1714.325	19.814
Phi(~age_class)p(~td + age_class * time)	97	1806.36	1585.005	85.382
Phi(~age_class)p(~1)	5	1835.724	1226.94	114.746

td = trap dependence, tids = proportion of time spent in dry season.

2. Survival Phi (with recapture fixed as p~td):

Model	Number of parameters	AICc	Deviance	ΔAICc
Phi(~age_class)p(~td)	**6**	**1739.86**	**1727.754**	**0**
Phi(~foal_old + yearl + adult + tids:foye)p(~td)	**7**	**1740.484**	**1726.342**	**0.624**
Phi(~foal_old + yearl + adult + tids:foal_old)p(~td)	**7**	**1740.523**	**1726.38**	**0.662**
Phi(~foal_old + yearl + adult + season:foal_old)p(~td)	**7**	**1740.851**	**1726.708**	**0.99**
Phi(~age_class + tids)p(~td)	**7**	**1741.097**	**1726.954**	**1.236**
Phi(~age_class + season)p(~td)	**7**	**1741.404**	**1727.261**	**1.543**
Phi(~foal_old + yearl + adult + tids:juve)p(~td)	**7**	**1741.434**	**1727.291**	**1.574**
Phi(~foal_old + yearl + adult + tids:yearl)p(~td)	**7**	**1741.632**	**1727.489**	**1.771**
Phi(~foal_old + yearl + adult + tids:foal)p(~td)	**7**	**1741.681**	**1727.538**	**1.82**
Phi(~foal_old + yearl + adult + season:yearl)p(~td)	**7**	**1741.839**	**1727.696**	**1.978**
Phi(~foal_old + yearl + adult + tids:foal_young)p(~td)	7	1741.893	1727.751	2.033
Phi(~foal_old + yearl + adult + tids:foal_old + tids:yearl)p(~td)	8	1742.1	1725.917	2.24
Phi(~foal_old + yearl + adult + tids:foal_young + tids:foal_old)p(~td)	8	1742.561	1726.377	2.7
Phi(~foal_old + yearl + adult + season:foal_old + season:yearl)p(~td)	8	1742.866	1726.683	3.006

Phi(~foal_old + yearl + adult + season:foal)p(~td)	8	1743.051	1726.868	3.191
Phi(~foal_old + yearl + adult + season:juve)p(~td)	8	1743.421	1727.238	3.561
Phi(~foal_old + yearl + adult + season:foye)p(~td)	8	1743.644	1727.46	3.784
Phi(~foal_old + yearl + adult + season:foal_young)p(~td)	8	1743.72	1727.536	3.86
Phi(~foal_old + yearl + adult + tids:foal_young + tids:foal_old + tids:yearl)p(~td)	9	1744.143	1725.913	4.283
Phi(~foal_old + yearl + adult + season:foal_young + season:foal_old)p(~td)	9	1744.647	1726.418	4.787
Phi(~age_class * tids)p(~td)	10	1745.445	1725.164	5.585
Phi(~age_class * season)p(~td)	10	1746.673	1726.392	6.813
Phi(~foal_old + yearl + adult + season:foal_young + season:foal_old + season:yearl)p(~td)	10	1746.674	1726.392	6.813
Phi(~age_class + time)p(~td)	28	1753.361	1695.235	13.501
Phi(~foal_old + yearl + adult + time:juve)p(~td)	29	1754.955	1694.675	15.095
Phi(~foal_old + yearl + adult + time:foal)p(~td)	29	1756.195	1695.915	16.335
Phi(~foal_old + yearl + adult + time:foal_young)p(~td)	29	1757.45	1697.17	17.59
Phi(~foal_old + yearl + adult + time:foal_young + tids:foal_old)p(~td)	30	1758.054	1695.613	18.193
Phi(~foal_old + yearl + adult + time:foal_young + tids:foal_old + tids:yearl)p(~td)	31	1759.814	1695.207	19.953
Phi(~foal_old + yearl + adult + time:foye)p(~td)	29	1762.422	1702.141	22.561
Phi(~foal_old + yearl + adult + time:yearl)p(~td)	28	1768.558	1710.432	28.698
Phi(~foal_old + yearl + adult + time:foal_old)p(~td)	28	1770.896	1712.77	31.035
Phi(~foal_old + yearl + adult + time:foal_old + tids:yearl)p(~td)	29	1772.66	1712.38	32.8
Phi(~1)p(~td)	3	1821.533	1815.503	81.673
Phi(~age_class * time)p(~td)	94	1865.301	1651.714	125.441

td = trap dependence; tids = proportion of time spent in dry season; foal = foal_young and foal_old gathered; foye =foal_old and yearling gathered; juve = foal_young, foal_old and yearling gathered.

3. Recapture p and survival Phi (combination of all the recapture and survival models with ΔAICc < 2):

Model	**Number of parameters**	**AICc**	**Deviance**	**ΔAICc**
Phi(~foal_old + yearl + adult + tids:foye)p(~td + time)	**29**	**1718.922**	**1658.641**	**0**
Phi(~foal_old + yearl + adult + tids:foye)p(~td + age_class + time)	**32**	**1719.827**	**1653.049**	**0.906**
Phi(~foal_old + yearl + adult + tids:foal_old)p(~td + time)	**29**	**1720.134**	**1659.853**	**1.212**
Phi(~age_class + tids)p(~td + time)	**29**	**1720.291**	**1660.011**	**1.37**
Phi(~age_class)p(~td + time)	28	1720.978	1662.852	2.056

Phi(~foal_old + yearl + adult + tids:foal_old)p(~td + age_class + time)	32	1721.011	1654.232	2.089
Phi(~foal_old + yearl + adult + tids:juve)p(~td + time)	29	1721.189	1660.908	2.267
Phi(~age_class + tids)p(~td + age_class + time)	32	1721.377	1654.598	2.455
Phi(~foal_old + yearl + adult + season:foal_old)p(~td + time)	29	1721.737	1661.456	2.815
Phi(~age_class + season)p(~td + time)	29	1721.926	1661.645	3.004
Phi(~age_class)p(~td + age_class + time)	31	1721.953	1657.345	3.031
Phi(~foal_old + yearl + adult + tids:yearl)p(~td + time)	29	1721.997	1661.717	3.076
Phi(~foal_old + yearl + adult + tids:juve)p(~td + age_class + time)	32	1722.258	1655.479	3.336
Phi(~foal_old + yearl + adult + tids:foal)p(~td + time)	29	1722.283	1662.003	3.362
Phi(~foal_old + yearl + adult + season:foal_old)p(~td + age_class + time)	32	1722.8	1656.021	3.879
Phi(~foal_old + yearl + adult + tids:yearl)p(~td + age_class + time)	32	1723.024	1656.245	4.103
Phi(~age_class + season)p(~td + age_class + time)	32	1723.053	1656.274	4.132
Phi(~foal_old + yearl + adult + season:yearl)p(~td + time)	29	1723.128	1662.848	4.207
Phi(~foal_old + yearl + adult + tids:foal)p(~td + age_class + time)	32	1723.264	1656.485	4.342
Phi(~foal_old + yearl + adult + season:yearl)p(~td + age_class + time)	32	1724.12	1657.341	5.198
Phi(~1)p(~td + time)	25	1807.532	1755.837	88.61
Phi(~1)p(~td + age_class + time)	28	1809.927	1751.801	91.005
Phi(~age_class)p(~1)	5	1835.724	1226.94	116.802
Phi(~age_class + season)p(~1)	6	1836.028	1225.213	117.106
Phi(~foal_old + yearl + adult + tids:foal_old)p(~1)	6	1836.36	1225.545	117.438
Phi(~foal_old + yearl + adult + season:foal_old)p(~1)	6	1836.432	1225.617	117.51
Phi(~foal_old + yearl + adult + tids:foye)p(~1)	6	1836.757	1225.942	117.835
Phi(~age_class + tids)p(~1)	6	1836.761	1225.946	117.839
Phi(~foal_old + yearl + adult + tids:juve)p(~1)	6	1837.007	1226.193	118.086
Phi(~foal_old + yearl + adult + tids:foal)p(~1)	6	1837.063	1226.249	118.142
Phi(~foal_old + yearl + adult + season:yearl)p(~1)	6	1837.641	1226.827	118.72
Phi(~foal_old + yearl + adult + tids:yearl)p(~1)	6	1837.699	1226.884	118.777
Phi(~1)p(~1)	2	1925.597	1322.874	206.675

td = trap dependence; tids = proportion of time spent in dry season; foal = foal_young and foal_old gathered; foye =foal_old and yearling gathered.

Mares

1. Recapture p (with survival fixed as S~sight and transition fixed as Psi~1):

Model	Number of parameters	AICc	Deviance	ΔAICc
S(~sight)p(~td + repro_status + time)Psi(~1)	**28**	**3327.278**	**3269.773**	**0**
S(~sight)p(~td + repro_status * time)Psi(~1)	50	3345.659	3240.834	18.382
S(~sight)p(~td + repro_status * season)Psi(~1)	8	3365.045	3348.914	37.768
S(~sight)p(~td + repro_status + season)Psi(~1)	7	3366.032	3351.93	38.754
S(~sight)p(~td + repro_status + tids)Psi(~1)	7	3388.819	3374.717	61.541
S(~sight)p(~td + repro_status * tids)Psi(~1)	8	3389.763	3373.632	62.485
S(~sight)p(~td + repro_status)Psi(~1)	6	3411.854	3399.778	84.577
S(~sight)p(~td + time)Psi(~1)	27	3552.193	3496.793	224.915
S(~sight)p(~td + season)Psi(~1)	6	3587.921	3575.845	260.643
S(~sight)p(~td + tids)Psi(~1)	6	3598.026	3585.949	270.748
S(~sight)p(~td)Psi(~1)	5	3605.565	3595.51	278.287
S(~sight)p(~1)Psi(~1)	4	3621.583	2566.376	294.306

td = trap dependence; tids = proportion of time spent in dry season; sight = first capture or not for a given female; repro_status = reproductive state.

2. Survival S (with recapture fixed as p~td and transition fixed as Psi~1):

Model	Number of parameters	AICc	Deviance	ΔAICc
S(~sight + repro_status + tids)p(~td)Psi(~1)	**7**	**3594.039**	**3579.937**	**0**
S(~sight + repro_status * tids)p(~td)Psi(~1)	**8**	**3595.366**	**3579.235**	**1.328**
S(~sight + repro_status)p(~td)Psi(~1)	6	3599.6	3587.524	5.561
S(~sight + tids)p(~td)Psi(~1)	6	3599.857	3587.78	5.818
S(~sight + repro_status + season)p(~td)Psi(~1)	7	3601.625	3587.524	7.587
S(~sight + repro_status * season)p(~td)Psi(~1)	8	3603.406	3587.274	9.367
S(~sight)p(~td)Psi(~1)	5	3605.565	3595.51	11.526
S(~sight + repro_status + time)p(~td)Psi(~1)	28	3606.548	3549.043	12.51
S(~sight + season)p(~td)Psi(~1)	6	3607.532	3595.456	13.493
S(~sight + time)p(~td)Psi(~1)	27	3609.906	3554.506	15.867
S(~1)p(~td)Psi(~1)	4	3618.612	3610.576	24.573
S(~sight + repro_status * time)p(~td)Psi(~1)	50	3635.119	3530.294	41.081

td = trap dependence; tids = proportion of time spent in dry season; sight = first capture or not for a given female; repro_status = reproductive state.

3. Transition Psi (with recapture fixed as p~td and survival fixed as S~sight):

Model	Number of parameters	AICc	Deviance	ΔAICc
S(~sight)p(~td)Psi(~time + repro_status:to_repro_status)	**28**	**3366.042**	**3308.537**	**0**
S(~sight)p(~td)Psi(~-1 + season:repro_status:to_repro_status)	8	3374.425	3358.294	8.383

S(~sight)p(~td)Psi(~season + repro_status:to_repro_status)	7	3375.155	3361.053	9.113
S(~sight)p(~td)Psi(~-1 + time:repro_status:to_repro_status)	50	3393.9	3289.075	27.858
S(~sight)p(~td)Psi(~tids + repro_status:to_repro_status)	7	3398.862	3384.76	32.82
S(~sight)p(~td)Psi(~-1 + repro_status:to_repro_status)	6	3410.582	3398.506	44.54
S(~sight)p(~td)Psi(~time)	27	3586.434	3531.034	220.392
S(~sight)p(~td)Psi(~season)	6	3599.911	3587.835	233.869
S(~sight)p(~td)Psi(~tids)	6	3605.206	3593.13	239.164
S(~sight)p(~td)Psi(~1)	5	3605.565	3595.51	239.523
S(~sight)p(~td)Psi(~-1 + tids:repro_status:to_repro_status)	6	3618.762	3606.686	252.72

td = trap dependence; tids = proportion of time spent in dry season; sight = first capture or not for a given female; repro_status = reproductive state of departure; to_repro_status = reproductive state of arrival.

4. Recapture p, survival S and transition Psi. When there was only one competing model emerging from the previous selection (*i.e.,* for recapture and transition models), we included the two first models in the present model selection, even if the second one was not within ΔAICc < 2 of the first one:

Model	**Number of parameters**	**AICc**	**Deviance**	**ΔAICc**
S(~sight + repro_status + tids)p(~td + repro_status + time)Psi(~-1 + season:repro_status:to_repro_status)	**33**	**3294.197**	**3226.108**	**0**
S(~sight + repro_status * tids)p(~td + repro_status + time)Psi(~-1 + season:repro_status:to_repro_status)	**34**	**3295.161**	**3224.943**	**0.964**
S(~sight + repro_status + tids)p(~td + repro_status + time)Psi(~time + repro_status:to_repro_status)	53	3299.564	3188.134	5.367
S(~sight + repro_status * tids)p(~td + repro_status + time)Psi(~time + repro_status:to_repro_status)	54	3300.039	3186.398	5.842
S(~sight + repro_status + tids)p(~td + repro_status * time)Psi(~-1 + season:repro_status:to_repro_status)	55	3301.739	3185.884	7.542
S(~sight + repro_status * tids)p(~td + repro_status * time)Psi(~-1 + season:repro_status:to_repro_status)	56	3301.809	3183.734	7.612
S(~sight + repro_status + tids)p(~td + repro_status + time)Psi(~1)	30	3310.19	3248.463	15.993
S(~sight + repro_status * tids)p(~td + repro_status + time)Psi(~1)	31	3312.076	3248.232	17.879
S(~sight + repro_status * tids)p(~td + repro_status * time)Psi(~time + repro_status:to_repro_status)	76	3318.984	3155.632	24.787
S(~1)p(~td + repro_status + time)Psi(~-1 + season:repro_status:to_repro_status)	30	3320.113	3258.386	25.916

S(~1)p(~td + repro_status + time)Psi(~time + repro_status:to_repro_status)	50	3325.235	3220.41	31.038
S(~sight + repro_status + tids)p(~td + repro_status * time)Psi(~time + repro_status:to_repro_status)	75	3326.789	3165.742	32.592
S(~1)p(~td + repro_status * time)Psi(~-1 + season:repro_status:to_repro_status)	52	3328.386	3219.161	34.189
S(~sight + repro_status + tids)p(~td + repro_status * time)Psi(~1)	52	3329.551	3220.326	35.354
S(~sight + repro_status * tids)p(~td + repro_status * time)Psi(~1)	53	3331.626	3220.195	37.429
S(~1)p(~td + repro_status + time)Psi(~1)	27	3336.137	3280.736	41.94
S(~1)p(~td + repro_status * time)Psi(~time + repro_status:to_repro_status)	72	3351.159	3197.002	56.962
S(~1)p(~td + repro_status * time)Psi(~1)	49	3355.938	3253.307	61.741
S(~sight + repro_status + tids)p(~1)Psi(~time + repro_status:to_repro_status)	29	3370.636	2263.852	76.439
S(~sight + repro_status * tids)p(~1)Psi(~time + repro_status:to_repro_status)	30	3372.15	2263.253	77.953
S(~sight + repro_status + tids)p(~1)Psi(~-1 + season:repro_status:to_repro_status)	9	3377.376	2312.041	83.179
S(~sight + repro_status * tids)p(~1)Psi(~-1 + season:repro_status:to_repro_status)	10	3378.891	2311.519	84.694
S(~1)p(~1)Psi(~time + repro_status:to_repro_status)	26	3398.165	2297.696	103.968
S(~1)p(~1)Psi(~-1 + season:repro_status:to_repro_status)	6	3406.7	2347.453	112.503
S(~sight + repro_status + tids)p(~1)Psi(~1)	6	3611.275	2552.028	317.078
S(~sight + repro_status * tids)p(~1)Psi(~1)	7	3612.627	2551.355	318.43
S(~1)p(~1)Psi(~1)	3	3637.862	2584.669	343.665

td = trap dependence; tids = proportion of time spent in dry season; sight = first capture or not for a given female; repro_status = reproductive state of departure; to_repro_status = reproductive state of arrival.

Supporting information 4

Another approach to estimating foals survival.

In addition to the CMR approach, we estimated foal survival using a different approach based on the assumption that a foal under six months of age (*i.e.,* younger foal in our analyses) is still fully dependent on its mother and cannot survive without its mother. Based on this assumption, we considered each foal seen at least once after its date of birth and for which the mother was re-observed at least once between the first observation of her foal and six months after her foal's date of birth (n = 37). Even if the results could be less reliable because after six months old, foals can sometimes survive without their mother (Smuts 1976), we also included this age class to estimate the probability of survival for older foals (*i.e.,* between six and 12 months old, n = 126). For both foal age classes (modelled as a categorical variable with two categories, *i.e.,* younger foal of less than six months old and older foal between six and 12 months old), if the mother was seen alone, the foal was considered to be dead (0), whereas if the foal was also seen during the same field session, the foal was considered to be alive (1). For foals whose mother was seen more than once between the first observation of the foal after its date of birth and 12 months after its date of birth, we kept the last observation only to prevent intra-individual repetitions.

We fitted two logistic regressions to the data, with (assumed) death or survival as response variable, and age class of the foal at the end of the interval considered and the proportion of days in dry season experienced since birth at the re-observation of the mother (*tids_2*) as predictors. In the first model, we added the interaction between the age class and *tids_2*, whereas in the second one we only looked at the effect of *tids_2* on older foals. When the foal was assumed dead, there was no way to precisely know the duration spent in dry season before death because this date was unknown. We also included the duration between the first observation of the foal and the re-observation of its mother as an additive predictor in both models to account for the fact that death is more likely as time passes.

Both models were less than 2 AIC units apart from each other ($AIC_{age_class*tids_2}$ = 195.673 and $AIC_{foal_young+foal_old*tids_2}$ = 194.144). We focused on the model where *tids_2* acts solely on older foals to compare with the CMR approach. We found a significant effect of duration between first observation of the foal and the re-observation of its mother (logit scale: β = -0.015 ± 0.003, $p < 0.001$), but no significant effect of *tids_2* on the survival of older foals (logit scale: β = -0.017 ± 0.014, p = 0.223). Nevertheless, even if the trend was not statistically

significant, the probability of survival of older foals tended to decrease with an increased proportion of time spent in dry season, similarly to what was found with the CMR approach (Fig. S4-1). Our results were also very similar to what we found with the CMR approach concerning younger foals, as they had a mean survival of 0.374 ± 0.090 SE, 85 % CI [0.255; 0.510] (see Results section).

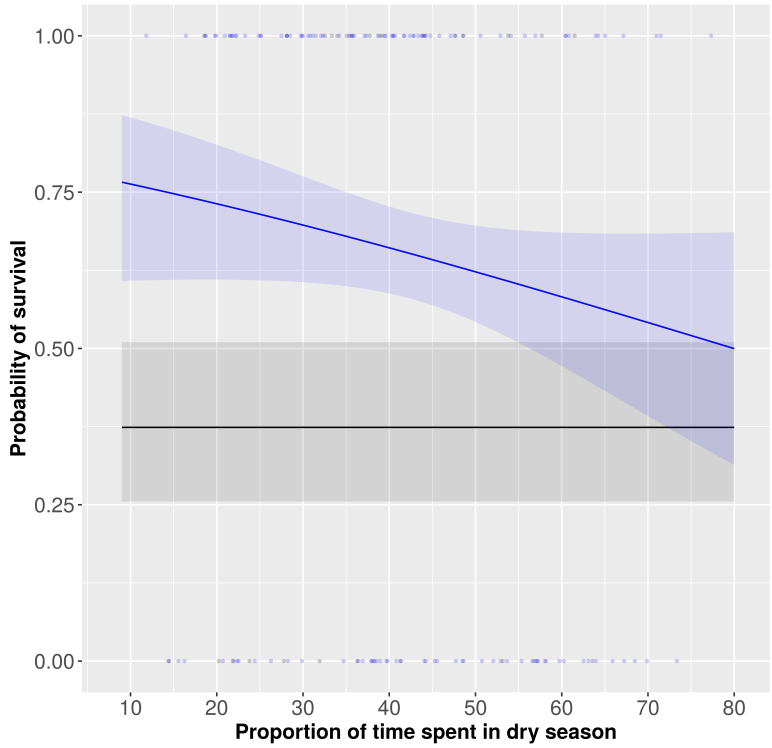

Figure S4-1: survival according to the proportion of time spent in dry season between birth and last re-observation of the mother (before the first year of the foal) for younger foals (black items, n = 67) and older foals (blue items, n = 126), in plains zebra foals born in Hwange National Park between 2008 and 2019. For representation purpose, the proportion of time spent in dry season was truncated to match the one of the CMR approach, i.e., between 9 % and 80 %. The time elapsed between the first observation of the foal and the re-observation of its mother was fixed to six months (to match the CMR framework). The shaded dots represent the state of the foal at its mother re-observation (0 = dead, 1 = alive). The solid lines represent the predicted values from the model, for younger (black) and older (blue) foals. The shaded areas represent 85% confidence interval (for comparison purpose with the CMR approach) of these predicted values.

The lower survival estimated using this approach, compared to the estimate from the CMR approach, could come from the fact that sometimes (*e.g.,* observations in dense habitats), mothers are seen without their foal even if the foal is still alive (foal seen again later while its

mother was seen alone before it reaches 12 months old), but it seems unlikely as we found only two foals in this case. However, the GLM was conducted on a smaller sample as the mother had to been seen at least once between parturition and one year after for the foal to be included in this analysis. The effect of the proportion of time spent in dry season on older foals survival was less strong with the GLM approach than with the CMR approach, but the overall older foals survival was quite similar (see Results section). It is worth noting that yearlings could not be considered in the GLM approach because their survival cannot be assessed according to their mother re-observation anymore. This could alter the comparability of the results of the CMR and the GLM approaches, as older foals and yearlings were gathered in the CMR approach only. They participated in the determination of the coefficient of the slope of *tids*, which thus could not reflect what happens with older foals only.

References Supporting information

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Ncube, H. *et al.* 2011. Pattern of faecal 20-oxopregnane and oestrogen concentrations during pregnancy in wild plains zebra mares. - Gen. Comp. Endocrinol. 172: 358–362.

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General discussion

Summary of the results

The aims of my thesis were to explore the different steps of the study of phenology, from data collection to the interpretation of final results, and to provide methodological and ecological prospects on the phenology of births in mammals. I intended to validate or invalidate a new data collection methodology, to provide a summary and some guidelines to best describe phenology and to explore the relationship between environment, timing of birth and survival in a tropical mammal. To do so, I focused my analyses on large herbivores, a group particularly suitable to achieve such goals as it illustrates a wide part of the variability of life history traits encountered in mammals in general and it is characterized by a high diversity of habitats and conditions. I first investigated the usability of camera trapping combined with citizen science as a data collection tool to assess the phenology of births of three large African herbivores as a study case. Then, I questioned the diversity of metrics used so far to describe the phenology of births in large herbivores, their pros and cons, and provided guidelines to encourage a common framework across studies. Finally, I explored the consequences of the timing of birth on juveniles and females survival in the plains zebra, according to the duration of the dry season they experienced during different life history stages.

In the first chapter, I addressed the question of data collection in the context of birth phenology. Camera traps are booming rapidly, and scientists start to glimpse their use not only to study the occupancy of the species, but also their behaviours and even phenology. Those new applications still need to be tested and validated. I highlighted the fact that, when working with camera traps, a high number of pictures are not relevant to study the specific question of birth phenology. Once those irrelevant data are removed, the final number of pictures available could be reduced by a factor of 10 000, as in my case study: the Snapshot Serengeti program, which is currently the largest dataset of its kind. The identification of the presence of very young individuals (< 1 month old) in the pictures thanks to morphological criteria provided consistent results between trained observers, particularly when studying large species living in small groups (*Fleiss'* $\kappa > 0.61$). However, volunteers were only able to detect the absence of very young individuals when they were asked to focus on the presence or absence of "young" in general. Without the good assessment of the presence of very young individuals in the pictures, it is not possible to estimate dates of birth. Thus, without additional guidelines and references for the volunteers to identify very young individuals, the combination of camera trapping and

citizen science do not provide accurate enough data to study the phenology of births in large African herbivores.

In the second chapter, I focused on the methods used to describe the phenology of births in the large herbivore literature. In the studies reviewed, I identified at least five different metrics (up to 25) used to describe each of the four main characteristics of phenology: timing, which corresponds to the position of births in the year; synchrony, which corresponds to the spread of births in the year; rhythmicity and regularity, which correspond to the consistency of timing and synchrony respectively across the years. Among each of those four categories, most of the metrics were significantly correlated when applied to the same simulated phenology of births, whatever the shape of the phenology (*i.e.,* normal or asymmetric, except in the case of random distributions). Using a set of criteria developed to favour comparison between studies to evaluate the relevance of the metrics, I identified at least one suitable metric for each phenology characteristic. With this simulation work, I also identified metrics that should be avoided because they are irrelevant or have undesirable statistical properties. I finally showed the low number of studies describing rhythmicity and regularity in the long term through the low number of metrics associated with both characteristics and the fact that each of them has rarely been used in empirical studies so far.

In the third chapter, I moved to a dataset based on direct field observations as camera trapping combined with citizen science was not satisfactory to study the phenology of births. I explored the impact of the timing of birth on individual survival through the environmental conditions experienced at birth and during the following stages of life. I found no effect of the season. The annual survival of foals of less than six months old (*i.e.,* still dependent on their mother) was not affected by the time spent in dry season since birth either. To the contrary, the annual survival of older foals (between six and twelve months old) and yearlings decreased with an increasing proportion of time spent in dry season at this period of their life. The annual survival of reproductive and non-reproductive mares was negatively affected by the proportion of time spent in dry season too, but the effect was stronger for non-reproductive mares, possibly denoting some quality difference between them. Thus, I illustrated that the phenology of births affects cohorts survival through the determination of the external conditions experienced by the juveniles at a critical period of their life. However, the precise mechanisms are still to be assessed. The phenology of births could affect population dynamics: as climate change should favour longer and harsher dry seasons in the near future, the consequences of such changes could be detrimental to the demography of tropical species of large herbivores such as plains zebra.

During my thesis, I have focused on the estimation and the study of the phenology of births *in natura*. Even if such data are particularly relevant to study the natural distribution of births governed by the numerous intertwining factors met in real life, it is nevertheless jeopardized by several methodological limitations, sometimes limiting our ability to draw clear conclusions.

Limits of observations in natura

Difficulties related to observations in natura

Direct observations *in natura*, such as done in **chapter 3**, are of particular interest to study populations in their natural environment, with limited disturbance and little equipment. However, observations when studying the phenology of births are particularly challenging to collect. As it is almost impossible to document births in natural conditions, the date of birth must be estimated from the age of the offspring when first spotted. In the case of altricial or hider species, it is possible to capture offspring soon after birth if the nest is accessible, which is a real advantage to precisely assign an age (*e.g.,* Gaillard *et al.* 1993b, Williams *et al.* 2013), but this technique requires searching for the offspring. When studying precocial species such as plains zebra, offspring can be identified during routine censuses, the method we used in our study. Although juveniles are theoretically visible as soon as they are born, age estimation can sometimes be less precise because most of the juveniles are seen when there are already few days to few months old, or because they are too numerous to be precisely spotted (*e.g.,* with zebra in Ogutu *et al.* 2008).

In our study, the uncertainty around the date of birth ranged between ± zero day (*i.e.,* when the birth is observed or when the foal is still wet from birth) and 90 days. Such uncertainty also comes from the short time window of presence in the field, ranging from 13 to 88 days every six months. Those uncertainties lead to coarse patterns of births and implies difficulties to clearly test the role of fine ecological and environmental processes with empirical data, such as the effect of food resource availability, but also predation or life history traits on the synchrony of births (Zerbe *et al.* 2012). This is also true for the estimation of the effect of the precise timing of birth on newborn survival in our case. Uncertainty on the date of birth may limit the statistical robustness and produce inconclusive results. That is why it is advisable, when possible, to reinforce the validity of the conclusions drawn using various methodologies or changing the data resolution/data quantity ratio, as done in **chapter 3**.

Besides, the date of birth can also be estimated *via* other field methods, such as using physical and behavioural observations of the mother (in both altricial and precocial species) if the observations occur soon after birth, or using opportunistic faecal sampling for dosage of reproductive hormones (see **chapter 3** and Ncube *et al.* 2011). Such methods are particularly useful in the case of early newborn loss (Williams *et al.* 2013), something happening quite frequently in our system because of a high level of predation (and probably of other forms of mortality too) on juveniles. In any case, an intensive monitoring of a population is necessary to characterise its phenology of births (Festa-Bianchet 1988). However, maintaining a sufficient search effort is time-consuming and expensive, particularly if births are not significantly synchronous, such as with plains zebra. Thus, the precision of the phenology of births often depends on the ability to precisely assign a date of birth to each juvenile, but also on the frequency of censuses in the field. Nevertheless, it has rarely been accounted for, nor has it been quantified in most of the studies so far: in **chapter 2**, I identified only a very few metrics accounting for data resolution (*e.g.,* Johnson *et al.* 2004).

Alternative methods to direct observations in natura

Automated data collection such as pictures provided by camera traps and classified by volunteers I illustrated in **chapter 1** offers an appealing solution to at least some of those limitations. However, I have shown that improvements are still needed to be able to use such methods for the study of the phenology of birth. Indeed, poorly documented phenology of births could lead to misinterpretations, such as over estimation of the level of synchrony because of multiple counting (similarly, Johansson and colleagues illustrated that identification errors lead to overestimation of the population abundance, Johansson *et al.* 2020) or a lack of information for a part of the year in the case of local migration. Although it is sedentary in our study site, the Serengeti National Park, topi can do short-distance migrations elsewhere, like in Uganda (Jewell1 972). Thus, even when considering that the age is correctly assessed, which seems unlikely in a wild population, the detection probability and the frequent multiple counting of the same individual need to be accounted for. Using models that describes the rate of contact between animals and camera traps developed for density estimation studies based on populations where individual recognition is impossible could be a solution (Rowcliffe *et al.* 2008). In addition, the location of the camera traps should be chosen according to the species biology, such as its home range, daily travelled distance, group size and population density in the study site (Rowcliffe *et al.* 2008). Individual identification is sometimes possible, depending

on the species studied and the size of the population. It has already been successfully tested on giraffes (Miele *et al.* 2021). It is also worth noting that camera trapping has proven to be efficient to determine the phenology of births in the case of species which are static during breeding, such as ground-nesting seabirds (Hinke *et al.* 2018).

To circumvent those limitations, it is also possible to study reproductive phenology in controlled conditions for a limited number of known individuals (*e.g.,* Berger *et al.* 1977, Gemmell and Sernia 1992, Porter and Wilkinson 2001). Such methods allow to assess the precise effect of the factor studied (*e.g.,* photoperiod or temperature variations, social cues, food availability), but they only provide a narrow vision of all the mechanisms at stake and of their interactions. Moreover, experimental designs are almost impossible to conduct on wild large mammals, because of their cost, and the space and husbandry requirements of those species. However, partially controlled conditions can be used with captive or temporarily held populations, which permit control over food resources or social cues. Using such framework, Sempéré and colleagues demonstrated that the reproductive cycle of roe deer is initiated by short days and interrupted by long days using melatonin implants and experimentally modified photoperiod (Sempéré *et al.* 1995). Calabrese and colleagues provided evidence that ovulation is synchronized by male rutting calls in wildebeest using playbacks on captured female (Calabrese *et al.* 2018).

As an intermediary method, it could be interesting to investigate the variations of the phenology of births in a wild population, well known in terms of demographic and reproductive parameters and living in a well characterized environment, as it is the case with the population of roe deer living in the Territoire d'Étude et d'Expérimentation of Trois Fontaines, France. This population, living in an enclosed area of 1 360 ha and intensively followed since 1985 fits this description (Gaillard *et al.* 1993b, Plard *et al.* 2014b, Gaudry *et al.* 2018). Building on the findings of **chapter 2**, it could be feasible to identify typologies of phenology of births (*e.g.,* early spread births, late synchronous births) and to relate them to combinations of environmental variables such as temperature, rainfall or NDVI (*e.g.,* hot productive year, cold unproductive year).

Several methodological limitations exist when studying the phenology of births *in natura*, which can be reduced or accounted for using the adequate sampling protocols and analytical methods. However, some biological limitations can also be raised. Mammals range from species of a few grams living around one year such as shrews, to species of more than a hundred tonnes living more than five decades, like the blue whale. Such differences are

responsible for many different life history traits related to their reproductive biology, and need to be accounted for if comparison and general conclusions are to be drawn.

Phenology of births and allometry

Allometry in the reproductive biology of mammals

Allometry, which initially refers to the study of proportional relationships between the growth of the different organs of an organism (Huxley and Teissier 1936), is nowadays also employed to describe the proportional relationship between physiological, behavioural, or ecological characteristics of organisms with their size or body mass. Allometric relationships participate in the regulation of the life cycle of the organisms by adding supplementary constraints to the existing environmental ones on organisms. The latter have thus to deal with both a specific physiological timing and a common astronomical timing in the regulation of their life cycle (Lindstedt and Calder 1981, Calder 1983). The role of allometric relationships in reproduction has already largely been illustrated, through differential gestation length (Kihlström 1972), energy allocation (Gittleman and Thompson 1988) and reproductive effort (Blueweiss *et al.* 1978) for instance. Small species whose energetic costs are huge during intensive reproductive periods (post-partum oestrus permits the production of several litters in a very short period of time) mainly depend on short term climatic variations (Bronson 1989). Large species with low energetic costs and slow offspring development (one complete reproductive cycle per year or even less) mainly depend on long-term climatic variations (Bronson 1989). Thus, the phenology of births in large mammals is more predictable, whereas it is more sensitive to intra-annual variations in small mammals.

Inclusion of allometry when considering phenology of births

Although the methods used to collect data about the phenology of births in mammals can be similar between small and large species (compare Lambin 1993 and Gaillard *et al.* 1993b), a unique monitoring and sampling design seem unlikely. With camera trapping explored in **chapter 1**, a basic consideration, the body size of the species, should be considered when placing the cameras, and restrict comparison to species of similar size only (Fig. 1). However, multi-specific comparisons have proven to be of particular interest to empirically testing theoretical hypotheses about life history traits related to the phenology of births. For instance, the level of birth synchrony should depend on the location of the species on the hider-follower continuum (follower species should be born more synchronously, Rutberg 1987), a theory

which is often questioned by empirical data because it frequently do not find strong support (*e.g.,* Ogutu *et al.* 2014).

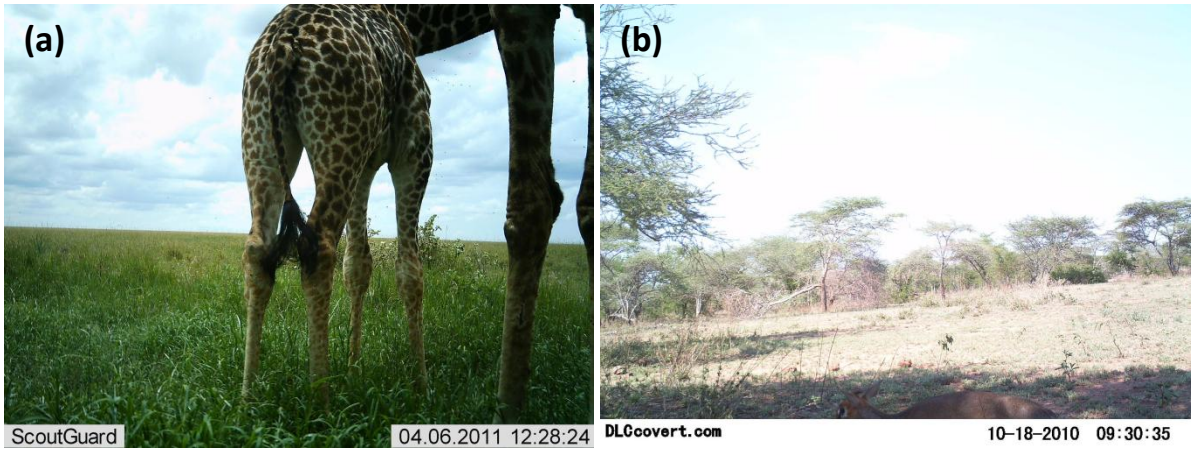

Figure 1: The choice of a standard height for camera traps is not adapted to small and large species at once, because they are not visible in the same scale. a) an adult giraffe with a calf of unknown age. Only the legs and the body of the adult and the juvenile respectively are visible, greatly obstructing age determination; b) an adult dik-dik, without possibility to assess the presence or absence of a juvenile. The adult is barely visible on the bottom of the picture, and a potential juvenile, which is even smaller, would necessarily be off-camera.

Whatever the size of the species, the shape of the phenology of births (*i.e.,* at the population level) can be similar. However, when taking into account the individual level, the phenology of small species is often more complicated than the one of large species, because it can be composed of the close succession of several complete reproductive cycles (*i.e.,* at least one offspring of a given litter reaches the age of independence) for the same female. Thanks to postpartum oestrus, the European rabbit produces three litters per reproductive season on average and can even theoretically reach seven (von Holst *et al.* 2002). Moreover, early born females of some rodent species can breed during the same breeding season in which they were born (Bronson 1989), what can reduce synchrony by extending the period of births to a variable extent every year (*e.g.,* Lambin 1993). Thus, although it is possible to describe the phenology of births *via* its timing and synchrony as illustrated in **chapter 2** when exploring the role of environmental factors, the meaning of those descriptors could be biologically different according to the size (associated with specific life history traits) of the organism at stake, regarding synchrony and social factors for example.

Timing is a neutral way to measure the position of births, *i.e.,* whatever the size of the species, the main drivers of their timing of births are often environmental factors. Thus, one can compare the absolute timing of births of a species with the timing of another one, without

any particular biological limitation. However, it could be interesting to study the relative synchrony of births (*i.e.,* level of synchrony corrected by the size or the body mass of the species) in addition to the absolute synchrony of births (*i.e.,* the number of days gathering a certain percentage of births, for instance), especially when comparing small and large mammals. Generally in bison, 50 % of births occur within 20-27 days (Berger 1992) whereas in banded mongoose, 100 % of births occur within the same night (Hodge *et al.* 2011). Both species are gregarious species, but bison are a hundred times larger than mongoose. Although the synchrony of births in bison seems dramatically lower than the synchrony of mongoose, it could be interesting to compare their synchrony relatively to other species of their magnitude and phylogenetic groups (order of *Artiodactyla* and *Carnivora* respectively) to assess the difference in terms of relative synchrony and the role of gregariousness on the phenology of births.

In general, the papers studied in **chapter 2** focused on one single species, but when comparing several species, none looked at the relative synchrony of births. This is partly because the principal interest of those studies lied in the exploration of the role of environmental factors in the shape of the phenology of births. Moreover, we focused our analysis on large herbivores, with body size of the same order of magnitude and thus no necessity to rescale synchrony. If we expand the comparison to several groups of mammals, then the comparison of relative synchrony (regarding the physiological time of the species) could add interesting interpretations to the comparison of absolute synchrony (regarding astronomical time), regarding social factors and active synchronization (similarly, *Phocidae* have a shorter period of lactation than expected for their body mass, Hayssen 1993). Eventually, it would be interesting to review the studies empirically investigating the factors influencing the shape of the phenology of births in different species of mammals. Identifying common or divergent drivers between small and large species, suspected determinants which have not been confirmed or even explored in certain species yet, but also identifying less represented species and compare the relative synchrony of births, could provide useful insight in the comprehension of the phenology of reproduction in mammals.

Each species has different life history traits and lives in varied environments, which lead them to respond differently to various cues to time their reproduction. In the context of the current climate change, the environmental cues are changing. Phenology of births having major consequences on the population dynamics, it is critical to continue studying the modifications climate change induces in mammals' reproductive phenology.

The study of the phenology of births in the days of climate change

The need for long-term and quality data

Working on the impact of climate change on the phenology of births, its determinants and consequences requires long-term data. It is important to limit the effect of inter-annual stochasticity and consider the effect of abnormal years, such as drought or flood years (Ogutu *et al.* 2014). It is also important to better know the demographic parameters of the population which play a role in reproductive ecology, and to have enough hindsight on the life history of the individuals and cohorts to explore the consequences of the date of birth on their life (Clutton-Brock and Sheldon 2010). Above all in the context of climate change, collecting data over several decades allows to detect potential trends across the years (*e.g.,* Paoli *et al.* 2018) or to the contrary, abnormally variable patterns. It is also valuable to have enough variability in the factor of interest (in **chapter 3**: the duration of the dry season) to make predictions about the behaviour of the species of interest in response to the expected changes due to climate change (in **chapter 3**: increased duration). Finally, historical data are valuable to provide a baseline when studying the changes of phenology (Kharouba and Wolkovich 2020). Such data are often hard to find, especially for tropical species, because most of the long-term studies there have started recently relatively to the current climate changes (Abernethy *et al.* 2018, Sakai and Kitajima 2019).

A social and conservation interest

The main advantage of citizen science often put forward is a practical one (*e.g.,* greater geographical range covered, increased field detection, cost-effective data collection and/or first data sorting). However, citizen science is also an important tool to inform, raise awareness and include people in the reflections about the consequences of climate change on biodiversity and the mitigation attempts (McKinley *et al.* 2017). Even if I showed in **chapter 1** that citizen science is not effective enough yet to study the phenology of births for a scientific purpose, this approach is still of great social value. The Snapshot Serengeti Program can be (and has already been, see https://cbs.umn.edu/hhmi-grants/science-education/research-experiences/serengeti) used in an educational context to train students while making them aware of general environmental and scientific questions using charismatic fauna (Swanson *et al.* 2015).

Moreover, the knowledge of the factors driving the phenology of births of a given species, and more generally of its consequences at the population scale, can play a determinant role in the conservation of this species. The drivers of the phenology of births can inform

indirectly about the sensitivity of a species and its ability to adjust to climate change. Species whose phenology of births is mainly regulated by photoperiod variations such as roe deer should be more sensitive to climate change because they are less prone to adjust their phenology of births to direct environmental conditions (*e.g.,* Plard *et al.* 2014b, Rehnus *et al.* 2020). Thus, populations with low evolutionary potential regarding phenology of births should be targeted by conservation policies as a priority concern (Hoffmann and Sgrò 2011).

Studying the phenology of births necessitates long-term quality data. It is essential to better predict the implications of climate change on the population dynamics and persistence. Public engagement can help in data collection and analysis *via* citizen science. This is also a way to make people aware and encourage them to participate in informing and advancing policymaking and resource management to improve species conservation.

Conclusions and perspectives

During my PhD thesis work, I have first tested a new method of data collection to study the phenology of births. The use of camera trapping coupled with citizen science still needs improvements before being applicable to assess the phenology of births in large mobile herbivores. Nevertheless, it is a promising field of research: the addition of guidelines on participatory platforms, the inclusion of species characteristics in the placement of the cameras and the development of adapted models extracting the phenology of births can be the next steps to improve the method. Then, I have provided a state of the art in terms of description and measure of the phenology of births. The comparison of the outputs of the metrics based on simulated phenology has helped to identify the main characteristics of phenology and the best metrics to quantify them. I have also provided guidelines and a common framework to describe the phenology of births in a comparative context. Using simple and as universal descriptors as possible (*i.e.,* which can adjust to a large diversity of patterns and data resolutions) enhances the comparability of the studies at the multi-specific scale. Finally, building on the findings of the two previous studies, I have explored the consequences of the timing of birth on juveniles and mares survival. I have provided evidence that the proportion of time spent in dry season negatively affects both older juveniles and mares. As climate change should lead to an increasing frequency of droughts and duration of the dry seasons, the demography of zebra could be altered if no phenotypic adjustment in the timing of birth occurs.

To go further with this work, the knowledge about the phenology of births of species relying on fixed factors such as photoperiod variations should be deepened. The use of species with long-term monitoring and well-known environments as study case should be prioritized, to provide representative models of less well known or hard to study species. This could also help making predictions about their behaviour facing climate change and thus, better manage their populations. Multi-specific comparisons and reviews of existing studies seem of particular interest too in this perspective. When based on standardized protocols of data collection and description, they can be used to draw general conclusions and identify the shortcomings in terms of knowledge of a given species or a given factor responsible for the shape of the phenology of births.

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