

COMMENTARY

SPECIAL ISSUE

INTEGRATING BIOMECHANICS, ENERGETICS AND ECOLOGY IN LOCOMOTION

An annual cycle perspective on energetics and locomotion of migratory animals

Judy Shamoun-Baranes^{1,*} and Kees C. J. Camphuysen²

ABSTRACT

Animal migrations, or long-distance movements, on land, through water or in the air, are considered energetically costly because of the investment in persistent locomotion typical for migration. Diverse strategies exist to manage these energetic costs. Yet migration is only one stage in an annual cycle and may not be the most energetically costly. To better understand how free-ranging animals adaptively organize energy expenditure and locomotion, an annual cycle perspective is needed. Bio-logging data are collected for a range of animal species and could facilitate a life cycle approach to study energy expenditure. We provide examples from several studies across different taxa, as well as a more in-depth exploration from our own recent research on time activity budgets based on field observations and bio-logging data to estimate daily energy expenditure in a migratory seabird throughout a year. Our research has shown that daily energy expenditure is highest (1.7× average daily energy expenditure) during the spring migration of long-distance migratory gulls, whereas short-distance migrants expend the most energy (1.4× average daily energy expenditure) during the breeding season. Based on the examples provided, we show how bio-energetic models create exciting opportunities to study daily energetics and behaviour of migratory animals, although limitations also still exist. Such studies can reveal when, where and why peaks and lulls in energy expenditure arise over the annual cycle of a migrant, if long-distance movements are indeed energetically expensive and how animals can adapt to fluctuating demands in their natural environment throughout the year.

KEY WORDS: Annual routine, Behaviour, Bio-logging, Breeding, Migration, Movement

An annual cycle perspective

Whether you have observed thousands of birds flying overhead, seemingly endless trails of grazers reshaping the Serengeti, rivers swelling with fish moving to spawning grounds or the return of a species heralding the onset of spring, migration is an awe inspiring phenomena in nature. Migratory behaviour is a life history strategy observed across the animal kingdom, anywhere on earth. Migration is considered a specialized behaviour, characterized by persistent and straightened out movement in which station-keeping behaviour (movements within a home range) is temporarily inhibited and specific organization of energy allocation may be needed to support

these movements (Dingle, 1996). That migration is considered energetically costly is due to the investment in persistent locomotion required to travel long distances, but whether indeed this is one of the most energetically costly activities within the life cycle of an animal remains to be proved (Carey, 1996).

Animals have evolved diverse behavioural and physiological strategies to meet the energetic demands of migration (Dingle, 1996; Sapir et al., 2011). Movements can be powered entirely by an animal's investment in locomotion or assisted by the environment. For example, birds and insects can use atmospheric flows (Chapman et al., 2011; Gatehouse, 1994; Shamoun-Baranes et al., 2017b) and aquatic species can use currents (Gaspar et al., 2006; Putman, 2018) to save time or energy during long-distance movements. Migrants may also differ in how they organize the storage and allocation of energy to fuel migration bouts. An energetics framework has been proposed, analogous to one used for avian reproduction, to describe and compare different migration strategies along a continuum (Evans and Bearhop, 2022). In this framework, capital migrants may spend days to weeks increasing their energy reserves to fuel extreme endurance migrations moving for days without stopping to rest (Battley et al., 2012; Carneiro et al., 2024; Hedlund et al., 2021). At the other end of the spectrum, income migrants may move for short durations interspersed with (short) pauses for refuelling, or even refuel while travelling (Amélineau et al., 2021; Imlay et al., 2020; Sawyer and Kauffman, 2011). Many species, however, may exhibit intermediate strategies to organize their energy expenditure during migration, and be flexible in how they manage energy expenditure (Halsey et al., 2019).

While persistent movements during migration are potentially energetically costly, migration is only part of the annual life cycle of an animal. For animals living in seasonal environments, life history stages such as migration, breeding and moult may be organized in an annual routine, with each stage occurring in different environments and incurring different energetic costs (McNamara and Houston, 2008b; Wingfield, 2008). Annual cycles will pose temporal and spatial constraints on animals through endogenous and external factors. The duration and timing of reproduction may be highly conserved and under strong endogenous control (Sharp, 2005; Stearns, 1992). Animals will also be constrained in space because of their movement capacity, central place foraging strategies or specific habitat requirements during different stages in the annual cycle. Thus, being in the right place at the right time may be important for survival or reproduction (Condit et al., 2022). Furthermore, migratory animals may exhibit site fidelity to breeding areas as well as non-breeding areas (Brown et al., 2021; Picardi et al., 2023), further constraining their movements. An annual cycle perspective can thus improve our understanding of different life history trade-offs, seasonal interactions and activity-related fluxes in energy expenditure and provide a more integrated approach to animal ecology (Marra et al., 2015; McNamara and Houston, 2008a; see also papers in this [Special Issue](#)). An annual cycle approach is important, especially in migratory animals, to

¹Institute for Biodiversity and Ecosystem Dynamics, Department of Theoretical and Computational Ecology University of Amsterdam, P.O. Box 94240, 1090 GE Amsterdam, The Netherlands. ²Department of Coastal Systems, Royal Netherlands Institute for Sea Research (NIOZ), P.O. Box 59, 1790 AB, Den Burg, Texel, The Netherlands.

*Author for correspondence (j.z.shamoun-baranes@uva.nl)

 J.S.-B., 0000-0002-1652-7646; K.C.J.C., 0000-0002-3469-9070

identify where and when the main energetic bottlenecks may arise for a species (Marra et al., 2015). In this Commentary, we reiterate earlier calls for an annual cycle perspective. In light of the theme of this Special Issue 'Integrating biomechanics, energetics and ecology in locomotion' (Biewener and Wilson, 2025), we focus on daily energy expenditure in migratory animals in the wild, moving in and experiencing variable and heterogeneous environments during their annual cycle. Using an example from our research, we demonstrate why studying energy expenditure in the context of an animal's annual cycle is valuable and feasible, in migratory as well as in non-migratory animals.

By incorporating an annual cycle perspective on energetics and locomotion, we can address several questions. (1) How does energy expenditure vary during the annual cycle, and why (Fig. 1)? (2) How does the relative contribution of locomotion to daily energy expenditure vary during the annual cycle (Fig. 2)? (3) At which stage in the annual cycle and where do energetic bottlenecks arise? (4) What behavioural adaptations can animals use to reduce the energetic costs of different (movement) strategies? (5) When and where are animals most susceptible to unpredictable and abrupt environmental change?

Estimating energy expenditure and locomotion throughout the annual cycle

Information on the time animals spend on various activities can be used to estimate daily energy expenditure in wild animals (Goldstein, 1988). In certain study systems, or stages of the annual cycle, time-activity budgets can be calculated based on visual observations in the

field. Time-activity budgets can then be integrated with field, lab-based or theoretical estimates of the energetic cost of different activities, including variable resting metabolic rates, to convert activity budgets into estimated energy budgets (Dasilva, 1992; Goldstein, 1988; Karasov, 1992). Such methods have been used to estimate energy expenditure throughout the annual cycle in mammals, for example, showing seasonal shifts in time and energy invested in foraging, reproduction and resting (Dasilva, 1992; Kenagy et al., 1989). However, visual observations to measure time-activity budgets are hardly feasible for migratory animals. Thus, without remotely monitoring animal behaviour, data availability is a major limiting factor.

Bio-logging has opened new opportunities for quantifying behaviour and assessing related energy expenditure (Hussey et al., 2015; Kays et al., 2015; Ropert-Coudert and Wilson, 2005; Watanabe and Papastamatiou, 2023). Positional data obtained by bio-logging can be annotated with a behaviour (e.g. using accelerometry) and relevant environmental conditions (e.g. using remote sensing data), and bio-energetic models can then be used to estimate energy expenditure at the temporal resolution of interest (Fig. 1). If information is only available on the position of an animal, its speed can be derived and used to distinguish between stationary periods and locomotion. An average cost of movement based on scaling laws could then be used to estimate the resulting energy expenditure attributed to locomotion (Alexander, 2005) and thermoregulatory costs can be estimated by integrating environmental information. Energetic costs of locomotion could be further refined by using

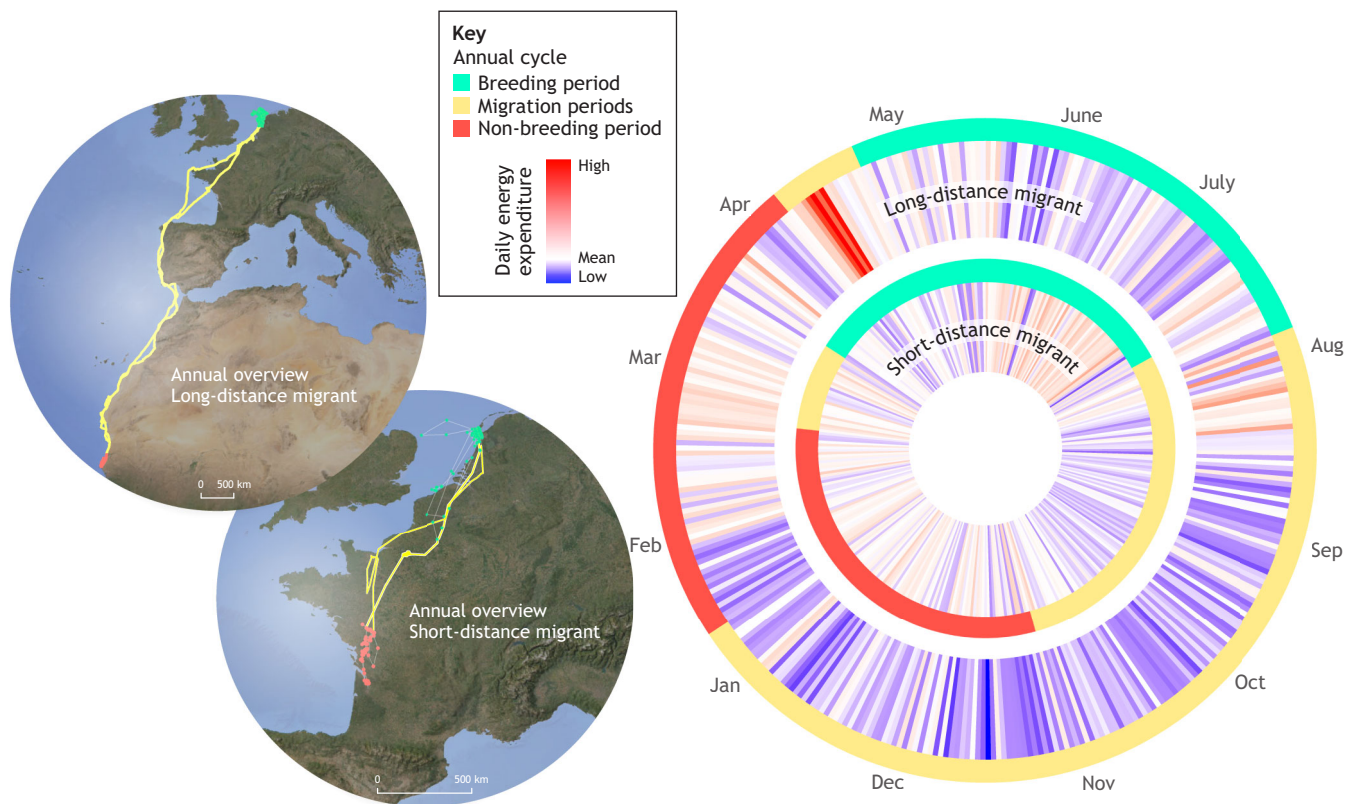


Fig. 1. Estimated daily energy expenditure and annual movements in the context of the annual cycle of two gulls. For comparison, data is shown for a long-distance migrant (individual 5416, 2016–2017, outer ring and upper map, Fig. 2) and a short-distance migrant (individual 5588, 2017–2018, inner ring and lower map). Circular plots show the periods in the annual cycle on the outer part of each ring and the estimated daily energy expenditure on the inner part of each ring. Shades of blue and red represent daily energy expenditure below and above, respectively, the annual daily energy expenditure (777 kJ day⁻¹, white) estimated for the species. Data from Brown et al. (2022b, 2023).

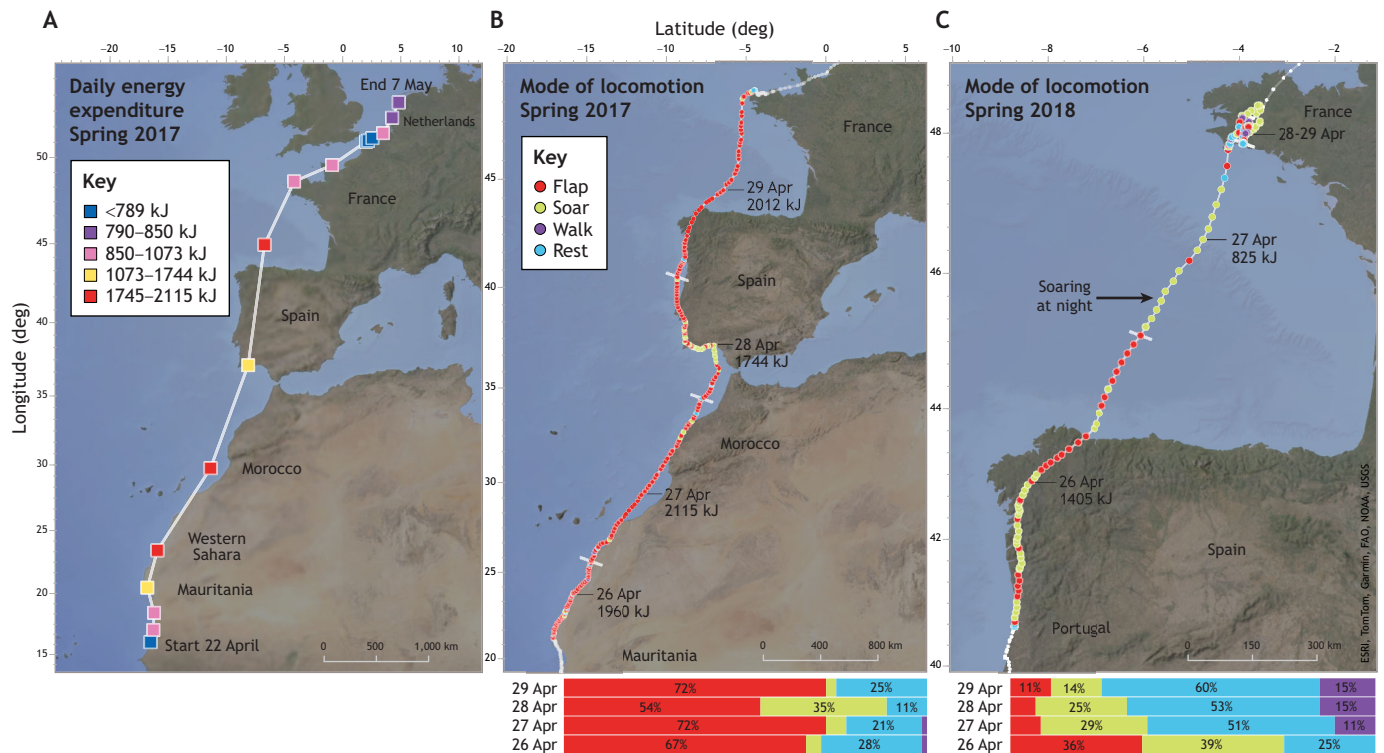


Fig. 2. Spring migration of a lesser black-backed gull (ID 5416) that overwinters in West Africa and breeds in The Netherlands. (A) Daily energy expenditure per day in spring 2017 when energy expenditure was highest that annual cycle. Icons are positioned at mean latitude and longitude per day, energy expenditure per day (kJ) indicated by colour. (B,C) Tracking positions and activity per position from 26–29 April 2017 for individual 5416 during days of peak energy expenditure (B) and from 26–29 April 2018 for the same individual (C). Estimated energy expenditure in B and C is indicated per day on the maps; white lines delineate days; proportion of time spent in flapping flight, soaring flight, walking and resting are indicated for each day (26–29 April) below each map. Data from Brown et al. (2022b, 2023).

theoretical or empirical relationships between the metabolic cost of locomotion and speed for a given species and mode of locomotion (Alexander, 2003; Taylor et al., 1982; Tobalske et al., 2003). However, annotating positional data with a behaviour based on speed alone is not always sufficient to distinguish between different activities, such as flapping and soaring flight, or resting from walking, which may have contrasting energetic costs (Shamoun-Baranes et al., 2012, 2016). Alternatively, a range of modelling approaches exist in which step lengths and turning angles can be used to estimate behavioural states (Williams et al., 2020). Once behavioural states are classified, the time in each state could be calculated and an average energy expenditure per behavioural state could then be applied.

Behaviours can also be classified, or energy expenditure directly estimated, using additional sensor data. For example, data collected from heart rate loggers (Bishop et al., 2015; Campbell et al., 2008; Grémillet et al., 2005; Seebacher et al., 2005), accelerometers (Collins et al., 2015; Resheff et al., 2014), time-depth recorders (Grémillet et al., 2005; Seebacher et al., 2005) or temperature sensors (Garthe et al., 2012) have been used to estimate energy expenditure. Heart rate loggers can account for various somatic costs such as moult and reproductive development which accelerometers cannot directly account for, whereas accelerometers can be used to distinguish between being stationary and different types of body movement. By converting sensor data into behaviour and incorporating this with the ecology of the study species, we can better understand how energy expenditure and behavioural adaptations are organized within the annual cycle. See Table 1 for several examples of studies in which locomotion and energetics or proxies thereof were studied throughout the annual cycle.

From sensor data to energy expenditure: examples from long-term research on gulls

Below we provide some examples from our earlier work (Brown et al., 2023), showing how an integrative approach can be used to study energetics and locomotion in the context of the annual cycle of the lesser black backed gull (*Larus fuscus*) and briefly address some of the questions posed in the Introduction. Long-term research on the breeding biology, demography and diet of gulls at a breeding colony on Texel, The Netherlands, was complemented with individual tracking data, providing insight into the annual movements (Camphuysen et al., 2024), migratory behaviour (Brown et al., 2021; Shamoun-Baranes et al., 2017a), foraging ecology (Camphuysen et al., 2015; Tyson et al., 2015) and fine-scale flight behaviour in the breeding stage (Sage et al., 2019, 2022; Shamoun-Baranes et al., 2016). In order to study energetics throughout the annual cycle and consequences of different migration strategies, it took additional lab and fieldwork work to calibrate energetic estimates of different activities (Brown et al., 2022a), and several years of tracking data collection from multiple colonies before enough knowledge and suitable data was available to study energy expenditure throughout the annual cycle (Brown et al., 2022b, 2023) (Fig. 1).

Despite breeding in close proximity and having a relatively synchronized breeding stage in the annual cycle (Camphuysen et al., 2024), birds from the same colony had very different migration and overwintering strategies, with destinations ranging from a few hundred (e.g. UK) to a few thousand kilometres (e.g. West Africa), either using predominantly urban, agricultural, coastal or marine habitats, and experiencing very different climates, from temperate to tropical (Shamoun-Baranes et al., 2017a). While the average

Table 1. A selection of examples of annual cycle analysis of energy expenditure or proxies of energy expenditure and locomotion in migratory (or highly mobile) animals

Common name	Species	EE	Research questions or aims	Reference
Antarctic fish	<i>Notothernia coriiceps</i>	Yes	Are seasonal changes in growth rate due to changes in ecological strategy, from maximizing food acquisition to minimizing the energetic cost of living?	Campbell et al. (2008)
Humpback whale	<i>Megaptera novaeangliae</i>	Yes	Estimate energetic cost of migration and describe migration route and phenology	Kettemer et al. (2022)
Alpine ibex	<i>Capra ibex ibex</i>	Proxy	What are the physiological and behavioural strategies that facilitate survival in challenging environments?	Signer et al. (2011)
Barnacle goose	<i>Branta leucopsis</i>	Yes	When do foraging constraints occur during the annual cycle?	Boom et al. (2023)
Northern gannet	<i>Morus bassanus</i>	Yes	What are the costs and benefits of wintering in different regions?	Garthe et al. (2012)
Common guillemot	<i>Uria aalge</i>	Yes	Where and when does variation in energy gain occur? How do environmental factors influence energy gain? Where and when do guillemots experience energetic constraints and increased susceptibility to mortality?	Dunn et al. (2022)
Lesser black-backed gull	<i>Larus fuscus</i>	Yes	What are the energetic consequences of different migration strategies? How does daily energy expenditure and activity patterns vary throughout the annual cycle among different migration strategies?	Brown et al. (2023)
Red-backed shrike	<i>Lanius collurio</i>	Yes	Comparison of activity levels during different stages in the annual cycle. Is the breeding period a period of peak activity? Do birds migrate faster in spring and adjust foraging activity accordingly?	Macías-Torres et al. (2022)
Common starling	<i>Sturnus vulgaris</i>	Yes	Compare activities budgets within and among individuals across different stages in the annual cycle	Vigants et al. (2023)

EE, energy expenditure; ‘yes’ indicates when energy expenditure is estimated; ‘proxy’ indicates when proxies such as travel speed, activity or dynamic body acceleration were used but not converted to energy expenditure.

estimated daily energy expenditure (777 kJ day⁻¹) did not differ among these diverse movement strategies, large variations within and among individuals were observed (Fig. 1). For example, during spring migration, a short period of highly elevated daily energy expenditure (1.7× average daily energy expenditure) was observed among the longest distance migrants, and for them it was the stage in the annual cycle in which energy expenditure was highest (Fig. 1), reaching >2000 kJ day⁻¹ in some cases (Fig. 2A). By integrating energetics and locomotion, it is possible to understand the source of these peaks as gulls transition from spending approximately 15% of time in flight per day to spending up to 70% of their time in flight (Fig. 2B). While such a strategy results in elevated energy expenditure, the extended temporal investment in locomotion resulted in a travel distance of more than 1000 km in 24 h, speeding up its return to the breeding colony.

Exploring data from the same individuals over different years can show how flexible they could be in how they organize their time and energy expenditure, for example, in response to weather conditions. Gulls can adopt different flight modes such as energetically costly flapping flight or soaring flight with much lower costs per unit time (Brown et al., 2022a). However, soaring flight requires suitable atmospheric conditions (Sage et al., 2019, 2022; Shepard et al., 2016; van Erp et al., 2023). An example of inter-annual and intra-individual variation in partitioning of energy expenditure during migration from Africa to The Netherlands is provided in Fig. 2B,C. In two consecutive years, the same individual spent 70–75% of time in flight on the same day of the year while migrating back to the breeding ground. Yet in 2018, it spent a larger proportion of time soaring (39% compared with 2%), greatly reducing daily energy expenditure (Fig. 2C). While crossing the Bay of Biscay, the gull spent 29% of its time soaring, with an estimated daily energy expenditure that was similar to the mean estimated daily energy expenditure for gulls throughout the entire annual cycle. These examples show how fine scale flexibility in flight behaviour and opportunistic response to environmental conditions can have important implications for daily energy expenditure.

In gulls, the breeding stage can be an extended period of elevated energy expenditure (Fig. 1) because of a relatively high investment in locomotion. During this stage, both males and females incubate eggs and care for their young, regardless of migration strategy. Time–activity budgets also change during the breeding season, for example, travel distances per foraging trip are higher during the chick-rearing stage compared with during incubation (Camphuysen et al., 2015), and adults spend less time at the nest and more time in flight (Spelt et al., 2019) as they need to acquire food for themselves and their young. While daily energy expenditure was generally above the annual mean for all individuals during the breeding season, for birds with relatively short migration distances, the breeding season tended to be the stage in the annual cycle with the highest estimated daily energy expenditure (1.4× average daily energy expenditure, Fig. 1). Despite such differences, on average, migration strategies had no impact on reproduction success or on adult survival (Kentie et al., 2023). Regardless of the strategy, gulls maintained levels of activity throughout the annual cycle below maximum theoretical thresholds considered sustainable (Drent and Daan, 1980; Dunn et al., 2020), suggesting that energetic bottlenecks may be quite rare in the study population.

Current challenges and future opportunities

While we advocate an annual cycle perspective where possible, we acknowledge that for some species, studying energetics and locomotion throughout the year is still impossible because of technological limitations. Nevertheless, increasingly small activity loggers are being used to study activity year round, for example, in smaller birds that weigh less than 100 g, which provide promising opportunities to study energetics throughout the annual cycle (Briedis et al., 2020; Wong et al., 2024). Estimates of the cost of locomotion, or other behaviours may still be lacking for quite a few species, but scaling laws (Alexander, 2003) or other theoretical frameworks (e.g. aerodynamic theory; Pennycuik, 1989) may provide reasonable alternative estimates. The computational work needed to annotate movement data with environmental data at the right temporal and

spatial scale and estimate daily energy expenditure is also a challenging component of such research. To some extent, artificial intelligence tools and data annotation software to help automate several of these steps will reduce the technical challenges (Chimienti et al., 2022; Dodge et al., 2013; Nathan et al., 2012).

An additional limitation to acquiring data throughout the annual cycle is that several tracking methods still require sensor retrieval or a second surgical intervention to remove implanted tags (Bishop et al., 2015; Macías-Torres et al., 2022). Furthermore, large numbers of individuals may be needed before sufficient data are available to address research questions. As a result, research may also be biased towards, or focus on, successful individuals (e.g. individuals that successfully complete an annual cycle), masking instances when animals die because they have exceeded an energetic ceiling. It would be interesting to compare patterns of daily energy expenditure between complete annual cycles and truncated annual cycles, to better understand potential causes of mortality. Similarly, animals may skip or abandon stages in the annual cycle, for example, birds may forego breeding or animals may enter so called 'emergency' life history stages (Spaans et al., 1998; Wingfield, 2003). Comparative analysis among alternative annual cycle structures could improve our understanding of energetic trade-offs among different stages in the annual cycle.

Although different methods exist for estimating daily energy expenditure, energy intake is still very challenging to estimate in free-ranging animals. Thus, studies of energetics and locomotion often focus on costs of resting and locomotion, rather than energy budgets which account for energy intake to better assess energetic benefits of different lifestyles. To some extent, foraging activity and food intake could be estimated from animal-borne sensors such as accelerometers or temperature loggers (Clermont et al., 2021; Grémillet and Plös, 1994; Lok et al., 2023). For parts of an annual cycle, field measurements could provide supplementary information on foraging activity and intake rates (Dasilva, 1992; Ginnett and Demment, 1997; Gloutney et al., 2001). In studies focusing on movement, the energetic costs of stationary activities are likely underestimated, even when accounting for variable thermoregulatory costs due to environmental conditions. For example, moult, lactation and egg production are periods of elevated metabolic costs (Croxall, 1982; Guillemette and Pelletier, 2022; Guillemette et al., 2007; Nilsson and Råberg, 2001; Thometz et al., 2021, 2016). Similarly, somatic growth and immune function also incur energetic costs (Buehler and Piersma, 2008; Piersma et al., 1996) that are not easily accounted for with time-activity budgets. Combining empirical work with theoretical frameworks for modelling dynamic energy budgets in combination with fine scale information on movement (Chimienti et al., 2020) may provide opportunities for better understanding of where and when animals reach energetic limits or surplus.

Annual cycles and thus energy partitioning is likely to differ between sexually immature animals and animals that have reached a reproductive stage. Juveniles may take time before they reach the locomotor (e.g. flight) and foraging efficiency of adults, thus costs of locomotion may be higher during early life stages (Enstipp et al., 2021; Jouma'a et al., 2024; Rotics et al., 2016; Weston et al., 2018). Their migration routes and timing, habitat requirements and space use may also differ from adults (Sergio et al., 2014; Vansteelant et al., 2017) and individuals will need time to develop effective foraging strategies and dietary specializations (Grecian et al., 2018; Jeglinski et al., 2012). Therefore, tracking studies of animals in their first years of life, will provide great potential for studying how past experience and spatio-temporal constraints in the annual cycle influence energy expenditure.

Concluding remarks

We hope this Commentary sparks interest in applying an annual cycle perspective when studying energetics and locomotion in the wild. An annual cycle perspective is likely feasible in many species considering the number of species that are tracked for a complete annual cycle (e.g. references in Table 1). The approach we describe will also be highly valuable for non-migratory species. While there are constraints to data collection, we are experiencing a golden age compared with the challenges faced by researchers studying annual cycles of energy expenditure in free-ranging animals just a few decades ago. We now have an opportunity to study relative investments in different activities, compare investments across taxa, or foraging and migration specializations. By combining energy expenditure, behaviour and environmental conditions, we can study the breadth of behavioural responses to variable environments and demands during an annual cycle and their energetic consequences. Hopefully, such an approach can improve our understanding of the capacity of animals to adapt to predictable and unpredictable environmental change.

Acknowledgements

J.S.-B. thanks participants from the symposium Integrating Biomechanics, Energetics and Ecology in Locomotion for stimulating discussions and The Company of Biologists for their organisation and sponsorship of the symposium. We thank Morgan Brown for earlier discussions and her research on energy expenditure of gulls. Our many gull collaborators have been invaluable in making our long term research possible. UvA-BiTS studies are facilitated by infrastructures for e-Ecology, developed with support of NLeSC and LifeWatch and carried out on the Dutch national e-infrastructure subsidized by the NWO Domain Science (2021.030) with support of the SURF Cooperative. Part of the tracking research presented in this paper were supported by Open Technology Program (17083), which is financed by NWO Domain Applied and Engineering Sciences, in collaboration with the following private and public partners: Rijkswaterstaat and Gemini Windpark. We thank Edwin Baaij and Willem Bouten for their years of support with UvA-BiTS. We thank Stacy Shinneman (IBED, UvA) for preparing the figures.

Competing interests

The authors declare no competing or financial interests.

Funding

The authors are supported by the Nederlandse Organisatie voor Wetenschappelijk Onderzoek (2021.030).

Special Issue

This article is part of the Special Issue 'Integrating Biomechanics, Energetics and Ecology in Locomotion', guest edited by Andrew A. Biewener and Alan M. Wilson. See related articles at https://journals.biologists.com/jeb/issue/228/Suppl_1.

References

- Alexander, R. M. (2003). *Principles of Animal Locomotion*. Princeton University Press.
- Alexander, R. M. (2005). Models and the scaling of energy costs for locomotion. *J. Exp. Biol.* **208**, 1645–1652. doi:10.1242/jeb.01484
- Amélineau, F., Merkel, B., Tarroux, A., Descamps, S., Anker-Nilssen, T., Bjørnstad, O., Bråthen, V. S., Chastel, O., Christensen-Dalsgaard, S., Danielsen, J. et al. (2021). Six pelagic seabird species of the North Atlantic engage in a fly-and-forage strategy during their migratory movements. *Mar. Ecol. Prog. Ser.* **676**, 127–144. doi:10.3354/meps13872
- Battley, P. F., Warnock, N., Tibbitts, T. L., Gill, R. E., Piersma, T., Hassell, C. J., Douglas, D. C., Mulcahy, D. M., Gartrell, B. D., Schuckard, R. et al. (2012). Contrasting extreme long-distance migration patterns in bar-tailed godwits *Limosa lapponica*. *J. Avian. Biol.* **43**, 21–32. doi:10.1111/j.1600-048X.2011.05473.x
- Biewener, A. A. and Wilson, A. M.. (2025). Integrating biomechanics, energetics and ecology perspectives in locomotion. *J. Exp. Biol.* **228** (Suppl_1), jeb249585. doi:10.1242/jeb.249585
- Bishop, C. M., Spivey, R. J., Hawkes, L. A., Batbayar, N., Chua, B., Frappell, P. B., Milsom, W. K., Natsagdorj, T., Newman, S. H., Scott, G. R. et al. (2015). The roller coaster flight strategy of bar-headed geese conserves energy during Himalayan migrations. *Science* **347**, 250–254. doi:10.1126/science.1258732
- Boom, M. P., Lameris, T. K., Schreven, K. H. T., Buitendijk, N. H., Moonen, S., de Vries, P. P., Zaynagutdinova, E., Nolet, B. A., van der Jeugd, H. P. and Eichhorn, G. (2023). Year-round activity levels reveal diurnal foraging constraints

- in the annual cycle of migratory and non-migratory barnacle geese. *Oecologia* **202**, 287–298. doi:10.1007/s00442-023-05386-x
- Briedis, M., Beran, V., Adamík, P. and Hahn, S. (2020). Integrating light-level geolocation with activity tracking reveals unexpected nocturnal migration patterns of the tawny pipit. *J. Avian Biol.* **51**, 10. doi:10.1111/jav.02546
- Brown, J. M., Bouten, W., Camphuysen, K. C. J., Nolet, B. A. and Shamoun-Baranes, J. (2022a). Acceleration as a proxy for energy expenditure in a facultative-soaring bird: Comparing dynamic body acceleration and time-energy budgets to heart rate. *Funct. Ecol.* **36**, 1627–1638. doi:10.1111/1365-2435.14055
- Brown, J. M., Bouten, W., Camphuysen, K. C. J., Nolet, B. A. and Shamoun-Baranes, J. (2022b). Data and code archive for 'Energetic and behavioral consequences of migration: An empirical evaluation in the context of the full annual cycle'. Amsterdam University of Applied Sciences. *Dataset*. doi:10.21942/uva.21583926.v3
- Brown, J. M., van Loon, E. E., Bouten, W., Camphuysen, K. C. J., Lens, L., Müller, W., Thaxter, C. B. and Shamoun-Baranes, J. (2021). Long-distance migrants vary migratory behaviour as much as short-distance migrants: An individual-level comparison from a seabird species with diverse migration strategies. *J. Anim. Ecol.* **90**, 1058–1070. doi:10.1111/1365-2656.13431
- Brown, J. M., Bouten, W., Camphuysen, K. C. J., Nolet, B. A. and Shamoun-Baranes, J. (2023). Energetic and behavioral consequences of migration: an empirical evaluation in the context of the full annual cycle. *Sci. Rep.* **13**, 1210. doi:10.1038/s41598-023-28198-8
- Buehler, D. M. and Piersma, T. (2008). Travelling on a budget: predictions and ecological evidence for bottlenecks in the annual cycle of long-distance migrants. *Philos. Trans. R. Soc. B Biol. Sci.* **363**, 247–266. doi:10.1098/rstb.2007.2138
- Campbell, H. A., Fraser, K. P. P., Bishop, C. M., Peck, L. S. and Egginton, S. (2008). Hibernation in an antarctic fish: on ice for winter. *PLoS ONE* **3**, e1743. doi:10.1371/journal.pone.0001743
- Camphuysen, C. J., Shamoun-Baranes, J., van Loon, E. E. and Bouten, W. (2015). Sexually distinct foraging strategies in an omnivorous seabird. *Mar. Biol.* **162**, 1417–1428. doi:10.1007/s00227-015-2678-9
- Camphuysen, K., van Donk, S. C., Shamoun-Baranes, J. and Kentie, R. (2024). The annual cycle, breeding biology and feeding ecology of the lesser black-backed gull *Larus fuscus*. *Ardea* **112**, 1–35. doi:10.37934/ard.112.1.17
- Carey, C. (1996). *Avian Energetics and Nutritional Ecology*. New York: Chapman & Hall.
- Carneiro, C., Gunnarsson, T. G., Kaasiku, T., Piersma, T. and Alves, J. A. (2024). Icelandic Whimbrel first migration: Non-stop until West Africa, yet later departure and slower travel than adults. *Ibis* **166**, 715–722. doi:10.1111/ibi.13282
- Chapman, J. W., Drake, V. A. and Reynolds, D. R. (2011). Recent Insights from Radar Studies of Insect Flight. *Annu. Rev. Entomol.* **56**, 337–356. doi:10.1146/annurev-ento-120709-144820
- Chimienti, M., Desforges, J. P., Beumer, L. T., Nabe-Nielsen, J., van Beest, F. M. and Schmidt, N. M. (2020). Energetics as common currency for integrating high resolution activity patterns into dynamic energy budget-individual based models. *Ecol. Model.* **434**, 9. doi:10.1016/j.ecolmodel.2020.109250
- Chimienti, M., Kato, A., Hicks, O., Angelier, F., Beaulieu, M., Ouled-Cheikh, J., Marciau, C., Raclot, T., Tucker, M., Wisniewska, D. M. et al. (2022). The role of individual variability on the predictive performance of machine learning applied to large bio-logging datasets. *Sci. Rep.* **12**, 19737. doi:10.1038/s41598-022-22258-1
- Clermont, J., Woodward-Gagné, A. and Berteaux, D. (2021). Digging into the behaviour of an active hunting predator: arctic fox prey caching events revealed by accelerometry. *Mov. Ecol.* **9**, 12. doi:10.1186/s40462-021-00295-1
- Collins, P. M., Green, J. A., Warwick-Evans, V., Dodd, S., Shaw, P. J. A., Arnould, J. P. Y. and Halsey, L. G. (2015). Interpreting behaviors from accelerometry: a method combining simplicity and objectivity. *Ecol. Evol.* **5**, 4642–4654. doi:10.1002/ece3.1660
- Condit, R., Beltran, R. S., Robinson, P. W., Crocker, D. E. and Costa, D. P. (2022). Birth timing after the long feeding migration in northern elephant seals. *Mar. Mamm. Sci.* **38**, 931–940. doi:10.1111/mms.12896
- Croxall, J. P. (1982). Energy costs of incubation and moult in Petrels and Penguins. *J. Anim. Ecol.* **51**, 177–194. doi:10.2307/4318
- Dasilva, G. L. (1992). The western black-and-white colobus as a low-energy strategist: activity budgets, energy expenditure and energy intake. *J. Anim. Ecol.* **61**, 79–91. doi:10.2307/5511
- Dingle, H. (1996). *Migration: The Biology of Life on the Move*. New York: Oxford University Press.
- Dodge, S., Bohrer, G., Weinzierl, R., Davidson, S., Kays, R., Douglas, D., Cruz, S., Han, J., Brandes, D. and Wikelski, M. (2013). The environmental-data automated track annotation (Env-DATA) system: linking animal tracks with environmental data. *Mov. Ecol.* **1**, 3. doi:10.1186/2051-3933-1-3
- Drent, R. H. and Daan, S. (1980). The prudent parent: energetic adjustments in avian breeding. *Ardea* **51**, 225–252.
- Dunn, R. E., Green, J. A., Wanless, S., Harris, M. P., Newell, M. A., Bogdanova, M. I., Horswill, C., Daunt, F. and Matthiopoulos, J. (2022). Modelling and mapping how common guillemots balance their energy budgets over a full annual cycle. *Funct. Ecol.* **36**, 1612–1626. doi:10.1111/1365-2435.14059
- Dunn, R. E., Wanless, S., Daunt, F., Harris, M. P. and Green, J. A. (2020). A year in the life of a North Atlantic seabird: behavioural and energetic adjustments during the annual cycle. *Sci. Rep.* **10**, 5993. doi:10.1038/s41598-020-62842-x
- Enstipp, M. R., Bost, C.-A., Le Bohec, C., Chatelain, N., Weimerskirch, H. and Handrich, Y. (2021). The early life of king penguins: ontogeny of dive capacity and foraging behaviour in an expert diver. *J. Exp. Biol.* **224**, jeb242512. doi:10.1242/jeb.242512
- Evans, S. R. and Bearhop, S. (2022). Variation in movement strategies: capital versus income migration. *J. Anim. Ecol.* **91**, 1961–1974. doi:10.1111/1365-2656.13800
- Garthe, S., Ludynia, K., Hüppop, O., Kubetzki, U., Meraz, J. and Furness, R. (2012). Energy budgets reveal equal benefits of varied migration strategies in northern gannets. *Mar. Biol.* **159**, 1907–1915. doi:10.1007/s00227-012-1978-6
- Gaspar, P., Georges, J.-Y., Fossette, S., Lenoble, A., Ferraroli, S. and Le Maho, Y. (2006). Marine animal behaviour: neglecting ocean currents can lead us up the wrong track. *Proc. R. Soc. B* **273**, 2697–2702. doi:10.1098/rspb.2006.3623
- Gatehouse, A. G. (1994). Insect migration - variability and success in a capricious environment. *Res. Popul. Ecol.* **36**, 165–171. doi:10.1007/BF02514932
- Ginnett, T. F. and Demment, M. W. (1997). Sex differences in giraffe foraging behavior at two spatial scales. *Oecologia* **110**, 291–300. doi:10.1007/s004420050162
- Gloutney, M. L., Alisauskas, R. T., Afton, A. D. and Slattery, S. M. (2001). Foraging time and dietary intake by breeding Ross's and Lesser Snow Geese. *Oecologia* **127**, 78–86. doi:10.1007/s004420000577
- Goldstein, D. L. (1988). Estimates of daily energy expenditure in birds: the time-energy budget as an integrator of laboratory and field studies. *Am. Zool.* **28**, 829–844. doi:10.1093/icb/28.3.829
- Grecian, W. J., Lane, J. V., Michelot, T., Wade, H. M. and Hamer, K. C. (2018). Understanding the ontogeny of foraging behaviour: insights from combining marine predator bio-logging with satellite-derived oceanography in hidden Markov models. *J. R. Soc. Interface* **15**, 20180084. doi:10.1098/rsif.2018.0084
- Grémillet, D., Kuntz, G., Woakes, A. J., Gilbert, C., Robin, J.-P., Le Maho, Y. and Butler, P. J. (2005). Year-round recordings of behavioural and physiological parameters reveal the survival strategy of a poorly insulated diving endotherm during the Arctic winter. *J. Exp. Biol.* **208**, 4231–4241. doi:10.1242/jeb.01884
- Grémillet, D. J. H. and Plöös, A. L. (1994). The use of stomach temperature records for the calculation of daily food intake in cormorants. *J. Exp. Biol.* **189**, 105–115. doi:10.1242/jeb.189.1.105
- Guillemette, M. and Pelletier, D. (2022). Egg-laying increases body temperature to an annual maximum in a wild bird. *Sci. Rep.* **12**, 11. doi:10.1038/s41598-022-05516-0
- Guillemette, M., Pelletier, D., Grandbois, J.-M. and Butler, P. J. (2007). Flightlessness and the energetic cost of wing molt in a large sea duck. *Ecology* **88**, 2936–2945. doi:10.1890/06-1751.1
- Halsey, L. G., Green, J. A., Twiss, S. D., Arnold, W., Burthe, S. J., Butler, P. J., Cooke, S. J., Grémillet, D., Ruf, T., Hicks, O. et al. (2019). Flexibility, variability and constraint in energy management patterns across vertebrate taxa revealed by long-term heart rate measurements. *Funct. Ecol.* **33**, 260–272. doi:10.1111/1365-2435.13264
- Hedlund, J. S. U., Lv, H., Lehmann, P., Hu, G., Anderson, R. C. and Chapman, J. W. (2021). Unraveling the world's longest non-stop migration: the Indian Ocean crossing of the globe skimmer dragonfly. *Front. Ecol. Evol.* **9**, 698128. doi:10.3389/fevo.2021.698128
- Hussey, N. E., Kessel, S. T., Aarestrup, K., Cooke, S. J., Cowley, P. D., Fisk, A. T., Harcourt, R. G., Holland, K. N., Iverson, S. J., Kocik, J. F. et al. (2015). Aquatic animal telemetry: A panoramic window into the underwater world. *Science* **348**, 1255642. doi:10.1126/science.1255642
- Imlay, T. L., Saldanha, S. and Taylor, P. D. (2020). The fall migratory movements of Bank Swallows, *Riparia riparia*: fly-and-forage migration? *Avian Conserv. Ecol.* **15**, 150102. doi:10.5751/ACE-01463-150102
- Jeglinski, J. W. E., Werner, C., Robinson, P. W., Costa, D. P. and Trillmich, F. (2012). Age, body mass and environmental variation shape the foraging ontogeny of Galapagos sea lions. *Mar. Ecol. Prog. Ser.* **453**, 279–296. doi:10.3354/meps09649
- Jouma'a, J., Orgeret, F., Picard, B., Robinson, P. W., Weimerskirch, H., Guinet, C., Costa, D. P. and Beltran, R. S. (2024). Contrasting offspring dependence periods and diving development rates in two closely related marine mammal species. *R. Soc. Open Sci.* **11**, 230666. doi:10.1098/rsos.230666
- Karasov, W. H. (1992). Daily energy expenditure and the cost of activity in mammals. *Am. Zool.* **32**, 238–248. doi:10.1093/icb/32.2.238
- Kays, R., Crofoot, M. C., Jetz, W. and Wikelski, M. (2015). Terrestrial animal tracking as an eye on life and planet. *Science* **348**, aaa2478. doi:10.1126/science.aaa2478
- Kenagy, G. J., Sharbaugh, S. M. and Nagy, K. A. (1989). Annual cycle of energy and time expenditure in a golden-mantled ground squirrel population. *Oecologia* **78**, 269–282. doi:10.1007/BF00377166
- Kentie, R., Morgan Brown, J., Camphuysen, K. C. J. and Shamoun-Baranes, J. (2023). Distance doesn't matter: migration strategy in a seabird has no effect on survival or reproduction. *Proc. R. Soc. B* **290**, 20222408. doi:10.1098/rspb.2022.2408

- Kettemer, L. E., Rikardsen, A. H., Biuw, M., Broms, F., Mul, E. and Blanchet, M.-A. (2022). Round-trip migration and energy budget of a breeding female humpback whale in the Northeast Atlantic. *PLoS ONE* **17**, e0268355. doi:10.1371/journal.pone.0268355
- Lok, T., van der Geest, M., Bom, R. A., de Goeij, P., Piersma, T. and Bouten, W. (2023). Prey ingestion rates revealed by back-mounted accelerometers in Eurasian spoonbills. *Animal Biotelemetry* **11**, 5. doi:10.1186/s40317-022-00315-w
- Macías-Torres, P., Alerstam, T., Andersson, A., Bäckman, J., Thorup, K., Tøttrup, A. P. and Sjöberg, S. (2022). Activity patterns throughout the annual cycle in a long-distance migratory songbird, the red-backed shrike *Lanius collurio*. *Mov. Ecol.* **10**, 55. doi:10.1186/s40462-022-00355-0
- Marra, P. P., Cohen, E. B., Loss, S. R., Rutter, J. E. and Tonra, C. M. (2015). A call for full annual cycle research in animal ecology. *Biol. Lett.* **11**, 2015.0552. doi:10.1098/rsbl.2015.0552
- McNamara, J. M. and Houston, A. I. (2008a). Introduction. Adaptation to the annual cycle. *Philos. Trans. R. Soc. B Biol. Sci.* **363**, 209-210. doi:10.1098/rstb.2007.2192
- McNamara, J. M. and Houston, A. I. (2008b). Optimal annual routines: behaviour in the context of physiology and ecology. *Philos. Trans. R. Soc. B Biol. Sci.* **363**, 301-319. doi:10.1098/rstb.2007.2141
- Nathan, R., Spiegel, O., Fortmann-Roe, S., Harel, R., Wikelski, M. and Getz, W. M. (2012). Using tri-axial acceleration data to identify behavioral modes of free-ranging animals: general concepts and tools illustrated for griffon vultures. *J. Exp. Biol.* **215**, 986-996. doi:10.1242/jeb.058602
- Nilsson, J.-Å. and Råberg, L. (2001). The resting metabolic cost of egg laying and nestling feeding in great tits. *Oecologia* **128**, 187-192. doi:10.1007/s004420100653
- Pennycuik, C. J. (1989). *Bird Flight Performance: a Practical Calculation Manual*. New York: Oxford University Press.
- Picardi, S., Abrahms, B., Gelzer, E., Morrison, T. A., Verzuh, T. and Merkle, J. A. (2023). Defining null expectations for animal site fidelity. *Ecol. Lett.* **26**, 157-169. doi:10.1111/ele.14148
- Piersma, T., Bruinzeel, L., Drent, R., Kersten, M., Van der Meer, J. and Wiersma, P. (1996). Variability in basal metabolic rate of a long-distance migrant shorebird (Red Knot, *Calidris canutus*) Reflects Shifts in Organ Sizes. *Physiol. Zool.* **69**, 191-217.
- Putman, N. (2018). Marine migrations. *Curr. Biol.* **28**, R972-R976. doi:10.1016/j.cub.2018.07.036
- Resheff, Y., Rotics, S., Harel, R., Spiegel, O. and Nathan, R. (2014). AcceRater: a web application for supervised learning of behavioral modes from acceleration measurements. *Mov. Ecol.* **2**, 27. doi:10.1186/s40462-014-0027-0
- Robert-Coudert, Y. and Wilson, R. P. (2005). Trends and perspectives in animal-attached remote sensing. *Front. Ecol. Environ.* **3**, 437-444. doi:10.1890/1540-9295(2005)003[0437:TAPIAR]2.0.CO;2
- Rotics, S., Kaatz, S., Resheff, Y. S., Feldman Turjeman, S., Zurell, D., Sapir, N., Eggers, U., Flack, A., Fiedler, W., Jeltsch, F. et al. (2016). The challenges of the first migration: movement and behavior of juvenile versus adult white storks with insights regarding juvenile mortality. *J. Anim. Ecol.* **85**, 938-947. doi:10.1111/1365-2656.12525
- Sage, E., Bouten, W., Hoekstra, B., Camphuysen, K. C. J. and Shamoun-Baranes, J. (2019). Orographic lift shapes flight routes of gulls in virtually flat landscapes. *Sci. Rep.* **9**, 9659. doi:10.1038/s41598-019-46017-x
- Sage, E., Bouten, W., van Dijk, W., Camphuysen, K. C. J. and Shamoun-Baranes, J. (2022). Built up areas in a wet landscape are stepping stones for soaring flight in a seabird. *Sci. Total Environ.* **852**, 157879. doi:10.1016/j.scitotenv.2022.157879
- Sapir, N., Butler, P. J., Hedenström, A. and Wikelski, M. (2011). Energy gain and use during animal migration. In *Animal Migration: A Synthesis* (ed. E. J. Milner-Gulland, J. M. Fryxell and A. R. E. Sinclair): Oxford University Press. doi:10.1093/acprof:oso/9780199568994.003.0005
- Sawyer, H. and Kauffman, M. J. (2011). Stopover ecology of a migratory ungulate. *J. Anim. Ecol.* **80**, 1078-1087. doi:10.1111/j.1365-2656.2011.01845.x
- Seebacher, F., Franklin, Craig E. and Read, M. (2005). Diving Behaviour of a Reptile (*Crocodylus johnstoni*) in the Wild: Interactions with Heart Rate and Body Temperature. *Physiol. Biochem. Zool.* **78**, 1-8. doi:10.1086/425192
- Sergio, F., Tanferna, A., De Stephanis, R., Lopez Jimenez, L., Blas, J., Tavecchia, G., Preatoni, D. and Hiraldo, F. (2014). Individual improvements and selective mortality shape lifelong migratory performance. *Nature* **515**, 410-413. doi:10.1038/nature13696
- Shamoun-Baranes, J., Bom, R., van Loon, E. E., Ens, B. J., Oosterbeek, K. and Bouten, W. (2012). From sensor data to animal behaviour: An Oystercatcher example. *PLoS ONE* **7**, e37997. doi:10.1371/journal.pone.0037997
- Shamoun-Baranes, J., Bouten, W., van Loon, E. E., Meijer, C. and Camphuysen, C. J. (2016). Flap or soar? How a flight generalist responds to its aerial environment. *Philos. Trans. R. Soc. B Biol. Sci.* **371**, 2015.0395. doi:10.1098/rstb.2015.0395
- Shamoun-Baranes, J., Burant, J. B., van Loon, E. E., Bouten, W. and Camphuysen, C. J. (2017a). Short distance migrants travel as far as long distance migrants in lesser black-backed gulls *Larus fuscus*. *J. Avian Biol.* **48**, 49-57. doi:10.1111/jav.01229
- Shamoun-Baranes, J., Liechti, F. and Vansteelant, W. M. G. (2017b). Atmospheric conditions create freeways, detours and tailbacks for migrating birds. *J. Comp. Physiol. A* **203**, 509-529. doi:10.1007/s00359-017-1181-9
- Sharp, P. J. (2005). Photoperiodic regulation of seasonal breeding in birds. *Ann. N. Y. Acad. Sci.* **1040**, 189-199. doi:10.1196/annals.1327.024
- Shepard, E. L. C., Williamson, C. and Windsor, S. P. (2016). Fine-scale flight strategies of gulls in urban airflows indicate risk and reward in city living. *Philos. Trans. R. Soc. B Biol. Sci.* **371**, 20150394. doi:10.1098/rstb.2015.0394
- Signer, C., Ruf, T. and Arnold, W. (2011). Hypometabolism and basking: the strategies of Alpine ibex to endure harsh over-wintering conditions. *Funct. Ecol.* **25**, 537-547. doi:10.1111/j.1365-2435.2010.01806.x
- Spaans, B., Blijleven, H. J., Popov, I. U., Rykhlikova, M. E. and Ebbsing, B. S. (1998). Dark-bellied Brent Geese *Branta bernicla bernicla* forego breeding when Arctic Foxes *Alopex lagopus* are present during nest initiation. *Ardea* **86**, 11-20.
- Spelt, A., Williamson, C., Shamoun-Baranes, J., Shepard, E., Rock, P. and Windsor, S. (2019). Habitat use of urban-nesting lesser black-backed gulls during the breeding season. *Sci. Rep.* **9**, 10527. doi:10.1038/s41598-019-46890-6
- Stearns, S. C. (1992). *The Evolution of Life Histories*. New York: Oxford University Press.
- Taylor, C. R., Heglund, N. C. and Maloiy, G. M. O. (1982). Energetics and mechanics of terrestrial locomotion. I. Metabolic energy consumption as a function of speed and body size in birds and mammals. *J. Exp. Biol.* **97**, 1-21. doi:10.1242/jeb.97.1.1
- Thometz, N. M., Kendall, T. L., Richter, B. P. and Williams, T. M. (2016). The high cost of reproduction in sea otters necessitates unique physiological adaptations. *J. Exp. Biol.* **219**, 2260-2264. doi:10.1242/jeb.138891
- Thometz, N. M., Hermann-Sorensen, H., Russell, B., Rosen, D. A. S. and Reichmuth, C. (2021). Molting strategies of Arctic seals drive annual patterns in metabolism. *Conserv. Physiol.* **9**, coaa112. doi:10.1093/conphys/coaa112
- Tobalske, B. W., Hedrick, T. L., Dial, K. P. and Biewener, A. A. (2003). Comparative power curves in bird flight. *Nature* **421**, 363-366. doi:10.1038/nature01284
- Tyson, C., Shamoun-Baranes, J., Van Loon, E. E., Camphuysen, K. and Hintzen, N. T. (2015). Individual specialization on fishery discards by lesser black-backed gulls (*Larus fuscus*). *ICES J. Mar. Sci.* **72**, 1882-1891. doi:10.1093/icesjms/fsv021
- van Erp, J., Sage, E., Bouten, W., van Loon, E., Camphuysen, K. C. J. and Shamoun-Baranes, J. (2023). Thermal soaring over the North Sea and implications for wind farm interactions. *Mar. Ecol. Prog. Series* **723**, 185-200. doi:10.3354/meps14315
- Vansteelant, W. M. G., Kekkonen, J. and Byholm, P. (2017). Wind conditions and geography shape the first outbound migration of juvenile honey buzzards and their distribution across sub-Saharan Africa. *Proc. R. Soc. B* **284**, 20170387. doi:10.1098/rspb.2017.0387
- Vigants, V., Keišs, O., Dinsbergs, I., Jaunzemis, V., Zaczane, E. M., Priedniece, A. and Briedis, M. (2023). Migration strategies, performance and annual activity budget in a short-distance migrant, the common starling *Sturnus vulgaris*. *J. Avian Biol.* **2023**, e03080. doi:10.1111/jav.03080
- Watanabe, Y. Y. and Papastamatiou, Y. P. (2023). Biologging and biotelemetry: tools for understanding the lives and environments of marine animals. *Ann. Rev. Anim. Biosci.* **11**, 247-267. doi:10.1146/annurev-animal-050322-073657
- Weston, E. D., Whitfield, D. P., Travis, J. M. J. and Lambin, X. (2018). The contribution of flight capability to the post-fledging dependence period of golden eagles. *J. Avian Biol.* **49**, 01265. doi:10.1111/jav.01265
- Williams, H. J., Taylor, L. A., Benhamou, S., Bijleveld, A. I., Clay, T. A., de Grissac, S., Demšar, U., English, H. M., Franconi, N., Gómez-Laich, A. et al. (2020). Optimizing the use of biologgers for movement ecology research. *J. Anim. Ecol.* **89**, 186-206. doi:10.1111/1365-2656.13094
- Wingfield, J. C. (2003). Control of behavioural strategies for capricious environments. *Anim. Behav.* **66**, 807-815. doi:10.1006/anbe.2003.2298
- Wingfield, J. C. (2008). Organization of vertebrate annual cycles: implications for control mechanisms. *Philos. Trans. R. Soc. B Biol. Sci.* **363**, 425-441. doi:10.1098/rstb.2007.2149
- Wong, J. B., Adamik, P., Bažant, M. and Hahn, S. (2024). Migration and daily flight activity patterns in the barred warbler *Curruca nisoria* over the annual cycle. *J. Vertebr. Biol.* **73**, 23085. doi:10.25225/jvb.23085