

Understanding the ecological and evolutionary function of stopover in migrating birds

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ABSTRACT

Global movement patterns of migratory birds illustrate their fascinating physical and physiological abilities to cross continents and oceans. During their voyages, most birds land multiple times to make so-called ‘stopovers’. Our current knowledge on the functions of stopover is mainly based on the proximate study of departure decisions. However, such studies are insufficient to gauge fully the ecological and evolutionary functions of stopover. If we study how a focal trait, e.g. changes in energy stores, affects the decision to depart from a stopover without considering the trait(s) that actually caused the bird to land, e.g. unfavourable environmental conditions for flight, we misinterpret the function of the stopover. It is thus important to realise and acknowledge that stopovers have many different functions, and that not every migrant has the same (set of) reasons to stop-over. Additionally, we may obtain contradictory results because the significance of different traits to a migrant is context dependent. For instance, late spring migrants may be more prone to risk-taking and depart from a stopover with lower energy stores than early spring migrants. Thus, we neglect that departure decisions are subject to selection to minimise immediate (mortality risk) and/or delayed (low future reproductive output) fitness costs. To alleviate these issues, we first define stopover as *an interruption of migratory endurance flight to minimise immediate and/or delayed fitness costs*. Second, we review all probable functions of stopover, which include accumulating energy, various forms of physiological recovery and avoiding adverse environmental conditions for flight, and list potential other functions that are less well studied, such as minimising predation, recovery from physical exhaustion and spatiotemporal adjustments to migration. Third, derived from these aspects, we argue for a paradigm shift in stopover ecology research. This includes focusing on why an individual interrupts its migratory flight, which is more likely to identify the individual-specific function(s) of the stopover correctly than departure-decision studies. Moreover, we highlight that the selective forces acting on stopover decisions are context dependent and are expected to differ between, e.g. K -/ r -selected species, the sexes and migration strategies. For example, all else being equal, r -selected species (low survival rate, high reproductive rate) should have a stronger urge to continue the migratory endurance flight or resume migration from a stopover because the potential increase in immediate fitness costs suffered from a flight is offset by the expected higher reproductive success in the subsequent breeding season. Finally, we propose to focus less on proximate mechanisms controlling landing and departure decisions, and more on ultimate mechanisms to identify the selective forces shaping stopover decisions. Our ideas are not limited to birds but can be applied to any migratory species. Our revised definition of stopover and the proposed paradigm shift has the potential to stimulate a fruitful discussion towards a better evolutionary ecological understanding of the functions of stopover. Furthermore, identifying the functions of stopover will support targeted measures to conserve and restore the functionality of stopover sites threatened by anthropogenic environmental changes. This is especially important for long-distance migrants, which currently are in alarming decline.

Key words: avian, behaviour, benefits, bird, costs, fitness, life history, migration, stopover, trade-off

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I INTRODUCTION

(1) Where do we stand?

Bird migrants may travel thousands and even tens of thousands of kilometres across continents and oceans during their seasonal movements, thereby linking different ecosystems (Shaffer *et al.*, 2006; Gill *et al.*, 2009; Egevang *et al.*, 2010; Bairlein *et al.*, 2012; Seyer *et al.*, 2021) (Fig. 1A). In addition to our general curiosity regarding such migrations, scientists try to unravel the behavioural (Jenni & Schaub, 2003; Hedenström, 2008; Alerstam, 2011), orientation/navigation (Wiltschko & Wiltschko, 1995; Mouritsen, 2018), morphological/mechanical (Pennycuik, 1969; Winkler & Leisler, 1992; Rayner, 1999; Hedenström, 2008; Pennycuik, 2008; Kelsey, Schmaljohann & Bairlein, 2021), physiological (Jenni & Schaub, 2003; McWilliams *et al.*, 2004; Weber, 2009; Rattenborg *et al.*, 2016; Eikenaar *et al.*, 2020c) and genetic (Berthold, 1991; Delmore *et al.*, 2020) adaptations and adjustments required to reach the migratory destinations in time, as well as the implications of migration for seasonal trophic interactions in various ecosystems (Bauer & Hoye, 2014). Studying bird migration is also essential for a holistic understanding of population

dynamics because bird mortality, a crucial demographic process, is highest during migration (Sillett & Holmes, 2002; Klaassen *et al.*, 2014; Loonstra *et al.*, 2019).

The seasonal movements of migratory birds can be divided into migratory endurance flights and stationary periods spent on the ground, water or, in airborne species, even in the air in between these flights (Fig. 1A). These periods are commonly referred to as stopovers. The total duration of all stopovers is generally far longer than the total duration of all migratory endurance flights (Green *et al.*, 2002; Wikelski *et al.*, 2003; Schmaljohann, Fox & Bairlein, 2012) and consequently, detailed knowledge on the causes of variation in stopover frequency and duration is essential for understanding why some birds arrive relatively early and others relatively late at their migratory destinations. Therefore, many studies have focussed on the causes and costs of variation in arrival timing (Bêty, Giroux & Gauthier, 2004; Smith & Moore, 2005; Saino *et al.*, 2011; Tøttrup *et al.*, 2012; Flack *et al.*, 2016; Rotics *et al.*, 2018; Briedis *et al.*, 2019; Schmaljohann, 2019). This is important because non-optimal arrival time can have immediate and delayed fitness costs (Smith & Moore, 2005; Both *et al.*, 2006; Lameris *et al.*, 2018) impacting populations and

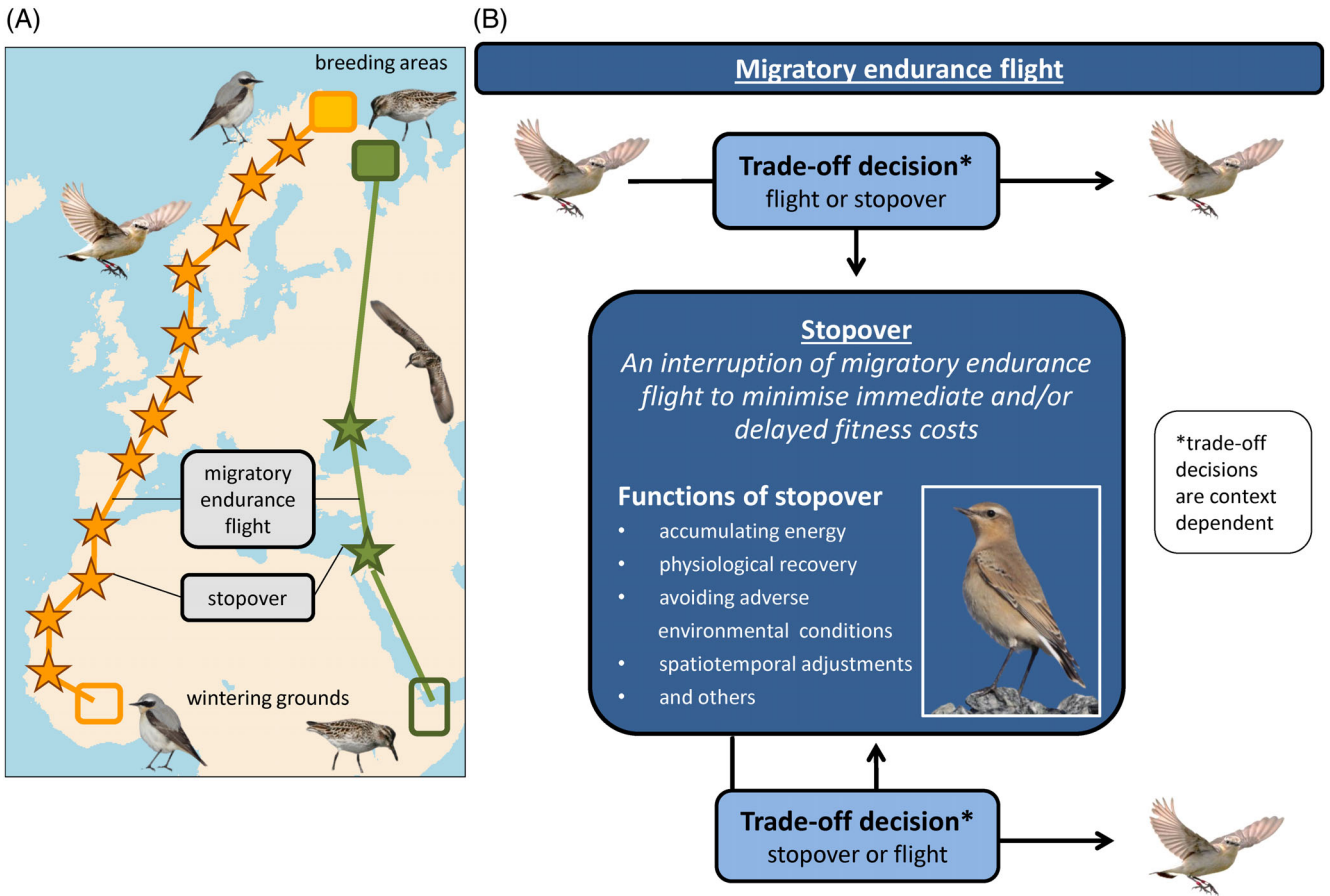


Fig. 1. (A) Potential migratory routes with series of migratory endurance flights (solid coloured lines) and stopovers (stars) for a wader (broad-billed sandpiper *Limicola falcinellus* Pontoppidan; green) and a songbird (northern wheatear *Oenanthe oenanthe* Linnaeus; orange) between their arctic breeding areas (filled rectangles) and sub-Saharan wintering grounds (open rectangles) on a Mercator projection, produced with the freely available R package “birdring” (Korner-Nievergelt & Robison 2019). (B) Simplified diagram showing that migrants (exemplified here by a northern wheatear) face a trade-off decision between continuing and interrupting the migratory endurance flight. In the latter case, migrants perform a stopover, which we define as ‘an interruption of migratory endurance flight to minimise immediate and/or delayed fitness costs’. Some possible functions of stopover are listed, for a more comprehensive list see Section III. During the stopover, migrants face a trade-off between continuing stopover and resuming migratory endurance flight. Both trade-off decisions should be considered in terms of the ultimate benefits to the individuals (for details, see Fig. 2). Moreover, these trade-off decisions are context dependent (for details, see Fig. 3). Photos by HS.

ultimately resulting in population declines (Both *et al.*, 2006; Saino *et al.*, 2011) and possibly extinction of the migratory species (Mayor *et al.*, 2017). Over recent years, significant advances have been made to our general understanding of (i) migratory endurance flights (e.g. Rattenborg *et al.*, 2016 and Loonstra *et al.*, 2019; for reviews see Linscott & Senner, 2021 and Moore, 2018), importantly as a result of the miniaturisation of tracking devices, and (ii) the importance of including the whole annual cycle in bird migration research (Marra *et al.*, 2015; Cohen *et al.*, 2019). Yet, our understanding of the stopover period has advanced much less, both in terms of theoretical developments and significant empirical discoveries. Specifically, after the development of optimal migration theory during the 1990s (Alerstam & Lindström, 1990; Lindström & Alerstam, 1992; Hedenström & Alerstam, 1997; Weber, Ens & Houston, 1998;

Hedenström, 2008; Alerstam, 2011), which transformed the field of stopover ecology from being almost purely descriptive to becoming hypothesis driven, less progress has been made in recent years. One important reason for this is that stopover studies tended to concentrate on specific aspects of stopover behaviour (e.g. departure decisions or migration strategies), and not on others (e.g. physiological aspects), such that we still do not understand all the different functions of stopover (Moore, 2018; Linscott & Senner, 2021).

The functions of stopover are manifold and vary among migration systems, species, populations and individuals such that not every migrant has the same reasons to stop-over at a certain time (Fig. 1B). Consequently, field studies focussing on how a specific trait affects particular stopover behaviour, without acknowledging the roles of other traits, may be unable to confirm their hypothesis and hence possibly

misinterpret the actual effect of that trait on stopover behaviour. To highlight that both are common phenomena in stopover ecology research, we present here a small selection of the variability found in migratory decisions in response to both intrinsic factors (e.g. energy stores), and extrinsic factors (e.g. wind support). Regarding energy stores, it is widely accepted that an important function of stopover is the accumulation of fuel (Schmaljohann & Eikenaar, 2017), mainly in the form of fat. Hence, the expectation is that migrants with large fuel stores will show a higher tendency to depart from stopover than migrants with low fuel stores. Although many stopover studies have provided data to confirm this expectation (e.g. Bairlein, 1985; Loria & Moore, 1990; Goymann *et al.*, 2010; Cohen, Moore & Fischer, 2014a; Deppe *et al.*, 2015), there are also many studies that failed to find an association between fuel stores and departure probability (e.g. Salewski & Schaub, 2007; Tsvey, Bulyuk & Kosarev, 2007; Schaub, Jenni & Bairlein, 2008; Schmaljohann & Klinner, 2020). These empirically demonstrated deviations from the expected departure pattern strongly suggest that the current level of fuel stores was not decisive for the departure decision in those birds. Another general migration pattern is the association between wind support and departure from stopover and migration intensity, which seems to be prevalent among migratory birds [reviewed in Richardson, 1978, 1990b, Liechti, 2006 and Shamoun-Baranes, Liechti & Vansteelandt, 2017]. This pattern reflects the birds' aim to optimise their journey through time and energy savings (Alerstam & Lindström, 1990; Liechti & Bruderer, 1998). Yet, substantial among-species and among-individual variability exists with regard to the response of migrating birds to wind conditions (Nilsson, Bäckman & Alerstam, 2014; Chmura *et al.*, 2020; Packmor *et al.*, 2020). For instance, Steidinger (1968) reported that nocturnal migration in Switzerland was not inhibited under headwinds and similarly Beason (1978) found that migration intensity in waterbirds was not related to wind direction. Regarding departure decisions, meteorological conditions did not affect the decision to resume migration in Eurasian Curlews (*Numenius arquata*) (Schwemmer *et al.*, 2021) and several passerine species (Bulyuk & Tsvey, 2006; Bolus *et al.*, 2017; Sjöberg *et al.*, 2017; Packmor *et al.*, 2020). Since flying into a headwind is costly in terms of time and energy, the reason for departure must, therefore, have included factors other than minimising the time and energy expenditure of that migratory flight. Hence, if we do not consider the trait(s) responsible for interrupting the migratory endurance flight, we misinterpret the function of stopover – in the above examples the importance of fuelling or wind – for the departure decision.

These issues are especially relevant for (potential) functions of stopovers that have been little studied and for which there is no current consensus. Is there really no effect of a given trait (e.g. physiological recovery) on stopover (departure) behaviour? Alternatively, is it masked by many individuals being at the stopover study site for reasons unrelated to that trait? Even if a trait has been studied for decades, among-

individual variation in the reasons to stop-over can still obscure the relationship between that trait and the likelihood of departure. Although many studies have observed a positive relationship between energy stores and departure likelihood, many others did not [reviewed in Schmaljohann & Eikenaar, 2017]. We are not suggesting that the latter group of studies is inferior to the former. What we wish to stress is that, given the many different functions of stopover, students of stopover ecology should not be surprised to find that many of their focal individuals may behave contrary to expectations. The notion that stopovers serve multiple functions is not new (e.g. Jenni & Schaub, 2003; Alerstam, 2011; Moore, 2018; Linscott & Senner, 2021). However, some of these functions have long remained, or still are, largely theoretical, with no attempts made to corroborate or refute them. Arguably the clearest is the widely accepted idea that stopovers function as periods of rest and recovery. This plausible idea has been around for many decades, but studies supporting it are only now beginning to accumulate (for details see Section III.2). Furthermore, even when multiple traits relating to various stopover functions are considered, much of the among-individual variation in departure likelihood may remain unexplained (e.g. Loria & Moore, 1990; Tsvey *et al.*, 2007; Schmaljohann *et al.*, 2013; Deppe *et al.*, 2015; Zenzal *et al.*, 2018), indicating that we are far from a complete understanding of the functions of stopover.

To fill parts of this knowledge gap, we need to be aware that migrants encounter a variety of different trade-offs, e.g. fuelling or making use of favourable wind, regarding their decision to interrupt or continue the migratory endurance flight. If we do not consider that migrants landed for other reasons than the focal trait of the study, we increase the likelihood of misinterpreting the biological importance of the focal trait for migratory decisions. To overcome this limitation, we suggest herein a paradigm shift to studying the reasons why migrants interrupt migratory endurance flights instead of focussing only on stopover departure decision making.

In addition, optimisation theories may allow us to infer key reasons for interrupting migratory movements, for example to optimise migration speed (McLaren, Shamoun-Baranes & Bouten, 2013) or even lifetime reproductive success, and ultimately individual fitness. That an optimisation approach can help us to understand behavioural strategies better, e.g. in terms of departure decisions, and to identify crucial research questions to be tested in the field has been convincingly demonstrated since the formulation of optimal migration theory (Alerstam & Lindström, 1990; Hedenström & Alerstam, 1997; Alerstam, 2011). Based on our new conceptual framework of stopover (Sections II–IV), we argue that it is time to expand optimal migration theory by including physiological recovery (Alerstam, 2011) and other potentially important trade-offs in addition to time, energy and predation risk and to incorporate a new component regarding the optimal interruption of migratory endurance flight (the transition from flight to stopover) in addition to the common practice of exploring the optimal timing of migration

departure (the transition from stopover to flight). We are convinced that corresponding optimisation analyses will provide a powerful tool to investigate the functions of stopover and the optimal behavioural decisions for the trade-offs encountered, but this is beyond the scope of the present review.

(2) **Aims and scope**

To fill parts of our knowledge gaps on the function of stopover, we provide a novel conceptual framework within an evolutionary ecological context on why birds make stopovers (Figs 1–3). We first propose a general definition in the broadest sense of what is a stopover for migrant birds (Fig. 1B), and then embed our new conceptual ideas on the multiple functions of stopover within a synthetic review of empirical studies. With this, we hope to stimulate a general scientific discussion about the functions of stopover in an evolutionary context (Figs 2 and 3), including the proposal that understanding stopover should not be limited to understanding

departure decisions but should also involve studying why migrants interrupt migratory endurance flights (Fig. 1). Since stopover ends with the bird’s decision to depart from stopover and resume migration, we briefly discuss departure decisions in light of our conceptual framework and stress the importance of taking an ultimate approach by expressing the decision to depart from stopover in fitness costs (Figs 2 and 3). We also emphasise that our conceptual framework is not limited to migratory birds but could also be applicable to other migratory animals. We then discuss a human perspective of why stopover is important, and finally put forward important open questions for stopover ecologists.

II A DEFINITION OF STOPOVER

We aim here to provide the broadest possible definition of stopover, as: *an interruption of migratory endurance flight to minimise*

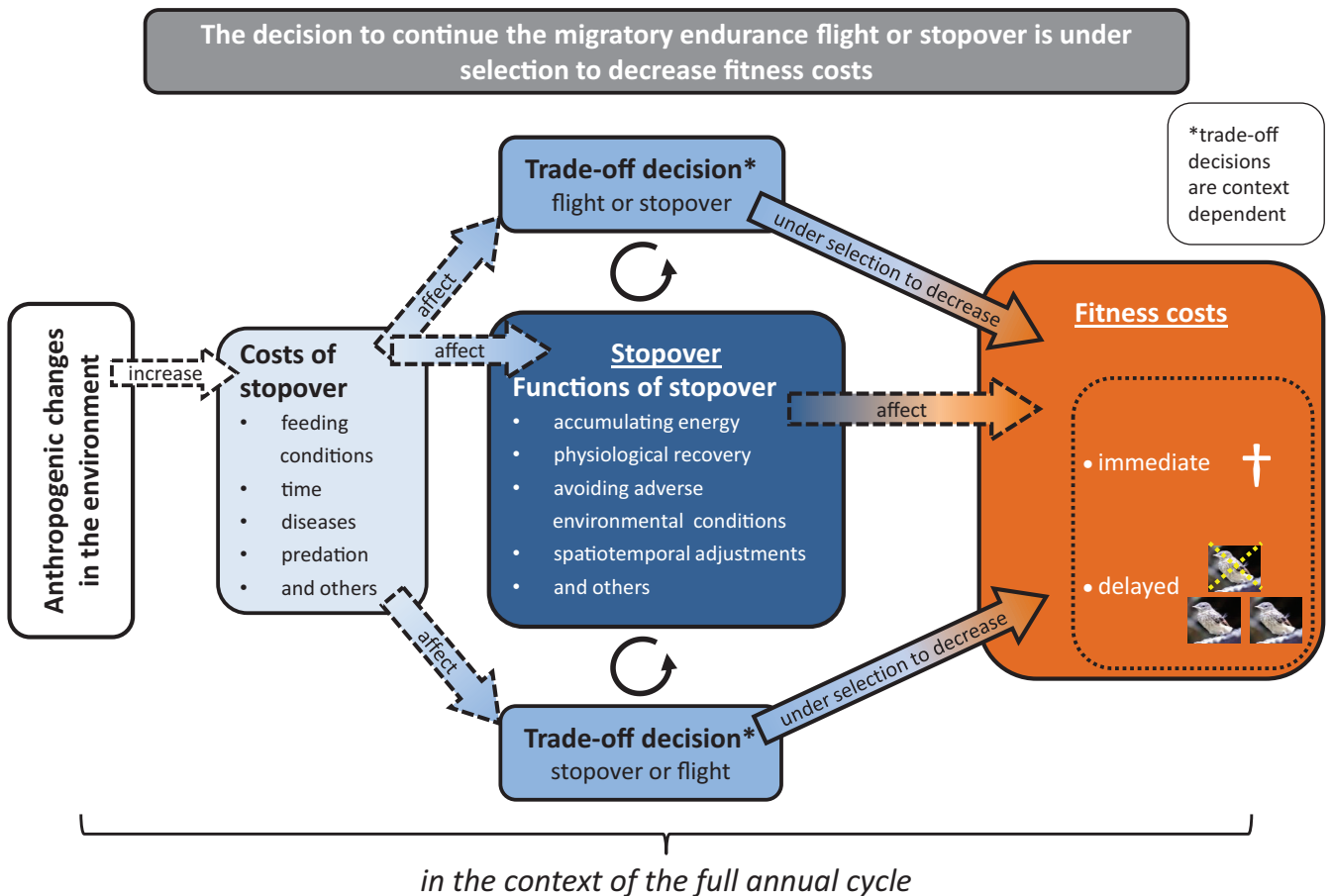


Fig. 2. The decision to continue the migratory endurance flight or stopover is under selection to decrease immediate and/or delayed fitness costs in the context of the bird’s full annual cycle. The functionality of the stopover affects the trade-off decisions during both the migratory endurance flight and the stopover period (for details, see Fig. 3). Both decisions are under selection to decrease immediate and/or delayed fitness costs. Anthropogenic changes in the environment (for instance, habitat degradation and fragmentation, intensified agriculture and global warming) often increase the costs of stopover through habitat loss, reduced arthropod communities (i.e. food availability) and unfavourable abiotic conditions. These may hamper the functionality of stopovers, and hence increase immediate and/or delayed fitness costs for migrants. Photos by HS.

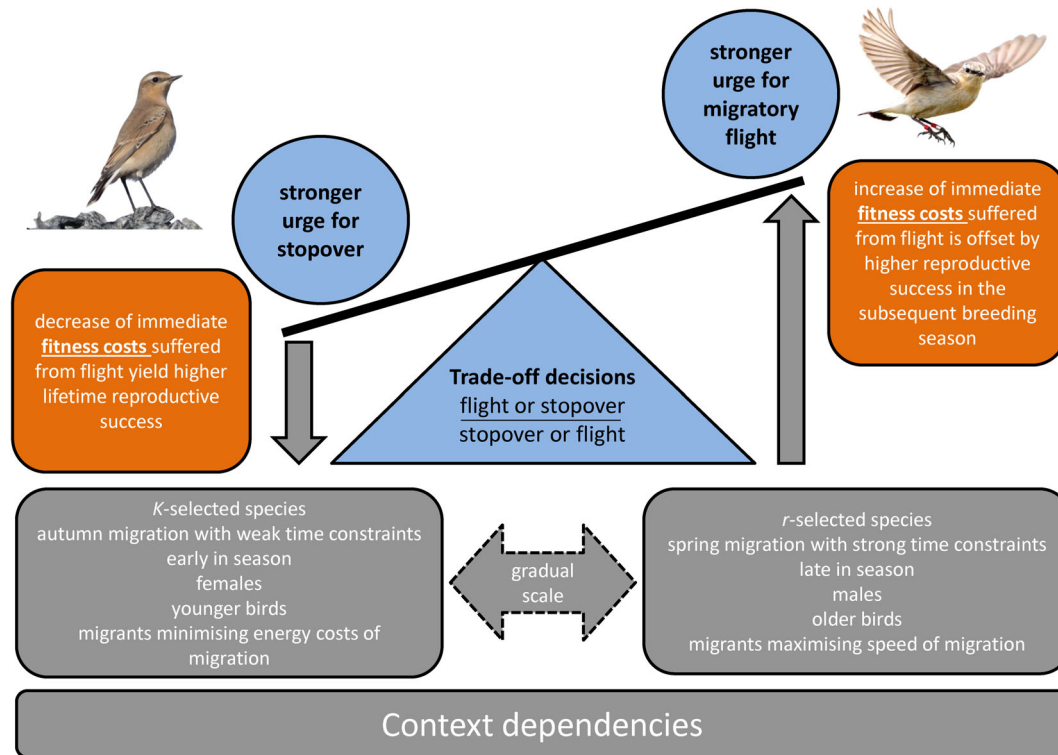


Fig. 3. The trade-off decisions between continuing and interrupting migratory endurance flight and between continuing stopover and resuming migratory endurance flight are context dependent (grey boxes). Note that this simplified presentation describes only the extremes, represented by the two grey boxes, to illustrate the most opposing context dependencies. In nature, there will be a continuum between these two extremes and most birds cannot be categorised as belonging to either of the two ends of the spectrum. For the left grey box, trade-off decisions lean towards interrupting the migratory flight and continuing stopover to decrease immediate fitness costs experienced from migratory endurance flight. This stronger urge for stopover should increase the probability of higher lifetime reproductive success at that time. Migrants at the other extreme (right grey box) are expected to be more prone to risk-taking. Here, the trade-off decisions lean towards continuing the migratory flight and resuming migration because the increase in immediate fitness costs suffered from the flight is counterbalanced by a higher reproductive success in the subsequent breeding season. Photos by HS.

immediate and/or delayed fitness costs (Fig. 1B). This definition is applicable to all migratory birds regardless of their life history and/or migration strategy. According to our definition, any interruption of a migratory endurance flight comprises a stopover, regardless of the reason(s) for landing and the temporal duration of the interruption (*cf.* Rappole & Warner, 1976; Warnock, 2010; Chernetsov, 2012; Cohen *et al.*, 2014a; Moore, 2018). The two ultimate reasons why migrants may interrupt a migratory endurance flight are to minimise either (i) immediate fitness cost, that is mortality, or (ii) delayed fitness costs, which include reduced reproductive success and/or lower survival probability at any later stage (Senner, Conklin & Piersma, 2015) (Fig. 2). First, if a migrant flies into a severe thunderstorm, this could significantly increase its risk of dying, that is increase immediate fitness costs. If, instead of continuing its migratory endurance flight, the migrant lands and makes a stopover, this would significantly reduce immediate fitness costs (Newton, 2007). Second, if the environment offers only a few suitable feeding areas, for example tidal flats for waders, continuation of the migratory endurance flight across such areas with later

stopovers at less suitable areas would increase the foraging time needed to accumulate fuel. This will reduce the speed of migration and delay arrival at the breeding area, potentially resulting in a reduced likelihood of obtaining high-quality territories and mates and hence in lower reproductive success (Kokko, 1999; Morbey & Ydenberg, 2001). Consequently, a decision to continue the migratory endurance flight over potentially beneficial feeding areas could result in delayed fitness costs. We must be aware that the decision to interrupt the migratory endurance flight or to continue the stopover is flexible with respect to trade-offs that depend on the bird's migration strategy (Fig. 3) and is ultimately driven by fitness considerations (*cf.* Paxton & Moore, 2017) (Fig. 2).

To exemplify our definition of stopover, we use a well-known concept in animal life-history theory: *r/K* selection theory (Dobzhansky, 1950; MacArthur & Wilson, 1967). This theory can be described by two scenarios when applied to migratory birds. First, the lifetime reproductive success of birds with a high fecundity rate and a low life expectancy (*r*-selected species) largely depends on the reproductive

outcome of the breeding season immediately following spring migration. Hence, such birds may attempt to maximise reproductive output at the expense of future survival and to achieve this goal may even risk their immediate survival during migration (Fig. 3; see also Ghalambor & Martin, 2001). Second, the lifetime reproductive success of birds with a low fecundity rate and a long life expectancy (K -selected species) depends, by contrast, on the cumulative reproductive outcome of their remaining lifespan, not only on a single breeding season. They should, therefore, reduce immediate risks resulting from the migratory endurance flight (Ghalambor & Martin, 2001) that may impact their survival. Overall, r -selected species will be more risk-prone in terms of maximising their immediate reproductive output, while K -selected species will consider also their future survival and reproduction (Fig. 3). Thus, they will be more risk-averse and apply a rather conservative migratory behaviour that will reduce their mortality probability, even at the expense of breeding (e.g. Tavera *et al.*, 2020). Most birds will fit somewhere along a continuum between these extremes. Moreover, even within a species, population or individual, the decision when to minimise immediate and/or delayed fitness costs during migratory endurance flight, that is when to make a stopover, might be context dependent (Fig. 3). We consequently expect to find stronger selection for more risk-prone decisions in spring, among males and older birds, in late-season migrants and for birds maximising the speed of migration instead of minimising energy costs of migration and/or predation risk (Fig. 3).

In spring, migrants will tolerate more of the general costs related to migratory endurance flight (e.g. reduced energy stores, physiological stress) because the reproductive fitness benefits of timely arrival at the final destination are higher than in autumn. This higher tolerance of costs may increase with the progression of the season, as the bird has less time left to arrive at its breeding area before the reproduction window closes; a response that should be especially pronounced in r -selected species (Fig. 3). Although considered overall to be of less importance, this effect may still hold true in the autumn as birds that arrive late at the wintering grounds may occupy poor wintering habitats, which may carry over to a late start of spring migration (Marra, Hobson & Holmes, 1998; Studds & Marra, 2005) and lower reproductive success in the next breeding season (Norris *et al.*, 2004). However, the manifestation of such carry-over effects differs among species and populations (Akresh, King & Marra, 2019). Yet, birds can reduce such delayed fitness costs, for example by moving into better habitats during the winter, by starting spring migration irrespective of wintering-grounds arrival time (Fayet *et al.*, 2016; Briedis *et al.*, 2018) and/or by adjusting spring migration speed to arrive in time at the breeding area (Alves *et al.*, 2012; Rotics *et al.*, 2018; González, Bayly & Hobson, 2020). Thus, birds can probably adopt a safer migration strategy during autumn, decreasing the costs of migratory endurance flight to their wintering grounds because delayed breeding-related fitness costs are less pronounced than in spring as the birds

have more time until breeding to compensate for these costs. Consequently, most bird groups migrate faster in spring compared with autumn (Nilsson, Klaassen & Alerstam, 2013; Schmaljohann, 2018, 2019).

Males typically arrive at their breeding areas before females in an attempt to maximise their mating opportunities and/or secure the best territories (Morbey & Ydenberg, 2001). Therefore, males are subject to greater costs from arriving late (Kokko *et al.*, 2006). Thus, they may be more prone to risk-taking during spring migration compared to females, although direct empirical support for this is still lacking.

Age may also play an important role. Younger birds have more time left for future reproduction than older birds, meaning that the immediate fitness costs (risk of dying) have a greater impact on decisions that result from a trade-off between immediate and future costs and benefits. Hence, younger birds are expected to follow more risk-averse behaviour (Fig. 3), and younger birds may be more inclined to interrupt migratory endurance flights than older birds. However, this does not imply *per se* that older birds follow a more risk-prone migration strategy. Migrants optimise their migratory decisions based on experience they have gained during previous migrations (Hake, Kjellen & Alerstam, 2003; Sergio *et al.*, 2014; Rotics *et al.*, 2018). From an evolutionary point of view, the frequency of high-quality individuals is greater in older than in younger birds through selective removal of low-quality individuals over time (van de Pol & Verhulst, 2006; Rotics *et al.*, 2018). Through both mechanisms, we predict older birds to adjust their landing decisions more optimally in terms of migration progress than younger birds, as demonstrated for stopover departure decisions in relation to environmental conditions (Mitchell *et al.*, 2015) and timing (Schmaljohann *et al.*, 2018). To the best of our knowledge, this prediction has not yet been empirically supported.

According to optimal migration theory (Alerstam & Lindström, 1990; Hedenström & Alerstam, 1997; Alerstam, 2011), time-minimisers maximise the speed of migration by using their rate of energy accumulation to time their departure, and usually resume migration with more energy stores than needed to reach the next stopover. Energy-minimisers time their departure irrespective of feeding conditions and minimise energy costs of transport by continuing migration with just sufficient energy stores required for the next flight bout. Other migrants are expected to minimise predation risk at the cost of decreasing their migration speed (the strategies are simplified here for the sake of clarity). Hence, the decision when to depart from stopover will not be the same for birds following different migration strategies. Analogously, we assume that the decision to interrupt migratory endurance flight may also differ between the three migration strategies, with time-selected migrants probably showing the most risk-prone decisions, that is they interrupt their flights less often than birds that adopt other optimisation criteria.

It is important to employ a holistic approach by investigating why birds interrupt their migratory endurance flight in addition to the traditional studies of why they resume

migration from stopover. Moreover, stopovers should be considered and studied within the annual cycle (Fig. 2), as previous life-history events may influence the reason for landing at a particular site and events at a particular stopover may carry over into subsequent life-history events (Moore, Smith & Sandberg, 2005; Paxton & Moore, 2015, 2017). More specifically, we argue that we can probably learn more about the functions of stopover from studying landing decisions than from studying departure decisions. Not all stopover sites are equally suitable to fulfil the reason(s) why a migrant decided to land. For example, a migrant may decide to interrupt flight because its energy stores are running low, but the site at which it lands holds little food for refuelling (e.g. Shochat *et al.*, 2002), and consequently, the migrant decides to depart soon after landing. A study focused on departure decisions will thus record a lean migrant departing, and such data sets could lead to the false conclusion that energy stores are unimportant for stopover departure decisions. Comparable scenarios can occur for other functions of stopover (see Section III). Our new definition of stopover may thus change our perception of stopover (Figs 2 and 3) and, importantly, our understanding of its ecological roles. The continuous technical progress and miniaturisation of recording devices now allow us to record multiple aspects of bird movement, behaviour and physiology in ever greater detail. Consequently, we can monitor birds' locations (Kays *et al.*, 2015; Taylor *et al.*, 2017), flight behaviour (Bäckman *et al.*, 2017; Liechti *et al.*, 2018), sleep behaviour (Rattenborg *et al.*, 2016), metabolism (Gumus *et al.*, 2015), body temperature (Guillemette *et al.*, 2017) and the environmental conditions they encounter (Liechti *et al.*, 2018) with great accuracy for the study of migratory decisions on a daily basis during entire journeys (Schmaljohann, Lisovski & Bairlein, 2017). Therefore, the time is ripe for exploring new ways of studying stopover ecology in general, why migrants interrupt their migratory endurance flights in particular, and to relate migratory decisions to individual relative fitness gain (*cf.* Bonier *et al.*, 2009).

III THE MULTIPLE FUNCTIONS OF STOPOVER

To facilitate a better understanding of the different functions of stopover, we present the various behavioural and physiological changes that birds undergo during the transition from the breeding or wintering season to the migration season. At the breeding areas and wintering grounds, most migrant birds sleep during part of the day (often at night), but exceptions can be found, for instance, during summer in the high Arctic (Lesku *et al.*, 2012). Furthermore, breeding birds and many over-wintering birds generally have low energy stores and are territorial (Greenberg, 1986; Salewski, Bairlein & Leisler, 2002; Blackburn & Cresswell, 2016) or at least largely sedentary (Newton, 2008). During migration, many diurnal birds travel during the night and consequently sleep less (Rattenborg *et al.*, 2004; Fuchs *et al.*, 2009), alternate extreme

anabolism at stopover (Bairlein & Gwinner, 1994; Bairlein, 2002) with extreme catabolism during migratory endurance flights (Klaassen, Kvist & Lindström, 2000; Kvist *et al.*, 2001; Wikelski *et al.*, 2003; McWilliams *et al.*, 2004; Jenni-Eiermann *et al.*, 2011), are less territorial and fly continuously for far longer distances than during the breeding and wintering periods. Therefore, to prepare for migration, significant behavioural and physiological adjustments must be made (Ramenofsky & Wingfield, 2017). These may include pre-migratory fuelling to accumulate sufficient energy stores for the first migratory endurance flight, adjustments of different organs (Ward & Jones, 1977; Metcalfe & Furness, 1984; Piersma, 1990; Bauchinger & Biebach, 2006; Kobylkov, Kosarev & Mukhin, 2014), as well as pre-migratory nocturnal flights (Mukhin, Kosarev & Ktitorov, 2005; Bulyuk *et al.*, 2009) and regional-scale flights (Arlt & Pärt, 2008; Mitchell, Taylor & Warkentin, 2010; Brown & Taylor, 2015). After such preparations, birds eventually depart on their initial migratory endurance flight. Before reaching their final destination, most birds will make a series of stopovers (Fig. 1A).

We strongly support the notion that we need to study stopover beyond its most obvious function, that is accumulating energy (Moore, 2018; Linscott & Senner, 2021), and expand the lists outlined by Linscott & Senner (2021) and Moore (2018). More importantly, we argue that a complete set of functions is necessary to avoid drawing incorrect conclusions regarding why migrants interrupt their migratory endurance flights. Depending on the reason(s), some stopovers are 'planned' or 'facultative', while others are 'forced' by unexpectedly harsh conditions. In this section, we attempt to outline why migrant birds interrupt their migratory endurance flights by separately discussing the different functions of stopover. This synthesis is based on functions for which there is currently at least some support from empirical studies, but we also list factors for which there is no empirical evidence to date but that may also be likely reasons for the interruption of migratory endurance flights. Undoubtedly, additional functions of stopover exist that will be discovered in the future.

Environmental conditions affect the energetic cost of bird flight, which in turn depends on the aerodynamic properties and the flight mode of the bird (Pennycuik, 2008; Bruderer *et al.*, 2010; Sapir *et al.*, 2011). In the following, we distinguish only between two fundamentally different flight modes: (i) flapping flyers, including different variants such as continuously flapping (e.g. waders, geese and gulls), flap-gliding (e.g. swifts, small raptors) and bounding flyers (e.g. songbirds); and (ii) soaring flyers (e.g. large raptors and storks) (Hedenström, 1993; Rayner *et al.*, 2001; Pennycuik, 2008; Bruderer *et al.*, 2010).

As this contribution deals only with the functions of stopover, we do not discuss the visual, acoustic, olfactory, geomorphological and/or magnetic mechanisms that may help migrants to choose their stopover habitats (e.g. Fransson *et al.*, 2001; Chernetsov, 2006, 2012; Buler, Moore & Woltmann, 2007; Mukhin, Chernetsov & Kishkinev, 2008; McLaren *et al.*, 2018; Cohen *et al.*, 2020). Furthermore, we do not include landscape movements because these are

“relocations that represent continued stopover at a broader spatial scale” (Taylor *et al.*, 2011, p. 1). Migrants probably perform such movements in order to search for better stopover habitats within a broader landscape (Taylor *et al.*, 2011; Schmaljohann & Eikenaar, 2017) which better meet their specific requirements.

(1) Accumulating energy

Hundreds of studies have investigated the link between migrants' energy stores and their stopover behaviour and physiology, although, to the best of our knowledge, there is no experimental evidence causally linking stopovers to fuelling. In other words, no study has removed, and in control birds replaced, fat tissue and studied the effect of this on the decision to interrupt a migratory flight (or to end a stopover). Still, there is no doubt that perhaps the most important function of stopovers is to accumulate energy: (i) birds burn energy (about 95% fat and 5% protein) to support migratory endurance flight (Jenni & Jenni-Eiermann, 1998), and hence, lose mainly fat but also protein in flight (Lindström & Piersma, 1993); (ii) migrants may arrive in rather lean body condition at stopovers (Bairlein, 1985; Biebach, 1985; Salewski & Schaub, 2007); (iii) they often accumulate energy stores during stopover [reviewed in Lindström, 1991]; and (iv) the size of the energy stores or the rate of accumulating energy typically affect the departure decision from stopover [reviewed in Alerstam, 2011 and Schmaljohann & Eikenaar, 2017].

Below we outline two different examples of fuelling during stopover; for a more complete list see Schmaljohann & Eikenaar (2017). In the first case, during a migratory endurance flight a bird may fully deplete its energy stores, forcing it to accumulate new energy stores before it can continue migrating (e.g. Bairlein, 1985; Loria & Moore, 1990). In the second case, a bird may interrupt its migratory endurance flight, despite having significant energy stores, to accumulate additional energy. This may happen just before an ecological barrier (e.g. Odum, 1963; Bayly, Atkinson & Rumsey, 2012; Gómez *et al.*, 2017), provide a safety margin for poor environmental conditions later along the migration route (Kerlinger & Moore, 1989; Yong & Moore, 1997), or confer time and energy benefits upon arrival at the breeding grounds (Gudmundsson, Lindström & Alerstam, 1991; Sandberg & Moore, 1996). These two examples highlight that, even though the function of stopover in both scenarios is fuelling, some stopovers may be ‘forced’ because survival is at stake and thus continuing flight could bear immediate fitness costs while other stopovers are, to a variable degree, facultative and have fitness costs that are carried over to later stages (survival and reproductive output in the subsequent season; Fig. 2). This gradient in forced and facultative stopovers makes it difficult to assess the function of stopover for an individual bird. Such complexity likely also exists for other functions of stopover that are discussed below.

(2) Physiological recovery

In addition to fuelling, it is widely believed that stopovers serve as periods during which migrants rest and/or recover from the preceding migratory endurance flight (e.g. Biebach, Friedrich & Heine, 1986; Latta & Brown, 1999; Dunn, 2000; Salewski & Schaub, 2007; Taylor *et al.*, 2011; Schofield *et al.*, 2018b; Holberton *et al.*, 2019; DeSimone *et al.*, 2020). That an organism needs to rest and recover physiologically after a period of endurance exercise seems a plausible explanation for stopping over. However, what exactly is meant by ‘rest and recovery’ is often not clearly defined (but see Biebach, 1998; Karasov & Pinshow, 1998; Guglielmo, Piersma & Williams, 2001; Schilch *et al.*, 2002b; Aborn & Moore, 2004; Skrip *et al.*, 2015; Ferretti *et al.*, 2019), and actual evidence for specific recovery processes is still scarce (Skrip *et al.*, 2015; Eikenaar, Hessler & Hegemann, 2020b; Eikenaar *et al.*, 2020c). Here we present several physiological processes and systems on which migratory endurance flight can have an adverse effect with potential fitness costs, from which the bird may need to recover during stopover.

(a) Oxidative balance

As an unavoidable side-effect of the high metabolic rate required for avian flight (Butler & Woakes, 1990; Videler, 2005; Jenni-Eiermann & Jenni, 2012), oxidative balance, that is the balance between the generation of damaging reactive oxygen species (ROS) and the protective antioxidant defence systems, is pushed towards ROS generation (Costantini, 2008; Costantini, Dell’Ariccia & Lipp, 2008; Jenni-Eiermann *et al.*, 2014; Skrip & McWilliams, 2016; Dick & Guglielmo, 2019; Eikenaar *et al.*, 2020a, c; but see Bairlein *et al.*, 2015). ROS can damage lipids, proteins and DNA (Gerschman *et al.*, 1954; Cadenas, 1995; Balaban, Nemoto & Finkel, 2005), which can, for example, result in malfunctioning of cell membranes (Birben *et al.*, 2012). Ultimately, the accumulation of oxidative damage may accelerate ageing and senescence (Beckman & Ames, 1998; Alonso-Álvarez *et al.*, 2010). Many migrating birds make multiple migratory endurance flights in a so-called ‘stop-and-go strategy’ (Delingat *et al.*, 2006; Åkesson & Hedenström, 2007), to reach the breeding or wintering grounds, during each of which ROS are generated at high rates. Instead of accumulating the oxidative damage over the migratory period, it is plausible that migrants use stopover to recover their oxidative balance. This has recently been supported, at least with regard to oxidative damage to lipids. In a study on garden warblers (*Sylvia borin* Boddaert), Skrip *et al.* (2015) found that at the population level, oxidative damage to lipids decreased with the time since presumed arrival at stopover. Interestingly, the decrease in oxidative damage at the population level was also observed intraspecifically in two birds that were sampled twice during their stopover (Skrip *et al.*, 2015). A study on northern wheatears (*Oenanthe oenanthe* Linnaeus) (Eikenaar *et al.*, 2020c)

corroborated these findings by showing that wild birds temporarily caged at stopover showed greatly reduced oxidative damage to lipids in just 2 days. Although the exact mechanisms behind these decreases in oxidative damage are currently unclear, it is evident that migrating birds are able to recover their oxidative balance during stopover.

(b) Constitutive immune function

Another physiological process that may be recovered during stopover is constitutive immune function, that is the immediate first defence responses (as opposed to long-term induced immune responses). Several studies have suggested that constitutive immune function can be compromised during migration (Owen & Moore, 2006; Hegemann *et al.*, 2012; Eikenaar & Hegemann, 2016), possibly because endurance flight negatively impacts this process (Nebel *et al.*, 2012, 2013; Eikenaar *et al.*, 2020a; but see Matson *et al.*, 2012). During stopover periods, increases in components of constitutive immune function have been observed, indicating recovery. Red knots (*Calidris canutus rufa* Linnaeus) that were in protein recovery, and hence presumably had recently interrupted their endurance flight, had lower constitutive immune function than conspecifics that were storing fat and thus presumed present for a longer time at stopover (Buehler, Tieleman & Piersma, 2010). These cross-sectional results were later supported by a longitudinal study showing improved constitutive immune function in northern wheatears temporarily caged at stopover, indicating a recovery from lower levels during flights (Eikenaar *et al.*, 2020b).

(c) Sleep

Migration may be physiologically demanding due to sleep deprivation. During migration, many bird species change from diurnally active to nocturnal because they restrict their migratory endurance flights mostly to the night (Dorka, 1966; Schmaljohann, Liechti & Bruderer, 2007; Müller *et al.*, 2016; Liechti *et al.*, 2018). Consequently, it might be predicted that sleep deprivation would lead nocturnal migrants to build up a sleep debt. Sleep debt in mammals was found to negatively affect alertness, working memory and cognitive function (Van Dongen *et al.*, 2003). However, in captive white-crowned sparrows (*Zonotrichia leucophrys* Forster), cognitive function was not reduced by sleep loss during the migration season, although it was reduced by sleep loss in the non-migratory season (Rattenborg *et al.*, 2004). Nocturnal migrants, thus, may have evolved behavioural or physiological mechanisms to cope with sleep deprivation during migration periods. Great frigatebirds (*Fregata minor* Gmelin) have been shown to sleep on the wing while soaring and flap-gliding (Rattenborg *et al.*, 2016), but whether this applies also to birds in lengthy migratory flight is still unclear. For example, bar-tailed godwits (*Limosa lapponica* Linnaeus) migrate in continuous flapping flight for periods up to 9 days (Gill *et al.*, 2009; Battley *et al.*, 2012). Another way that nocturnal migrants may avoid or reduce sleep debt and its

negative effects is by sleeping for prolonged periods during stopovers. This has been confirmed by field observations on various nocturnal migrants (Schwilch *et al.*, 2002b; Aborn & Moore, 2004; Németh, 2009; Bäckman *et al.*, 2017), as well as by studies on temporarily caged wild migrants (Ferretti *et al.*, 2019). Thus, stopovers may function to allow recovery from sleep loss, although further detailed studies are required to confirm this.

(d) Water stress

In addition to energy, birds need to balance their water budget, and this might be difficult during migratory endurance flights. Although metabolically produced water from fat and protein catabolism might counterbalance water loss due to evaporative cooling (Dawson, 1982; Michaeli & Pinshow, 2001) and in faeces (Giladi & Pinshow, 1999), long flights could potentially lead to dehydration (Yapp, 1956; Carmi *et al.*, 1992; Klaassen, 1995, 1996, 2004). If so, migrants could seek stopovers for rehydration (Leberg, Spengler & Barrow Jr, 1996). However, whether water loss rates are sufficiently high to force stopovers for rehydration is unclear (Landys *et al.*, 2000; Klaassen, 2004; Schmaljohann, Bruderer & Liechti, 2008). In addition, there is at least correlative evidence that migrants select flight altitudes that minimise energy costs rather than water loss (Schmaljohann, Liechti & Bruderer, 2009). Furthermore, Gerson & Guglielmo (2011) demonstrated that the ratio of fat to protein catabolism shifts towards protein when flying at warm ambient temperatures, yielding about five times more water per unit energy as fat. This shift may have evolved to compensate for the higher water loss at higher temperatures. Part of the digestive system or other organs may be catabolised to fuel migratory endurance flight (Karasov & Pinshow, 1998; Battley *et al.*, 2000; Schwilch *et al.*, 2002a), but also to produce metabolic water, suggesting that migrants can probably offset water loss more efficiently than anticipated. As the organs catabolised during flight are re-built during stopover (Biebach, 1998; Piersma, Gudmundsson & Lilliendahl, 1999; Battley *et al.*, 2000; Lindström *et al.*, 2000), one could argue that this is also represents refuelling or recovery. However, when substantial parts of particular organs or muscles are catabolised during flight, migrants may be forced to make a stopover because vital organs start losing their function and recovery is necessary to be able to continue migration. Interrupting the migratory endurance flight in this sense represents repair of physiological damage rather than refuelling. Interestingly, for energy storage following the recovery of the digestive tract, migrants may need to consume water in addition to food, particularly when consuming dry fruits as opposed to water-rich fleshy fruits (Sapir *et al.*, 2004; Tsurim *et al.*, 2008; Domer *et al.*, 2019).

(e) Hyperthermia

Birds are endothermic and keep their body temperature relatively constant (Clarke & Pörtner, 2010), although some birds use torpor to reduce metabolic rate to conserve energy

(Prinzinger, Preßmar & Schleucher, 1991; Ruf & Geiser, 2015). Most energy metabolised for flapping flight is transferred as heat to the body and therefore may increase body temperature. To avoid detrimental levels of hyperthermia, birds cool their body through evaporation/respiration (Salt, 1964; Dawson, 1982; Michaeli & Pinshow, 2001) and/or heat transfer from the body to the surrounding air layers (Ward *et al.*, 1999; Schraft, Whelan & Elliott, 2019). If these mechanisms are not sufficient, birds may interrupt the migratory endurance flight to prevent body temperature from rising above the normothermic zone (Guillemette *et al.*, 2016, 2017). The importance of this function of stopover probably depends on species-specific heat tolerance (Gerson *et al.*, 2019), including the length of time birds can endure facultative hyperthermia during their flight, as well as the environmental conditions in which they are flying.

(f) *Trade-offs in the recovery of physiological functions*

There may be trade-offs among the recovery of various physiological functions: macro- and micronutrients may be required for more than one type of recovery, and allocating these to a particular recovery process may delay the recovery of a different function. For example, Piersma (1997) suggested that muscle damage could impair immune defence function because phagocytes invading and removing damaged muscle cells are unavailable for other immune tasks. Originally this trade-off was suggested to manifest during intense bouts of exercise, that is during migratory endurance flight (Piersma, 1997). Nevertheless, this trade-off might also occur during stopover. Eikenaar, Isaksson & Hegemann (2018) provided data that support the presence of a physiological trade-off during stopover in migratory common blackbirds (*Turdus merula* Linnaeus). In these birds, microbial killing capacity (a constitutive immune function) was negatively correlated with non-enzymatic antioxidant capacity and positively associated with oxidative damage to lipids, whereas these correlations were absent in resident conspecifics sampled at the same location and time (Eikenaar *et al.*, 2018). This suggests that migrants during stopover may trade off recovery of oxidative balance against recovery of constitutive immune function.

Whether recovery of physiological processes and systems (muscle repair, recovery of organs, water stress) are linked to environmental conditions during stopover in general and specifically to food intake and the rate of energy accumulation, is currently unknown. In migrants temporarily caged during stopover under *ad libitum* food conditions (mealworms, *Tenebrio molitor* Linnaeus), the extent of recovery of oxidative balance and constitutive immune function was not explained by food intake or rate of energy accumulation (Eikenaar *et al.*, 2020b, c). However, it is conceivable that under natural conditions, food abundance and quality will affect the recovery rate, especially when food is scarce and/or of low quality. Under conditions of food shortage, the available energy may be allocated primarily to the maintenance of vital body functions, with little surplus available for the recovery of processes

and systems required for migration. We speculate that environmental stressors (cold, rain, high predation risk, competition) at stopover sites could have comparable effects on the recovery process, but do not discuss these further because our focus is on physiological aspects leading to the interruption of the migratory endurance flight.

(3) Avoiding adverse environmental conditions for the migratory endurance flight

A stopover may also function to minimise the costs of transport. In other words, a stopover could be made to avoid flying in particular environmental conditions that induce a high metabolic cost, which could lead to lower survival, either immediately or at a future time (Carneiro, Gunnarsson & Alves, 2020). Specific meteorological factors such as wind vector (speed and direction) and convective thermal availability and intensity may strongly influence avian flight. It is, therefore, important that migrants regularly assess the suitability of environmental conditions for flight and explore the availability of suitable stopover habitats for emergency landings, to reduce costs (e.g. flight against strong headwinds) and risks (e.g. drowning in the sea) during migratory endurance flights (Shamoun-Baranes *et al.*, 2010; Arizaga *et al.*, 2011; Overdijk & Navedo, 2012).

(a) *Wind*

Wind may have multiple effects on migrating birds, including disruption of flight control, increased metabolic cost that may influence survival and reproduction after the flight, as well as large-scale displacement that requires a later correction of the migration route (Liechti, 2006; Shamoun-Baranes *et al.*, 2010, 2017). Wind significantly affects the ground speed of birds (Liechti & Schaller, 1999; Richardson, Wakefield & Phillips, 2018) and costs of transport per unit distance (Liechti & Bruderer, 1998) because wind speed is typically in the same order of magnitude as birds' airspeed (Liechti, 2006). The strength and direction of wind thus have a pronounced effect on migrants' decisions on when and where to fly (Shamoun-Baranes *et al.*, 2017). Flying into a headwind decreases ground speed and thus, may significantly increase the costs and time of transport per unit distance (Shamoun-Baranes *et al.*, 2010; Loonstra *et al.*, 2019). Therefore, migrants could use stopovers to avoid strong headwinds. Storms may cause birds to drift far from their migratory route, and terrestrial birds displaced over extensive waterbodies may drown (Thorup *et al.*, 2003). While emergency landing to avoid adverse meteorological conditions could be beneficial (Shamoun-Baranes *et al.*, 2010; Arizaga *et al.*, 2011; Overdijk & Navedo, 2012), when landing sites offer suboptimal conditions, birds may experience an increased risk of mortality due to starvation (Newton, 2007; Loonstra *et al.*, 2019).

(b) *Thermal and updraft conditions*

Migrants that mainly use low-energy soaring flight, such as pelicans, large raptors and storks, generally depend on

atmospheric lift, that is thermals and updrafts (Norberg, 1990; Hedenström, 1993; Horvitz *et al.*, 2014; Duerr *et al.*, 2015). As thermals and updrafts are absent during the night (Kerlinger & Moore, 1989; Norberg, 1990; Hedenström, 1993), soaring flyers usually land before these subside during the last hours of the day (Kerlinger, 1989; Spaar & Bruderer, 1996; Nourani & Yamaguchi, 2017) to avoid switching to a flapping, and hence energetically more costly, flight. However, some birds may switch their flight mode from soaring to flapping to continue migration into the night and/or across the sea, where thermals and updrafts become increasingly less reliable (Meyer, Spaar & Bruderer, 2000; Becciu *et al.*, 2020; Santos *et al.*, 2020). These (mostly exceptions, but see Lopez-Ricaurte *et al.*, 2021) are often found in species with a low gliding performance, for which flapping is not too costly, and when adopting a time- rather than energy-minimising migration strategy (Hedenström, 1993; Spaar, 1997). The general function of landing when thermal and updraft conditions deteriorate is to minimise transport costs (Hedenström, 1993).

Intense thermals above ground during the day that are exploited by soaring migrants create air turbulence (Merry & Panofsky, 1976; Kerlinger & Moore, 1989; Sapir *et al.*, 2011). As powered flight is more costly in turbulent air than in laminar air layers (Ortega-Jimenez *et al.*, 2014), it was suggested that one reason for the restriction of migratory endurance flights over land mainly to the night or to the first hours of the day is to avoid the increased metabolic costs due to turbulent air later in the day (Kerlinger & Moore, 1989; Alerstam, 2009).

(c) *Precipitation, clouds and fog*

Migrating birds generally avoid flying in heavy rain, clouds and fog (Cochran, 1975; Erni *et al.*, 2002; Panuccio *et al.*, 2019) because this significantly impairs flight kinematics (Ortega-Jimenez *et al.*, 2016), thermoregulation (Webb & King, 1984), atmospheric lift (Kerlinger, 1989) and visual orientation (Griffin, 1973; Becciu *et al.*, 2021). Under these conditions, migrants may be forced to land when the energy costs of flight exceed the available energy stores or when, due to poor visibility, the risk of deviating from the intended flight path becomes too high. If the birds cannot find suitable stopover habitats in such situations, these unforeseen interruptions can lead to mass mortality of migratory birds [for an extensive review see Newton, 2007].

(4) **Other potential functions of stopover**

Below we list other plausible reasons why a migrant would interrupt a migratory endurance flight, but for which there is very little or no empirical support. We hope to encourage empirical exploration, as testing of these potential functions will be important for our understanding of the ecology of landing decisions. We do not consider interruptions of migratory endurance flight in order to moult (Stresemann & Stresemann, 1966; Jenni & Winkler, 2020), or when migrants

are attracted to artificial light at night (Gätke, 1895; McLaren *et al.*, 2018) or collide with novel features in the environment, such as wind turbines or tall buildings, and as a consequence rest on the ground (Loss *et al.*, 2014).

(a) *Temperature, humidity and oxygen partial pressure*

In flying animals, water loss increases with increasing temperature and decreasing humidity (Torre-Bueno, 1976; Biesel & Nachtigall, 1987; Adams, Pinshow & Gannes, 1997; Michaeli & Pinshow, 2001; Engel, Biebach & Visser, 2006). It has, therefore, been suggested that migrants interrupt their endurance flight in warm and dry air to prevent dehydration (see Section III.2d; reviewed in Schmaljohann *et al.*, 2008). However, we still lack evidence that birds experience dehydration after long flights (Gerson & Guglielmo, 2011) or interrupt their migratory flight because of high ambient temperature (see Section III.2d).

Some migrants fly at very high altitudes (e.g. Liechti & Schaller, 1999; Bishop *et al.*, 2015; Senner *et al.*, 2018), where they encounter very low temperatures, absolute humidity and oxygen partial pressures (Faraci, 1991; Scott, 2011). Since they actively choose these flight altitudes, we assume that these variables are unlikely to lead to the initiation of stopover. However, a radio-tracked Swainson's thrush (*Catharus ustulata* Nuttall) interrupted its migratory flights much earlier when encountering a cold front than at higher ambient temperatures (Cochran, 1987), providing the only empirical evidence to date suggesting that birds may land in response to temperature.

(b) *Air density*

Air density affects the two major aerodynamic forces, lift and drag, in birds. Since birds migrate at altitudes sometimes exceeding 5,000 m above sea level (e.g. Liechti & Schaller, 1999; Bishop *et al.*, 2015; Senner *et al.*, 2018), they must adjust their flight behaviour to air density (Chai, Harrykisson & Dudley, 1996; Pennycuik, 2001; Schmaljohann & Liechti, 2009; Bishop *et al.*, 2015). These behavioural adjustments, which include higher wingbeat frequency and wingbeat amplitude, require a higher energy input, raising the heart rate and causing an increase in the metabolic cost of flight (Bishop *et al.*, 2015). Bar-headed geese (*Anser indicus* Latham) crossing the Himalaya during migration appear to reduce their flight altitude when possible during the crossing to avoid the higher flight costs at low air densities (Bishop *et al.*, 2015). However, we do not know whether the effects of air density on flight costs could lead to interruption of migratory endurance flight by stopovers.

(c) *Minimising predation risk*

Predation risk could potentially affect trade-off decisions between flight and stopover. When encountering birds of prey (Walter, 1979; Rosén *et al.*, 1999) and/or bird-eating bats (Ibáñez *et al.*, 2001; Popa-Lisseanu *et al.*, 2007) birds

most likely show escape behaviours such as vertical or zigzag avoidance (Hedenström & Rosén, 2001; Kane, Fulton & Rosenthal, 2015), which may also include landing if habitat allows.

(d) *Recovery from physical exhaustion*

Considering the strenuousness of migratory endurance flight, one would expect migrants to become physically exhausted. However, muscle fatigue, a marked effect of endurance exercise in mammals (Loke, Mahler & Virgulto, 1982; Bogdanis, 2012), does not appear to occur in migrating birds (Jenni-Eiermann & Jenni, 2012). A tracking study of swifts (flap-gliding flyers) showed that they remain airborne for more than three quarters of a year (Liechti *et al.*, 2013; Hedenström *et al.*, 2016) and waders (continuously flapping flyers) have been shown to fly non-stop for nine consecutive days (Gill *et al.*, 2009; Battley *et al.*, 2012). Migratory endurance flight, however, can result in flight muscle damage (Guglielmo *et al.*, 2001; Dick & Guglielmo, 2019). Whether birds interrupt their migratory endurance flight due to such damage, and if it can be repaired during stopover, remains unknown, and likely depends on species-specific adaptations to migratory endurance flight (Weber, 2009).

(e) *Spatiotemporal adjustments to migration*

When migrants are still far from their final migratory destination, local environmental conditions are not necessarily good predictors for future conditions at the destination (Both, 2010). Regular stopovers thus may allow migrants to assess seasonal progression systematically, e.g. through changes in air temperature (Klinner & Schmaljohann, 2020) or vegetation growth rate (van der Graaf *et al.*, 2006; but see Wang *et al.*, 2019). Consequently, migrants may adjust their flight duration (Paxton & Moore, 2017) or departure probability (Eikenaar *et al.*, 2016) to optimise arrival time at breeding areas (van der Graaf *et al.*, 2006; Bauer, Gienapp & Madsen, 2008; van Wijk *et al.*, 2012; Lameris *et al.*, 2017; Paxton & Moore, 2017). For orientation and navigation, birds use cues from the sun, the stars, the Earth's magnetic field, odour and landmarks (Mouritsen, 2018), which they can probably also perceive during flight (Wiltschko & Wiltschko, 1995; Chernetsov, 2017; Mouritsen, 2018). However, it is possible that they can orient/navigate less accurately in flight than when on the ground/sea, where they also (re)calibrate their heading before resuming migration (Cochran, Mouritsen & Wikelski, 2004). Consequently, a potential function of stopovers could be to collect navigation/orientation information to determine their map position and/or to calibrate the magnetic compass through celestial cues (Cochran *et al.*, 2004; Muheim, Phillips & Åkesson, 2006), which likely takes place shortly before departure (Mouritsen *et al.*, 2004; Schofield *et al.*, 2018a).

IV DEPARTURE DECISIONS

After landing, a migrant eventually will have to depart from a stopover site. With stopover duration pivotal to shaping overall migration time (Alerstam & Lindström, 1990; Lindström & Alerstam, 1992; Schmaljohann & Both, 2017; Schmaljohann, 2018), hundreds of studies have investigated factors that influence migrants' departure likelihood, so-called 'departure cues'. Classical departure cues are energy stores and weather conditions, such as wind direction and speed (Richardson, 1990a; Jenni & Schaub, 2003; Liechti, 2006; Alerstam, 2011; Chernetsov, 2012; Cohen *et al.*, 2014a; Deppe *et al.*, 2015; Schmaljohann & Eikenaar, 2017; Moore, 2018; Linscott & Senner, 2021). Although we fully embrace the notion of departure cues, this does not lend itself well to our conceptual framework of stopover (Figs 1B, 2 and 3) because departure decisions are typically studied in a proximate fashion, with each cue having its own currency, such as grams of fat for energy stores and meters per second for wind support. Similar to the decision to interrupt migratory flight, we propose instead an ultimate approach, with the decision to depart from stopover expressed in fitness costs (Figs 2 and 3) (Alerstam & Lindström, 1990).

Given our definition of stopover, a migrant should depart when staying at a stopover site no longer contributes to lowering, but instead starts to increase immediate and/or delayed fitness costs (Fig. 2). This moment is reached when the sum of fitness costs associated with stopover is the smallest (*cf.* Paxton & Moore, 2017), irrespective of why the migrants initiated the stopover, and other potential associated cost(s), such as increased infectious disease risk (Altizer, Bartel & Han, 2011) and predation danger (Lank *et al.*, 2003) which might be context dependent for instance in relation to energy stores (Cimprich & Moore, 2006) (Figs 2 and 3). To exemplify this concept, consider a spring migrant with ample energy stores which lands in fair weather to recover from the oxidative damage incurred from endurance flight. After two days the oxidative balance is restored, so the initial purpose of the stopover is fulfilled. However, the weather has worsened and the migrant would face strong headwinds when departing. Whether or not the migrant should depart now depends on the fitness costs associated with each of the functions of stopover, each of which may affect the trade-off decision for stopover or flight (Fig. 3). For our spring migrant, the fitness costs of an imbalanced oxidative state are currently low; however, there are now substantial fitness costs to flying under unfavourable wind conditions, which may result in prolongation of the stopover. Likewise, for all other functions of stopover there may be fitness costs, which have to be incorporated into the decision to depart. For example, if our bird was traveling relatively late in the migration season (thus risking late arrival at the breeding areas, and hence losing the opportunity to reproduce), the associated fitness cost may exceed that of flying into headwinds, increasing the chances that the bird would depart (Fig. 3).

We believe that interpreting/assessing departure decisions in ultimate terms clarifies why the fulfilment of a single function of stopover may not always be informative for the likelihood that a migrant departs from stopover (Figs 2 and 3). Additionally, it explains why proximate departure cues sometimes appear to be ‘ignored’, for example when migrants depart in headwinds (Bulyuk & Tsvey, 2006) or remain at stopover sites despite having high energy stores [for reviews see Jenni & Schaub, 2003 and Schmaljohann & Eikenaar, 2017]. We emphasise that it is essential to study both the decision to interrupt the migratory endurance flight as well as the decision to depart. Moreover, we strongly suggest framing results of departure studies in terms of the ultimate fitness benefit for the individuals.

V RELEVANCE TO OTHER MIGRATORY ANIMALS

In our definition of stopover (Fig. 1B), ‘flight’ means movement through the air which could be relevant to other volant animals such as bats and insects. If in our definition ‘flight’ is replaced with ‘locomotion’, the concept of stopover could be applicable to any animal that makes migratory movements. Indeed, migratory animals from a wide variety of taxa interrupt their migratory movement once or several times before reaching the journey’s final destination. Even though it is not always clear if, and then which, immediate and/or delayed fitness costs are minimised, it is likely that such interruptions can be considered as stopovers. Examples of non-bird species that are known to make stopovers include silver-haired bats (*Lasiorycteris noctivagans* LeConte), common green darters (*Anax junius* Drury), fin whales (*Balaenoptera physalus* Linnaeus), monarch butterflies (*Danaus plexippus* Linnaeus), green turtles (*Chelonia mydas* Linnaeus), giant honeybees (*Apis dorsata* Fabricius), mule deer (*Odocoileus hemionus* Rafinesque) and chinook salmon (*Oncorhynchus tshawytscha* Walbaum) (e.g. Wikelski *et al.*, 2006; McCord & Davis, 2010; Sawyer & Kauffman, 2011; McGuire *et al.*, 2012; Robinson, 2012; Silva *et al.*, 2013; Baudouin *et al.*, 2015; Chalde & Fernández, 2017).

Similar to birds, some species need to accumulate energy between bouts of locomotion (e.g. Wikelski *et al.*, 2006; McCord & Davis, 2010) and/or appear to avoid particularly unfavourable weather conditions for migratory travel (e.g. Wikelski *et al.*, 2006; McGuire *et al.*, 2012). Stopovers have also been suggested to allow the animals to ‘rest’ (McCord & Davis, 2010; McGuire *et al.*, 2012; Baudouin *et al.*, 2015) or to maximise energy intake during the plant growing season (Sawyer & Kauffman, 2011). Additionally, stopovers may have functions that are unknown or irrelevant for birds. Some insects at times rely on sun-basking to raise thoracic temperature in order to reach a threshold required to initiate flight (Chapman, Reynolds & Wilson, 2015). In juvenile salmon, seaward migration may be interrupted and the fish may reside for some time in brackish estuaries, which

could facilitate physiological adaptations necessary for the transition between freshwater and ocean habitats (Chalde & Fernández, 2017). Clearly, the functions of stopover are myriad and, irrespective of the focal species, acknowledging this in future studies will considerably enhance our understanding of migration ecology in animals.

VI A HUMAN PERSPECTIVE OF WHY STOPOVER IS IMPORTANT

Humans should have an intrinsic motivation to conserve their natural environments and the ecosystems in which they live. These ecosystems are communities involving biotic and abiotic interactions, all parts of which are necessary for ecosystem functionality, as well as providing ecosystem services (e.g. pollination of crops, pest control and biomass production) to humans (Semmens *et al.*, 2018; Grilli, Bildstein & Lambertucci, 2019; Wotton *et al.*, 2019). Importantly, migratory animals may have significant roles in ecosystems thousands of kilometres apart, where they reside for several hours to several months (López-Hoffman *et al.*, 2017). The ability of migratory birds to survive and reproduce in the breeding period depends upon their capacity to forage and accumulate fuel in unfamiliar environments during migration (Fig. 1A) that may be characterised by extreme environmental conditions (e.g. hot and dry weather in deserts). The current anthropogenically induced accelerating rate of species extinction, alterations in habitat integrity and various climatic changes decrease the stability of ecosystems and thereby are harmful to the ecosystem services they provide (Fig. 2). Even if we could foresee which parts of the environment are indispensable to secure ecosystem services essential for human survival and economic benefits, it should remain a matter of international concern to prevent human-induced species extinction. In the context of migratory species, international collaboration constitutes a critical component for maintaining viable populations of almost all migratory species, which are subject to various risks in their breeding, wintering and stopover areas that are typically thousands of kilometres apart.

Special attention should be given to the worldwide declines in migratory species (Wilcove & Wikelski, 2008; Runge *et al.*, 2014). For example, about 19% of all bird species are migratory (Kirby *et al.*, 2008), and of these, the long-distance migrants have suffered the largest population declines (Vickery *et al.*, 2014; Bairlein, 2016). It is thought that this decline partly results from the migrants’ inability to adapt to advances in the peak availability of the food sources used to feed their offspring, that is they are unable to advance their arrival date sufficiently (Both & Visser, 2001; Both *et al.*, 2006). Arrival timing depends to a large extent on the total duration of stopover (Tøttrup *et al.*, 2012; Schmaljohann & Both, 2017; Schmaljohann, 2019), which in turn is affected by the functions provided by the stopover areas (e.g. feeding conditions;

Lindström, Alerstam & Hedenström, 2019). Hence, detailed knowledge of migrants' stopover ecology is required to understand the limits and potential for adjustments of arrival timing to breeding areas under scenarios of global warming (Fig. 2).

There are at least two questions that need answers if we want to conserve migratory species: what defines a suitable stopover habitat, and how many does a migrant need? Regarding habitat conditions, we need to understand which functions (e.g. availability of food and freshwater, places to rest, recover and hide from predators, spatial extent, etc.) a stopover habitat may offer at different times of year. A number of studies (Sapir *et al.*, 2004; Mehlman *et al.*, 2005; Buler *et al.*, 2007; Bonter, Gauthreaux & Donovan, 2008; Buler & Moore, 2011; Cohen, Pearson & Moore, 2014b; Cohen *et al.*, 2017, 2020) have explored features of stopover landscapes to characterise the habitat used by migrant birds. Although these studies provide a valuable description of important abiotic and biotic factors of stopover habitats, it is unknown whether and how they affect the decision of birds to interrupt their migratory endurance flights. However, we need to understand the reasons for landing in order to evaluate the migrants' requirements of the stopover landscapes for identifying and conserving these areas. By so doing, we could substantially improve the birds' chances of successful migration.

To address the second question of how many stopovers a migrant needs, we should identify how stopover habitats are spatially distributed and assess whether migrants are able to bridge the distance between them (Runge *et al.*, 2015; Choi *et al.*, 2019; Xu *et al.*, 2020). Degradation and loss of natural habitats, changes in agriculture, anthropogenic changes in the environment, poaching and recreational activities are significant threats to key properties of stopover habitats, with implications for the functions they may offer to migrants. Modelling of complete migration journeys could be helpful for our understanding how many stopover sites are required and what could be the consequences of their degradation and loss. Since migration has long been under strong selection, migrant birds are generally well adapted to the challenges encountered naturally during migrations. Therefore, migrants' capacity to tolerate such physically and physiologically demanding periods of exercise is likely to be well matched to the flight conditions experienced and to stopover functions. Anthropogenic changes in the environment, e.g. land use, climate change, nitrogen deposition (Sala *et al.*, 2000), create many novel and often unfavourable conditions that may push migrants towards or beyond their physical or physiological limits (Fig. 2). Notably, if stopovers offer insufficient opportunity to refuel, rest and recover, it is not only the deterioration of a single function, but rather the cumulative effect of all these functions along the migration route that could reduce bird fitness (Fig. 2). Such threats may be greatest for those species requiring unique stopover landscapes, such as waders that rely on tidal mudflats (Studds *et al.*, 2017), for species preparing to cross ecological barriers (Bairlein, 2016) or for species with unique stopover

sites, such as the Amur falcons (*Falco amurensis* Radde) in Nagaland (India) (Kasambe, 2014). If we do not improve or at least conserve the current functionality of stopover areas, many migrant species will likely experience lower fitness (Fig. 2). This could result in significant and accelerated population declines in the future (Studds *et al.*, 2017), which may eventually lead to extinctions of migratory species and entire migration systems (Wilcove & Wikelski, 2008).

VII IMPORTANT OPEN QUESTIONS FOR STOPOVER ECOLOGISTS

- (1) How can we assess the ultimate mechanisms regulating both departure and landing decisions?
- (2) What is the migratory history of a migrant before it lands at a specific stopover site?
- (3) Do we find the predicted context dependencies (Fig. 3) in freely moving animals, and what can we learn from them?
- (4) Do migrants learn from 'wrong' migratory trade-off decisions by adjusting their future decisions?
- (5) How does bird physiology affect ecological decisions (habitat selection, foraging)?
- (6) How can we assess fitness costs of migration and more specifically those leading to stopover landing and departure decisions?
- (7) How can we assess whether specific landscape types accommodate (all) the required functions of stopover?

VIII CONCLUSIONS

- (1) This review provides a revised conceptual framework within an evolutionary ecological context on why migratory birds make stopovers. This framework is also applicable to other migratory animals. We define stopover as: *an interruption of migratory endurance flight to minimise immediate and/or delayed fitness costs*. The decision to stop-over could be influenced by intrinsic factors and may differ between individuals depending on their life history (e.g. r/K -selected species) and even for the same individual depending on, for example, its age and ecological situation.
- (2) We list many functions of stopover, including several potential ones, and stress that individual migrants may have a different reason, or a set of diverse reasons, for making a stopover. Consequently, studies focussing on how a specific trait affects particular stopover behaviour, without acknowledging the roles of other traits, may be unable to examine their hypotheses properly and hence possibly misinterpret the actual effect of that trait on stopover behaviour. The traditional currencies of energy, time and predation in optimal migration theory should be complemented with

new currencies, pertaining to the state of the individuals, such as physiological recovery.

- (3) To allow for better identification of the functions that need to be fulfilled at the stopover before resuming migration, we propose not only to study stopover departure decisions, but also to investigate the reasons why migratory flights are terminated, leading to bird landing. Although it currently remains challenging to study why birds interrupt migratory endurance flights, the on-going miniaturisation of bio-logging devices and their remote data transmission will substantially facilitate identifying the energetic, physiological and environmental reasons for interruption of endurance flights. Optimisation analyses will provide a further powerful tool to investigate the functions of stopover. Bio-logging devices and optimisation analyses together will allow us to assess the consequences of certain stopover(s) for later annual cycle events.
- (4) Shifting the focus from proximate to ultimate mechanisms controlling the landing and departure decisions of migrants will help to identify the selective forces shaping stopover decision making within a full annual cycle perspective. It may also clarify why the fulfilment of a single function of stopover may not always be informative regarding whether a migrant resumes migration, or why proximate factors that are thought to stimulate departure (e.g. wind support and energy stores) sometimes appear to be 'ignored' by the birds.
- (5) Our work aims to stimulate the scientific discussion and empirical work on stopover decisions in particular and movement ecology of migrating animals in general. We list important open questions that should be addressed by stopover ecologists to advance understanding of stopover evolutionary ecology. Furthermore, we hope that our novel concept of stopover will provide significant input for conservation measures that may help to save long-distance migrants from extinction in response to anthropogenic changes in the environment.

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