**Seasonal biases in data collection cause conceptual gaps in animal ecology**

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**Author contribution**

Samuele Ramellini and Damien R. Farine conceived the ideas, designed the study and analysed the data; all authors contributed to data collection; Samuele Ramellini led the writing of the manuscript with insights from Damien R. Farine. All authors contributed critically to the drafts and gave final approval for publication.

**Statement of inclusion**

Our study was a global review of ecological research. This study brought together several young scientists (mostly PhD students) from different countries and backgrounds. Together, we worked from the start to define the research and design the study, which ensured diverse sets of perspectives when interpreting results.

**Conflict of Interest Statement**

The authors declare no competing interests.

## Data Availability Statement

The data used in this manuscript will be made available in figshare.

## Abstract

1. Animal life cycles are structured into seasons with major differences in behaviour. Yet much of the data that inform policy and predictive modelling is drawn from studies conducted when animals breed. This temporal research bias overlooks key seasonal and life stages in the ecology of animal populations, such as high over-winter mortality periods. Yet, it is unclear whether this bias also extends to the conceptual focus of the research questions in the ecological literature.
2. Here, we test whether there is a bias in research focused on breeding vs. non-breeding research questions. We evaluate the animal ecology literature by reviewing >6,000 studies in the last decade, discriminating between when the data were collected from what the focus of the research was. We also evaluate the methods and approaches used in each study to explore how different methodologies have contributed (or not) to closing the gap between breeding and non-breeding studies.
3. Our analysis shows that while most studies in ecology collect data during the breeding season—a pattern that has not changed over the last decade—the majority of this research asked questions about non-breeding ecology. We also show that studies conducted during the breeding season are more likely to conduct experiments and have larger sample sizes. By contrast, studies conducted during the non-breeding periods of organisms' lives relied more on indirect methodological approaches, such as biologging.
4. Our results show that the seasonal bias in ecology is one of data collection rather than research focus. While this suggests the bias in research may not be as severe as previously thought, our results reveal that our understanding of ecological processes outside of breeding are likely to have limited seasonal coverage, with persistent gaps in capturing how animals survive some of the harshest conditions that they experience.

**Keywords**:

full annual cycle; movement ecology; reproductive biology; seasonality

## 1. Introduction

The life-history of most animals is structured in distinct phases, often corresponding to seasonal environmental dynamics. One of the simplest distinctions is between the breeding and non-breeding season, which has often been linked to the differences between reproduction and survival. Understanding the interplay of these two fitness components, the survival of one generation and the production of the next, is key to provide robust predictions on which species will persist under rapid environmental change, and how. Studies commonly use modelling approaches to predict population viability (Selwood, McGeoch & Mac Nally 2015; Heinsohn *et al.* 2022), species interactions (Preisser & Strong 2004; Toby Kiers *et al.* 2010), how shifting climatic envelopes will shape the future distribution of species (Guisan & Thuiller 2005; Simoncini *et al.* 2025), and population responses to changes in phenological timing (Charmantier *et al.* 2008; Iler *et al.* 2021). However, most of these approaches are primarily informed by data collected during the reproductive period.

The presence of this strong seasonal research bias in the literature was highlighted over a decade ago by Marra *et al.* (2015). Their study showed that, on average, 61% of the research on terrestrial vertebrates has been conducted during the breeding season. In some taxa, such as amphibians and birds, this pattern was even stronger (73% and 71%, respectively). More recently, a review of studies on birds also showed a similar picture over the last 60 years, with 84.9% of the papers published in the journal "Ornithology" collecting data during the breeding season (Stewart & Conway 2026). Such a bias is not only prevalent in research but also pervasively informed policy and management practices. For example, IUCN risk assessments or distribution atlases are mostly based on breeding population evaluations, often neglecting non-breeding patterns and processes. Such focus on the breeding period has been linked to the greater ease and feasibility of obtaining data when animals are breeding.

Collecting data from wild animals is costly, logistically challenging, and time consuming. One reason why there is a persistent bias on collecting data during the breeding period is that it is far easier to do, as animals repeatedly return to the same location or restrict their movements while caring for their young. By contrasts, it is much more challenging to study the same individuals when their location and behaviour are less predictable (Farine 2025). This is exacerbated by many species expanding their home ranges outside of the breeding period (Chambers, Singleton & Krebs 2000; Volampeno, Masters & Downs 2011; Camerlenghi *et al.* 2021; Papageorgiou *et al.* 2021), or migrating to the non-breeding grounds. Similarly, many species display during the breeding period, making their presence more easily detected using breeding season surveys (e.g. because they produce and/or respond to territorial calls) than surveys outside of breeding (Zuberogoitia *et al.* 2020). Conversely, non-breeding surveys can have reduced detection probability or detections that are more context-dependent (Ramellini *et al.* 2024). The practicalities of collecting data during breeding periods also allows for collecting fitness-relevant data related to reproduction (e.g. on how many offspring are produced), which is simpler and faster to characterise than having to continuously observe individuals to estimate their survival.

While the bias in when data are collected is evident, this does not necessarily translate to a corresponding bias in what questions researchers ask. It is therefore important to distinguish between when data are collected and what questions those data are applied to. Much of evolutionary theory—going at least as far back as Darwin's theory of sexual selection (Darwin 1872)—has placed reproductive ecology firmly at the centre of our research focus. Subsequent major theories, like Hamilton's kin-selection theory (Hamilton 1964), have further reinforced this interest. Consequently, a research culture (*sensu* (Smaldino & McElreath 2016)) that has rewarded studying animals during breeding periods might have emerged. Yet many non-breeding questions, like responses to risk, personality, and communication, can be addressed when animals are breeding. Hence, the seasonal biases that we could observe could either (1) be driven by a greater focus on research questions related to breeding than non-breeding, (2) reflect both the focus and ease of collecting data when animals are breeding, or (3) could show a different pattern between when data are collected and the focus of the research being conducted. Hence, focusing only on when data were collected (Marra *et al.* 2015; Stewart & Conway 2026) might over-estimate the bias or, conversely, worsen the bias if questions not related to reproductive ecology are under-explored in the non-breeding season.

Here, we conduct a literature review of the animal ecology literature over the past decade to re-evaluate the seasonal research bias from a conceptual point of view, testing whether research questions in ecology are also biased towards studying animals during the breeding period. We quantify both when data were collected and whether the research questions are specifically focused on breeding versus non-breeding (limiting our sample to primary empirical research conducted on wild animals). We then also collect metrics allowing us to explicitly test the feasibility versus cultural (i.e. 'sexy research questions') drivers that might shape the seasonal research bias. Specifically, we record information on the approaches used in each study (e.g. direct observation, biologging), the use of experimental manipulations (as we expect that conducting manipulative experiments in the wild should be much simpler during breeding periods), and sample sizes (including the number of individuals and the tendency to re-study the same individuals in subsequent cycles). Throughout, we collate data from journals focusing on conservation biology, broad ecology, and behaviour, while also splitting our data across taxonomic groups (birds, reptiles, amphibians, non-primate mammals, and primates), allowing us to reflect on differences across these fields.

## 2. Materials and Methods

### *2.1. Literature review and data collection*

Similar to the methods used in Marra *et al.* (2015), we conducted a literature review of the ecological literature focusing on amphibians, birds, mammals, and reptiles. We reviewed papers published in the last decade (2012, 2015, 2018, 2021 and 2024), covering nine peer-reviewed journals (Ecology, Conservation Biology, Oecologia, Journal of Animal Ecology, Behavioural Ecology, Herpetologica, The Auk/Ornithology, Journal of Avian Biology, Journal of Mammalogy). Our full rubric is outlined in the Supplemental Information (SM1).

Briefly, for each study, we first evaluated whether it fits into our rubric. We included all studies with primary data collection, thus excluding models, studies based on museum specimens, or studies conducted in captivity (because seasonality is unclear). For each included study, we recorded the taxon (Aves, Mammalia, etc.) and geographic location of the study as a means of obtaining metadata on the coverage of studies we captured. We included three large-scale latitudinal regions: Tropics (i.e. between +23º and -23º latitude), North (>23º latitude) and South (<-23º latitude). Further, we recorded administrative areas to obtain a finer scale representation of the geographical coverage and separate regions that might be part of a country but spatially distinct (e.g. Alaska). We also recorded whether the study was conducted in urban or non-urban environments.

To evaluate seasonal trends in data collection, we collated information on when data were collected. We first recorded the specific months of data collection (start and end month) and whether these months fell under the focal species' breeding, non-breeding and transit periods. For breeding, we included studies conducted on breeding establishment through to offspring rearing. However, studies focused on the development of the offspring themselves (e.g. after independence) were considered non-breeding. Finally, we evaluated whether data were collected from a single seasonal replicate (e.g. one breeding season) or from multiple replicates (e.g. more than one breeding season).

*2.2 Are we asking questions or collecting data during breeding?*

To disentangle methodologically versus question-driven biases in the literature, we then distinguished between when data were collected and the specific focus of the question the study addressed. For example, a study could collect data on individual responses to a predator during the breeding season [e.g. (Cooper *et al.* 2012)], which would represent a non-breeding question that uses data collected during the breeding season. Conversely, a study could collect data on pair bond formation during the non-breeding season [e.g. (Beck, Farine & Kempenaers 2020)], which would be a question focused on breeding. We used the seasonal definitions as for our assessment of when data were collected.

*2.3 What approaches are we using to collect data and answer questions?*

To test whether the breeding season facilitates data collection, we recorded sample sizes (number of individuals and how many years of data were collected, where available) and whether experiments were conducted. We also collected information on the methodological approach(es) used in each study to determine if and how technological and methodological advances are facilitating data collection in different seasons.

## 3. Results

*3.1 Overview of the data*

From our initial review (N = 6,461 papers), we extracted information from 1,825 papers that met our inclusion criteria (see also SM1 for the PRISMA flowchart). Some papers reported data for more than one taxonomic group (two taxa, N = 13; three taxa, N = 5; and four taxa, N = 2) resulting in a total of 1,854 entries in our database (SM2). Studies mostly focused on a single species (Fig. 1c), with birds and mammals being the most commonly represented (Fig. 1d). These studies were widely distributed globally, with the notable exception of central- and northern-Africa and the Middle East (Fig. 1a-b). Very few studies were conducted in urban environments (5.2%) or in both urban and non-urban environments (6.3%).

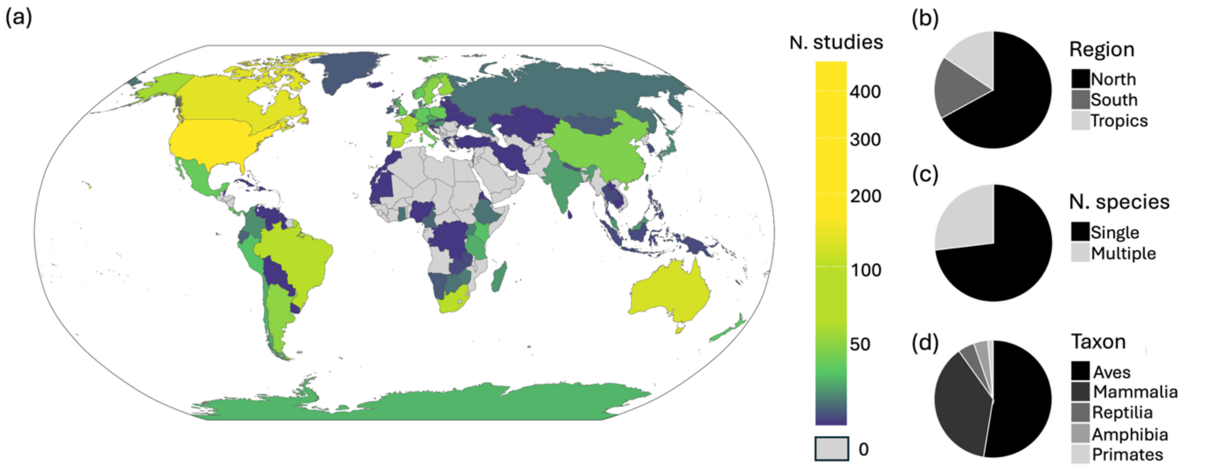


**Figure 1. Spatial and taxonomic coverage of reviewed studies.** (a) Map of the distribution of studies that reported data for a single administrative region (N = 1,639). (b) Breakdown of the major latitudinal regions in which studies have been conducted (sample sizes: North = 1,282, Tropics = 332, and South = 298). (c) Information on whether the study included one (N = 1,355) or more (N = 499) study species. (d) Distribution of studies across taxonomic groups (birds = 975, non-primate mammals = 696, reptiles = 84, amphibians = 72, primates = 27).

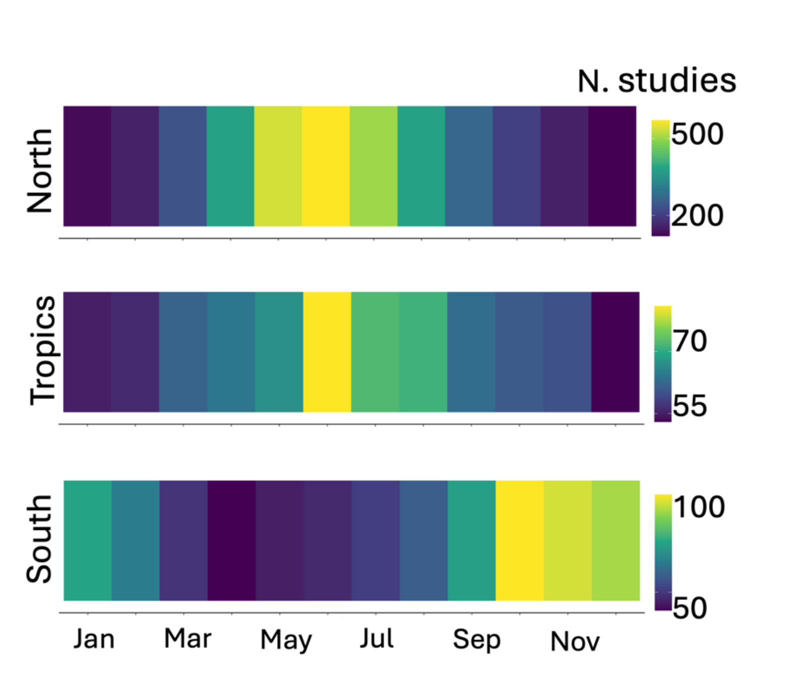


**Figure 2. The seasonal bias in when data are collected varies latitudinally**. Colours show the within-year variation in research effort across the world's three main major latitudinal regions.

*3.2 The bias in data collection does not reflect a bias in research questions*

The majority of studies collected data during the breeding season. Specifically, excluding studies conducted year-round, 72.6% collected data during the breeding season (51.1% were exclusively during breeding), whereas 37.7% collected data during the non-breeding season (21.4% were exclusively during the non-breeding), while 10.4% collected data on transit periods (3.0% were exclusively on transit periods). Out of all the studies, 7.3% reported data on carry-over effects. The time of the year when data were collected also varied across latitudinal regions, mostly occurring during the boreal or austral summers for northern and southern latitudes, respectively, while studies in tropical areas were mostly conducted during the boreal summer (Fig. 2).

While data collection was clearly biased towards breeding season, most studies addressed questions that were not directly related to breeding (61.5%, as compared to 43.7% answering breeding-related questions, Fig. 3a). Among studies conducted during the breeding season, more studies addressed questions on non-breeding ecology (48.6%) than on breeding ecology (43.2%) with the remaining focusing on transit (8.2%).

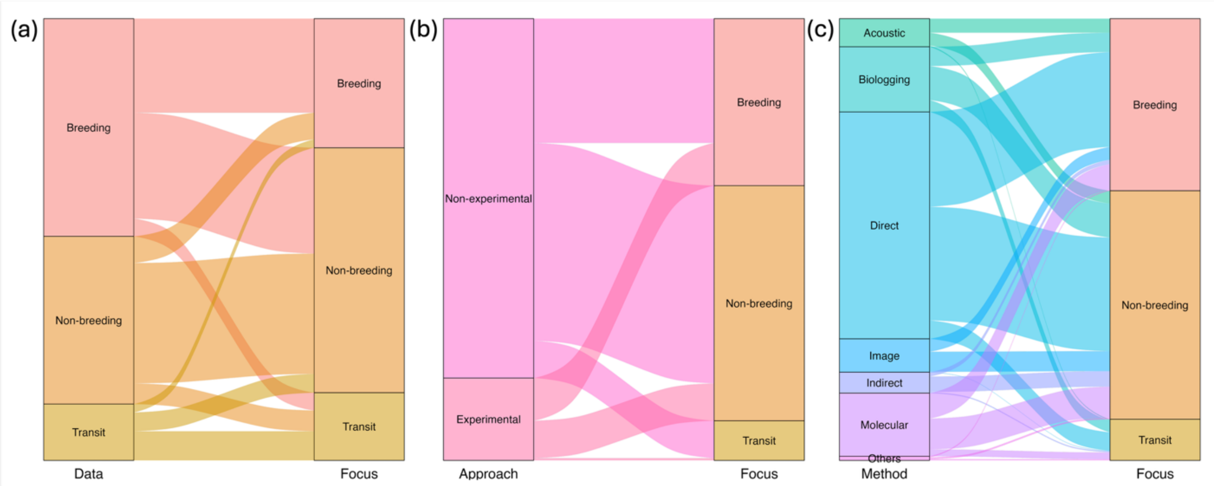


**Figure 3. The breeding season facilitates data collection, notably for direct observations and conducting experiments.** Sankey flow charts showing (a) the flow of when the data were collected into the focus of the study, (b) the use of experiments across seasonal research focuses, and (c) how methods were distributed across seasonal research focuses.

*3.3 The bias in data collection is clearly driven by feasibility*

There were significant differences in sample size between studies conducted during the breeding and non-breeding seasons. Studies that collected data during the breeding season (including breeding establishment, breeding and rearing) had a higher sample size (linear model on $log_{10}$-transformed number of individuals: Estimate ± SE: 0.14 ± 0.04, $t_{1,1355} = 3.08$, $P = 0.002$, full model formulation and results in SM3, Fig. 4a) and did so over a longer timespan (linear model on $log_{10}$-transformed maximum number of years: Estimate ± SE: 0.14 ± 0.03, $t_{1,1816} = 5.61$, $P < 0.001$, see also SM3, Fig. 4b) than studies that did not.

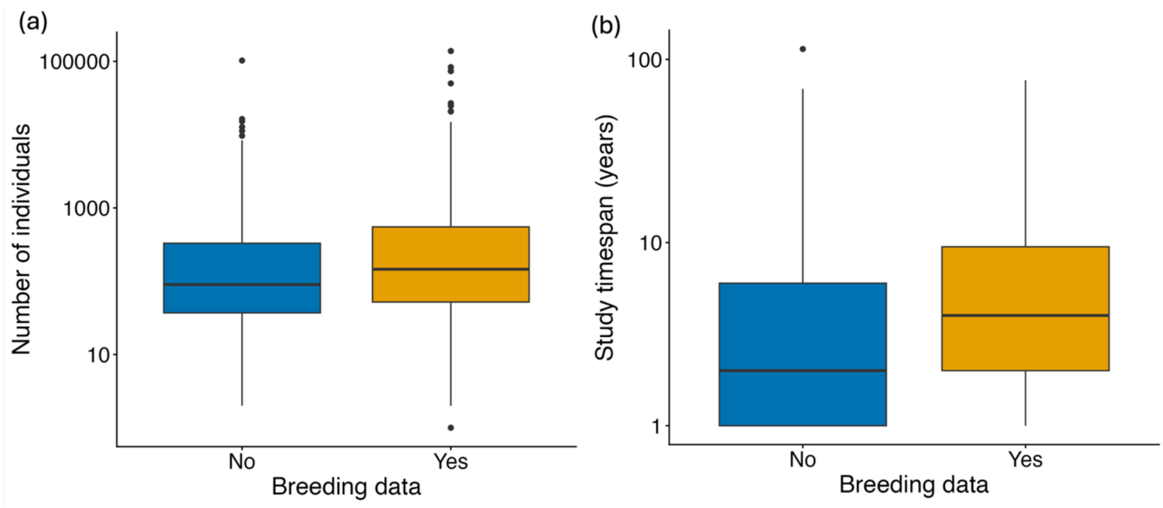


**Figure 4. The breeding season facilitates collecting larger sample sizes.** Boxplots showing (a) the number of individuals in studies collecting data during the breeding season or not and (b) the timespan in years for studies collecting data during the breeding season or not. Both plots are on $\log_{10}$ scale.

The majority of studies with an experimental treatment (N = 292) were conducted during the breeding season (65.9%) as compared to the non-breeding season (31.5%) and transit periods (2.6%; Fig. S2). Of the studies that conducted experiments, 51.9% addressed breeding-related questions and 45.4% addressed non-breeding-related questions (the remaining 2.7% was on transit; Fig. 3b). The opposite pattern was found in non-experimental studies, where 34.6% were answering breeding-related questions, 55.0% non-breeding-related questions, and the remaining 10.4% on transit (Fig. 3b).

Finally, the methods used also showed seasonal differences. Most papers relied on the direct observation of animals (51.4%, Fig. S2), with 41.8% of these answering breeding-related questions, 50.0% non-breeding-related questions and 8.2% transit-related questions (Fig. 3c). Biologging was the second most used data collection method (14.5% of the studies), with biologging studies being more twice more likely to address non-breeding related questions (14.8% of all studies asking non-breeding related questions) as compared to 8.5% on breeding-related questions (Fig. 3c). Biologging was mostly used in birds and mammals, while being less often used in other taxa (amphibians, reptiles and primates, see Fig. S3). In these other taxa, direct observations – and acoustic methods for amphibians – were the primary approach for data collection.

## 4. Discussion

Our results show that the temporal research bias towards the breeding season remains pervasive, that it is much more nuanced than previously reported, and that it is clearly driven by the increased methodological challenge associated with collecting data from non-breeding animals. We show that despite most of the data collection occurring during the breeding season, more studies overall were conducted to address questions that were not related to breeding. By recording what data were collected, we can clearly show that the bias in when studies are conducted is driven by feasibility rather than research focus. For example, studies that collected data during breeding were more likely to have experimental treatments and had larger sample sizes, both in terms of number of individuals and research timespan. Recent technological advances—notably in biologging—are playing an important role in facilitating data collection during the non-breeding season. However, our results reveal a potentially deeper problem associated with the seasonal bias in ecological research, which is that critical knowledge about the non-breeding ecology of animals is itself biased towards what animals do during the breeding period.

When data were collected does not necessarily correspond with what research question are being studied. For example, only about half the studies conducted during the breeding season actually addressed a breeding-related question. Interestingly, while many studies collect data during breeding to answer non-breeding questions, the opposite pattern is much rarer. This represents a major gap considering that there is now increasing evidence that many breeding-related behaviours occur before breeding activities start. For instance, in several species, pair bond formation starts during the non-breeding season, often months before the breeding season (Beck, Farine & Kempenaers 2020). Or, in many species of birds, males acquire the breeding plumage (van de Pol & Cockburn 2011) or start advertising in their territories (Cockburn *et al.* 2009) much earlier, often more than a month, than when they start breeding. Hence, by mostly collecting data during the breeding season we have greatly limited our scope in terms of understanding the reproductive ecology of many species. One way forward to increase the balance between data collection and research focus would be to address breeding-related questions during the non-breeding season.

A central prediction of Marra *et al.* (2015) was that new technologies and methodological approaches (e.g. biologging, molecular, and citizen science approaches) will play an important role in capturing more of the annual cycle. Our results confirm this prediction, with the increased use of biologging and the growth of movement ecology (Joo *et al.* 2022) contributing to a greater coverage of data across the annual cycle. Nevertheless, we highlight that biologging remains critically underused in taxa other than birds and mammals. We also found that other indirect methods (such as the use of scats for presence/absence studies) were disproportionately used in non-breeding-focused studies. Tools such as molecular technologies or citizen science were rarely represented in our dataset. One limitation to our study is that some patterns might be influenced by the journals that we surveyed. This was done in order to follow the same methodology as (Marra *et al.* 2015), allowing us to draw comparisons. However, the selected journals may overlook many papers in more methodologically focused journals. For example, molecular studies may be more likely to be published in journals specialising on this technique rather than those with a greater taxonomic focus. The emergence of biologging also includes a journal specifically for movement ecology studies (Movement Ecology was founded in 2013). Looking ahead, the most important methodological advances in the past decade have involved machine and deep learning, which are only starting to be used in animal ecology. For instance, deep learning has been used to determine mother-infant associations in mandrills *Mandrillus sphinx* (Charpentier *et al.* 2022). Similar models were also used in birds (Ferreira *et al.* 2020), even enabling the detection of sexual dimorphism, which was much less detectable to humans (Silva *et al.* 2025). Such advancements have opened the door to observational studies without having to trap or mark individuals and can provide key insights when tracking and direct observations are more challenging.

While feasibility explains why ecologists collected data during the breeding season and we found no strong evidence for a conceptual bias towards breeding-related questions, our results potentially point to a deeper issue with the ecological knowledge that we have. They suggest that much of what we know about non-breeding behaviours, such as strategies that are critical for survival, comes from studying animals during their breeding period. Yet there is now increasing evidence that animals can dramatically change their behaviour between the breeding and non-breeding periods. For instance, while breeding lesser kestrels *Falco naumanni* move over very restricted small ranges (Ramellini *et al.* 2022), they can roam over very large (often hundreds of km) areas during the non-breeding season (Assandri *et al.* 2024). Furthermore, many seasonal territorial breeders show very low tolerance to conspecifics while maintaining their breeding territory and are much more social during the non-breeding season [e.g. superb fairywrens (Camerlenghi *et al.* 2021), see also (Ramellini *et al.* 2025) for a review]. Thus, addressing non-breeding questions (such as movement ecology or social behaviour) by collecting data during the breeding season only might have severely under- or mis-represented the prevalence of key behaviours outside of the breeding season. This is becoming especially critical given the increased understanding that patterns of population declines might be linked to high mortality during harsh, non-breeding periods (Lv *et al.* 2023; Lv *et al.* 2026).

What compounds the potential issues with a lack of data from the non-breeding period is that studies conducted during this period typically have smaller samples sizes and shorter temporal coverage than studies collecting data during breeding. Specifically, breeding season studies had on average 1.42 times more study individuals and ran for 1.21 years longer than studies collecting data in non-breeding periods. Further compounding this issue is that experimental studies were more likely to be conducted during the breeding season. The lack of experiments in the non-breeding season likely reflects the challenges associated with conducting individual-level studies during this period. However, it could also reflect a conceptual gap in theory and influential hypotheses. In the past decades, many discoveries were driven by major bodies of theory related to breeding, such as sexual selection (Kuijper, Pen & Weissing 2012) or kin selection (Griffin & West 2002). While there are exceptions, such as the Marginal Value Theorem (Charnov 1976) for foraging decision making, these have also been challenging to test (Pierce & Ollason 1987). Inferring behaviours using biologging approaches (Christensen *et al.* 2025) could provide a valuable alternative to test experimental predictions in the wild. For instance, GPS-tracking has been used to assess how bushbucks *Tragelaphus sylvaticus* responded to experimentally manipulated predation risk (Atkins *et al.* 2019). These experimental tests could also be conducted with other forms of biologging such as animal-borne thermal loggers (Barratt *et al.* 2025). We urge for more theory and experimental method to be developed to facilitate addressing important questions about non-breeding ecology with similar power to studies conducted during breeding.

Overall, obtaining a systemic view of animal ecology will require understanding the complete set of life-history stages. Our analysis has shown that while there is a clear interest in studying non-breeding questions, the bias in when data are collected remains persistent. While we recognise that breeding outputs and behaviours are key in contributing to future generations, we must also acknowledge the equally important contribution of surviving the non-breeding season in affecting population dynamics. Neglecting, or (as we have found) obtaining an incomplete picture, of this key period means that our ecological understanding likely overlooks important aspects of animal biology. At worst, the disconnect between when we study animals and the questions we ask means that we may be introducing fundamental mistakes in the assumptions underlying our foundational theories, predictive models, policy and conservation actions.

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