Received: 18 December 2020 | Accepted: 8 March 2021

DOI: 10.1111/1365-2656.13484

RESEARCH ARTICLE

Journal of Animal Ecology | BRITISH ECOLOGICAL SOCIETY

Longer days enable higher diurnal activity for migratory birds

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Funding information
Russian Foundation for Basic Research, Grant/Award Number: 18-428 05-60057; Max-Planck Institute of Animal Behavior; German Air and Space Administration; Russian Ministry of Science and Higher Education, Grant/Award Number: AAAA-A19-119022190168-8

Handling Editor: Annette Fayet

Abstract

1. Seasonal geophysical cycles strongly influence the activity of life on Earth because they affect environmental conditions like temperature, precipitation and day length. An increase in daylight availability during summer is especially enhanced when animals migrate along a latitudinal gradient. Yet, the question of how day length (i.e. daylight availability) influences the activity patterns of long-distance, latitudinal migrants is still unclear.
2. Here, we ask whether migration provides benefits to long-distance migrants by enabling them to increase their diurnal movement activities due to an increase in daylight availability. To answer this question, we tested whether four vastly different species of long-distance migratory birds—two arctic migrants and two mid-latitude migrants—can capitalise on day length changes by adjusting their daily activity.
3. We quantified the relationship between daily activity (measured using accelerometer data) and day length, and estimated each species' daily activity patterns. In addition, we evaluated the role of day length as an ultimate driver of bird migration.
4. All four species exhibited longer activity periods during days with more daylight hours, showing a strong positive relationship between total daily activity and day length. The slope of this relationship varied between the different species, with activity increasing 1.5-fold on average when migrating from wintering to breeding grounds. Underlying mechanisms of these relationships reveal two distinct patterns of daily activity. Flying foragers showed increasing activity patterns, that is, their daytime activities rose uniformly up to solar noon and decreased until dusk, thereby exhibiting a season-specific activity slope. In contrast, ground foragers showed a constant activity pattern, whereby they immediately increased their activity to a certain level and maintained this level throughout the day.
5. Our study reveals that long days allow birds to prolong their activity and increase their total daily activity. These findings highlight that daylight availability could be an additional ultimate cause of bird migration and act as a selective agent for the evolution of migration.

KEYWORDS
animal activity patterns, animal movement, behavioural ecology, biologging, bird migration, global change, life history, seasonality

1 | INTRODUCTION

Seasonal and daily cycles strongly influence the activity of life on Earth. Within these cycles, different environmental conditions like temperature, precipitation, food availability and the number of daylight hours (day length) change regularly. The extent of these regular changes depends on latitude. Summer days are, for example, longer at high latitudes compared to mid-latitude regions. These seasonal cycles can provide temporal cues for many life-history stages of animals, including moult, growth, reproduction, hibernation (Hazlerigg & Wagner, 2006; Wingfield et al., 1993) and migration (Berthold, 1996; Gwinner, 1996). Research on animal migration drivers has shown that suitable atmospheric conditions, resource availability and predation risk affect the timing and characteristics of these journeys (Alerstam et al., 2003; Hurlbert & Haskell, 2003; McKinnon et al., 2010; Somveille et al., 2018). The proximate effect of day length on long-distance, latitudinal migrants has been studied in detail (Gwinner, 1990; Gwinner et al., 1993). Yet, it is still unclear whether migration benefits migrants because it enables them to increase their diurnal movement activities with the increasing daylight availability.

A raised daylight availability, especially when enhanced through poleward migration, increases fecundity in a wide diversity of taxa (Anderson & Jetz, 2005; Bryant, 1997; Lack, 1947, 1948, 1954; Schekkerman et al., 2003). In birds, different hypotheses for the latitudinal gradient in reproductive outcome have been suggested, including nest predation (McKinnon et al., 2010), adult mortality (Ghalambor & Martin, 2001) and gradients of resource availability and seasonality (Ashmole, 1963; Ricklefs, 1980). There is, however, one hypothesis for such a latitudinal gradient that has received much less attention: the daylight availability hypothesis. In a recent theoretical framework, Sockman and Hurlbert (2020) formulated the daylight availability hypothesis as 'diurnal birds for whom daylight is a resource incur fitness benefits from migration because, as the models reveal, the act of migration (compared to permanently residing at one latitude) almost always elevates an individual's annual exposure to daylight'. A link between day length and activity duration has been shown on captive birds (Daan & Aschoff, 1975). However, the hypothesis that birds can increase their foraging time during longer days, detectable through an increase in diurnal movement activity, has not been examined under natural conditions. At the same time, one main prediction of this hypothesis is that daylight availability could be an additional ultimate (but non-exclusive) cause of bird migration, and act as a selective agent for the evolution of migration (Sockman & Hurlbert, 2020). Many other ultimate factors of migration have been studied and quantified (Alerstam et al., 2003; Laird, 1961; McKinnon et al., 2010; Schekkerman et al., 2003). To evaluate the role of daylight availability as a driver of bird migration, we need to quantify the benefit of longer days for migratory birds.

Two main theoretical arguments question the assumption that birds can increase their total daily activity during longer days. First, it has been suggested that birds need to sleep for a certain amount of time (Cirelli & Tononi, 2008), limiting their potential ability to increase foraging time even when experiencing longer days. Second, estimations from the allometric relationship have implied that animals have an absolute upper limit of their daily energy budget (Kirkwood, 1983; Weiner, 1992). This would mean that they cannot benefit from longer days because they are unable to surpass a predicted ceiling in their energy budget. However, recent studies have shown that birds can adjust their sleep duration to varying ecological demands rather than to different restorative needs (Lesku et al., 2012; Rattenborg et al., 2016; Siegel, 2009). In addition, regarding the second theoretical argument, estimations of the total daily energy budget are often based on studies of captive animals and may be biased by differences in the measurement (Weiner, 1992). Studies have shown that with controlled foraging time (i.e. animals were able to feed all day long), the predicted maximum energy budget (Kirkwood, 1983) was exceeded by up to 126% for laboratory studies (Kvist & Lindström, 2000, 2003) and up to 150% for the studies in the wild (Klaassen et al., 2010). Thus, neither sleep requirements nor maximum daily energy budgets are constraining birds' activity levels. Also, previous studies have examined individual birds only over short periods, not covering their entire annual cycle in natural conditions. This means it is still unclear to what extent variation in day length may influence birds' energy budgets throughout their life.

Here we hypothesise that birds can benefit from longer days by increasing their daily activity. First, we explored whether birds can increase their activity period during longer days under natural conditions. Second, we examined whether total daily activity increased with longer days by analysing how birds adjust their daily activity patterns to different day length regimes. We expected that birds with different foraging modes exhibit different patterns of daily activity. Unlike ground foragers, flying broadwing foragers depend a lot on thermal updrafts (Bildstein, 2006; Cone, 1962; Hedenström & Bone, 1993), whose strengths covary with solar radiation and are stronger during midday. Thus, the birds' daily activity patterns will most likely have a bell shape (Cone, 1962; Friedemann et al., 2016). In contrast, ground foragers' activity would be more stable during the day (Raveling et al., 1972; Systad et al., 2000). Simultaneously, birds migrating to the Arctic for breeding will experience a more significant day length increase (even constant daylight during polar days) than mid-latitude migrants. Therefore, Arctic migrants could increase their total daily activity stronger than temperate breeders and/or decrease their activity level during the day. Thus, we predict that birds with different foraging modes will exhibit different daily activity patterns, and these patterns will change during the year to a greater degree for Arctic migrants than for mid-latitude migrants.

These questions can only be answered when we study the birds' movements and activity patterns during a whole year (i.e. complete life cycle) and compare the sum of their daily activities. Modern tracking technologies provide new possibilities for following migrating birds through their annual cycle with extreme detail. High-resolution Global Positioning System (GPS), together with tri-axial acceleration, allows us to monitor the behaviour and measure animals' activity (Green et al., 2009; Halsey et al., 2011; Payne et al., 2011). Thus, using advanced tracking technology (Wikelski et al., 2007), we are now able to compare the behaviour of migrating birds that experience various daylight regimes throughout their life cycles.

Here we examine the relationship between activity and day length in four long-distance migratory bird species. By

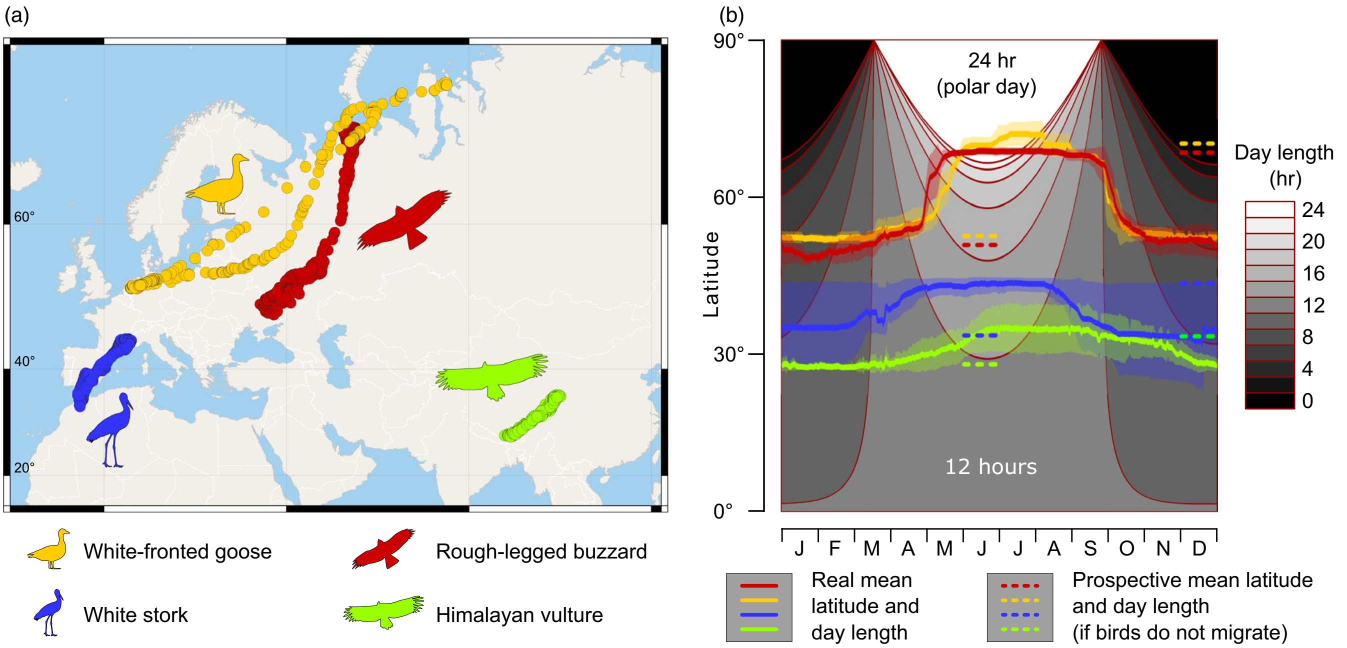

FIGURE 1 Migration paths and duration of the day length. (a) Migration paths of 63 birds of four species tracked with GPS/GSM. Circles represent the mean daily locations of each species throughout the year. (b) Real (solid line) and prospected (if birds did not migrate; dashed line) mean latitudes in June/December of the four studied species on the spatiotemporal map of day length. Shadows represent the standard deviation of the mean; colours indicate the four species

TABLE 1 A number of birds of each species, sex ratio, dates and duration of tracking, and energy expenditure variables

	Rough-legged buzzard *Buteo lagopus*	White stork *Ciconia ciconia*	Greater white-fronted goose *Anser albifrons*	Himalayan Vulture *Gyps himalayensis*	Total	Mean ± *SD*
Number of individuals	14	14	18	17	63	
Sex ratio (male/female/ unknown)	1/13/0	8/4/2	11/7/0	0/0/17	20:24:19	
Tracking duration per animal (days), mean ± 95% CI	679 ± 169	924 ± 119	494 ± 119	588 ± 54		671 ± 185
Years of tracking	2013–2016	2013–2016	2013–2016	2014–2016	2013–2016	
Activity sun angle[a] (*p*-values for piecewise regression)	−6.4 <0.001	−7.7 0.002	−6.5 <0.001	−10.7 <0.001		−7.8 ± 1.9
Activity slope[a] (mean ± *SD*)	0.0030 ± 0.0013			0.0017 ± 0.0005		
Activity level[a] (mean ± *SD*)		0.18 ± 0.02	0.27 ± 0.03			
Activity threshold	0.035	0.040	0.100	0.028		

[a] See Figure 3b for explanation.

determining the species-specific daytime activity patterns, we explore whether migratory birds can benefit from longer days by increasing their total daily activity levels. We analysed data on the annual movements and activity patterns of 63 individuals of four different species: rough-legged buzzards *Buteo lagopus* (hereafter buzzards), white storks *Ciconia ciconia* (storks), greater white-fronted geese *Anser a. albifrons* (geese) and Himalayan vultures *Gyps himalayensis* (vultures). These species differ in their foraging behaviour in that geese and storks are ground foragers, and vultures and buzzards search for food in flight. At the same time, these species experience different amplitudes of the annual daylight changes, as two species migrate to the Arctic (buzzards and geese), whereas the other two (storks and vultures) stay in middle latitudes. Therefore, our study covers a range of behavioural features (flight/ground foragers, arctic/temperate breeders, Figure 1; Table 1), providing us with a diverse set of parameters to explore our hypothesis that the activity of arctic migrants will increase stronger than that of mid-latitude migrants (Sockman & Hurlbert, 2020).

2 | MATERIALS AND METHODS

2.1 | Dataset

For this study, we used 45 g solar GSM–GPS–ACC loggers (e-obs GmbH) that were attached with a Teflon harness. Sixty-three birds of four species were trapped in 2013–2016 using different catching techniques (Flack et al., 2016; Kölzsch et al., 2016). Buzzards, geese and vultures were tagged as adult birds, and storks were juveniles. However, for storks, first-year tracks were not included in our analyses (see Table 1 for further details).

We recorded GPS locations and 3D body acceleration 24 hr/day for buzzards, geese and vultures and 19 hr (between 2:00 and 20:00) for storks. GPS positions were recorded every 5 min for storks, vultures and geese and every 1 hr for buzzards. For all species, three-axial body acceleration was measured every 5 min for 3.8 s at 10.54 Hz (i.e. 40 data points per axis and 120 data points per ACC burst). Because the tracking devices were solar-charged, they could run out of energy on days with little sunlight, affecting the GPS and ACC sampling scheme independently from each other (i.e. ACC sensors require less energy than GPS). For each tracked individual, we selected for our analyses only days of data that included both GPS and acceleration measurements.

Data were stored and then downloaded via GSM using GPRS technology or via UHF radio link using handheld base stations. Raw acceleration data were converted from millivolts to gravitational acceleration (g) (rate of change of velocity; $1\ \text{g} = 9.81\ \text{ms}^{-2}$) using tag-specific calibration values.

Here we used overall dynamic body acceleration (ODBA) data for measuring the birds' movement activities. ODBA has been used as a proxy for the energy an animal spends for body movements (Green et al., 2009; Halsey et al., 2011; Payne et al., 2011). But it is clear that other individual physiological and behavioural processes, such as moult, egg production or thermoregulation, contribute to an animal's overall energy expenditure. ODBA was calculated as follows: the static acceleration was determined by individual smoothing of the three axes' measures using running means over each 3.8 s segment. Next, for each axis, the dynamic acceleration was determined by subtracting the static acceleration from the corresponding (unsmoothed) raw acceleration data. The sum of all three axes then provided a value of ODBA experienced by the animal (Flack et al., 2016; Gleiss et al., 2011).

2.2 | Activity and sun angle above the horizon

To investigate whether birds' activity was related to daylight conditions, we calculated the mean ODBA for each hour each day. Then, we selected only data of those days with 24 values (19 for storks), that is, one ODBA mean value per hour. Finally, we averaged all daily/hourly values over the different years and combined them with monthly/hourly ODBA values. Thus, for buzzards, geese and vultures, we worked with 288 values (24 hr × 12 months) and for storks with 228 values (19 hr × 12 months). These represented the mean daily dynamic of the activity in each month of the year. In the same way, we calculated the mean GPS positions. Using mean values of the resulting latitudes, we calculated sun angles above the horizon that were set into relation with each value of ODBA (R function 'sunAngle' in library 'oce', Kelley & Richards, 2016).

The predicted relationship between activity and sun elevation (*activity pattern*) was analysed in the following way. First, we determined the threshold of the sun angle at which the birds started and stopped to be active (*activity sun angle*), using an iterative search procedure for piecewise regression described by Crawley (2007). We continued to work only with data to the right side of the threshold, that is, with sun angles of activity. Second, we analysed the relationship of sun angle and ODBA (*activity slope*) for buzzards and vultures using linear mixed-effects models (R function 'lmer' in library 'lme4', Bates et al., 2015). ODBA was the response variable, sun angle and month were fixed effects, and individuals were included as a random effect. The analysis was done separately for each species. Likelihood ratio tests were used to compare four candidate models: including sun angle as a fixed effect, including month as a fixed effect, including both with and without interaction. Third, for storks and geese, we examined the same relationship using nonlinear mixed-effects models (R function 'nlme' in library 'nlme', Pinheiro et al., 2020) with a nonlinear function of the following form:

$$f(x) = a - be^{-cx},$$

where x is the sun angle, $f(x)$ is the ODBA value, a is the upper asymptote (*activity level*), b is the growth rate and c is the time of maximum growth. We used likelihood ratio tests to compare two candidate models: with and without month as a fixed effect of the upper asymptote.

For presenting the results in a more informative way, we determined a generalised local time (i.e. so that the sun angle above the horizon is maximum at noon). Considering that the Earth makes a complete rotation (360°) every 24 hr [or 1° in 4 min (1/15 of an hour)], we calculated this local time using the following equation:

$$t_{\text{loc}} = t_{\text{UTC}} + \frac{lon}{15},$$

where t_{loc} is the generalised local time, t_{UTC} is the time in UTC format as obtained from the logger (in decimal hours) and *lon* is the mean longitude calculated in a way described above (in decimal degrees).

2.3 | Activity and length of the day

For investigating whether migration to higher latitudes allowed a change in total daily activity and duration of the activity period, we used mean ODBA values for each hour, calculated as described above. Then for each day, we calculated the total ODBA (sum of the ODBA values for that day) and mean day length (using R function 'daylength' in the library 'geosphere' (Hijmans, 2016)). For each day, we calculated the period of activity as the number of hourly mean ODBA values, which were greater than a certain threshold of activity. This threshold was estimated as a mean ODBA value for the non-moving bird. The bird was considered as non-moving when two consistent hourly GPS coordinates were equal, and there were at least six ODBA bursts between these GPS values, and they did not differ between each other for more than one standard error of the mean. For each species, we used 10 measurements from 10 different birds. The values of the activity threshold for each species are presented in Table 1.

The overall relationship between daily ODBA values (and duration of activity period) and day length was then analysed using a linear mixed-effects model (R function 'lme' in library 'nlme') with total daily ODBA (and duration of activity period) as response variables, day length as explanatory variable and individuals as a random effect. Temporal autocorrelation was included in the model as a first-order autoregression (corAR1). Total daily ODBA and duration of activity period were analysed separately. The likelihood ratio test was then used to compare two candidate models: with and without day length as a fixed factor. The analysis was done independently for each species.

All calculations were performed using R 3.6.2 (R Development Core Team, 2019).

3 | RESULTS

3.1 | Duration of activity and total daily activity

The length of the activity period of all four species depended strongly on day length (Figure 2a). Activity duration was increasing when the day got longer, as the model with day length as a fixed factor received higher support from the likelihood ratio test ($p < 0.001$, Table 2; Tables S1 and S2). Mid-latitude migrants—storks and vultures—started and stopped their activity during twilight throughout the entire year. Therefore, the length of their activity period was always longer than the total day length and increased linearly

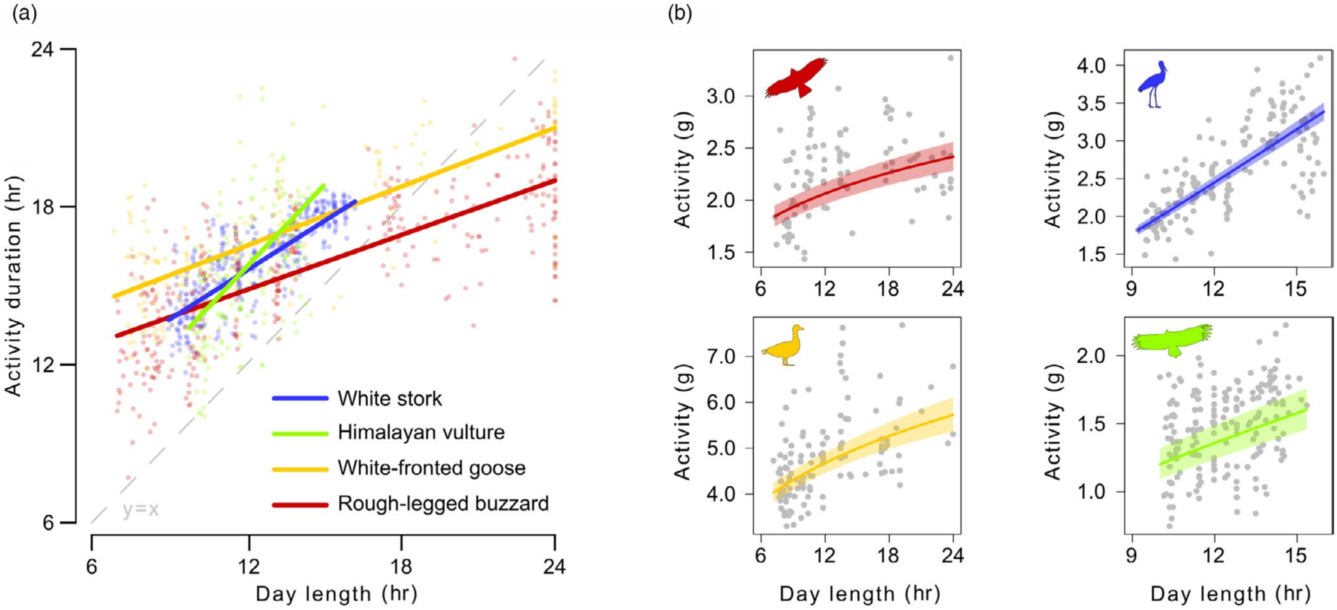

FIGURE 2 Activity in relation to day length. (a) Daily activity duration (mean number of active hourly ODBA averages) as a function of day length. See Table 2; Tables S1 and S2 for model output. (b) Daily activity (sum of hourly ODBA averages) as a function of day length. See Table 3; Tables S3 and S4 for model output. Shadows represent the 95% confidence interval for the mean

TABLE 2 The relationship between duration of activity and day length. Linear mixed-effect model, fixed effects. Response variable—daily duration of activity. Fixed effect—day length. Random effect—individuals. Temporal autocorrelation—autoregression of order 1. For the plot of the model, see Figure 2a. For the random effects and correlation structure, see Table S2

Species		Estimate	*SE*	*t* value	*p* value
Rough-legged buzzard	Intercept	10.51	0.27	39.06	
	Day length	0.35	0.01	28.75	<0.001
Himalayan vultures	Intercept	3.97	0.71	5.61	
	Day length	0.95	0.05	19.67	<0.001
White storks	Intercept	7.75	0.19	41.58	
	Day length	0.65	0.01	52.98	<0.001
Greater white-fronted geese	Intercept	12.00	0.31	38.95	
	Day length	0.37	0.02	23.46	<0.001

TABLE 3 The relationship between total daily activity and day length. Linear mixed-effect model, fixed effects. Response variable—total daily activity (ODBA). Fixed effect—day length. Random effect—individuals. Temporal autocorrelation—autoregression of order 1. Effect sizes are on the log scale. For the plot of the model, see Figure 2b. For the random effects and correlation structure, see Table S4

Species		Estimate	*SE*	*t* value	*p* value
Rough-legged buzzard	Intercept	0.15	0.06	2.61	
	Day length	0.23	0.02	11.29	<0.001
Himalayan vultures	Intercept	−1.36	0.12	−11.33	
	Day length	0.67	0.04	15.17	<0.001
White storks	Intercept	−1.91	0.09	−22.63	
	Day length	1.13	0.03	34.12	<0.001
Greater white-fronted geese	Intercept	0.81	0.07	11.00	
	Day length	0.29	0.03	10.15	<0.001

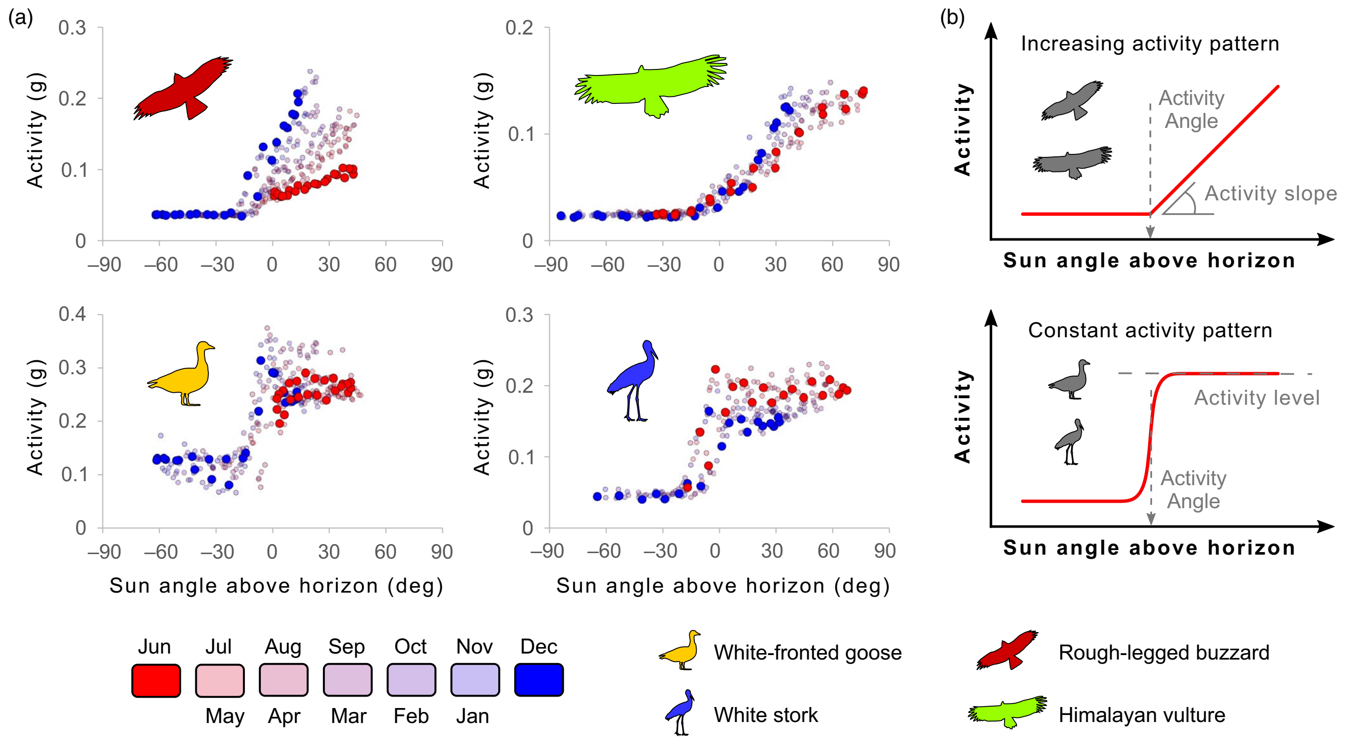

FIGURE 3 Activity in relation to sun angle above the horizon. (a) Hourly activity (hourly mean of ODBA values) as a function of sun angle above the horizon. See Tables 4 and 5; Tables S5 and S6 for model output, and Figures S1 and S2 for the plots of the models. (b) Activity patterns of two different forager types, flying and walking

(Figure 2a). The activity duration of storks and vultures increased from 13.7 to 18.2 and from 13.4 to 18.8 hr when the day length increased from 9.1 to 16.1 and from 9.9 to 15.6 hr, respectively (Figure 2a). In contrast, for arctic migrants—buzzards and geese—the sun was always above the horizon during the summer. Thus, the activity periods of arctic migrants were longer than the overall day length in the mid-latitudes and shorter than day length in the Arctic (Figure 2a). The activity duration of buzzards and geese increased from 13.1 to 19.0 and from 14.6 to 21.0 hr when the day length increased from 7.2 to 24 and from 7.0 to 24 hr, respectively. These findings resulted in different values of the regression slopes (activity duration vs. day length) for mid-latitude and arctic migrants. Buzzards and geese had a slope of 0.35 ± 0.01 (hereafter mean ± *SE*, estimated from the model) and 0.37 ± 0.02, respectively. Storks and vultures had a slope of 0.65 ± 0.01 and 0.95 ± 0.05, respectively (Figure 2a; Table 2).

The total daily activity of all four species increased with day length (Figure 2b). The model with day length as a fixed factor received higher support from the likelihood ratio test ($p < 0.001$, Table 3; Tables S3 and S4). The magnitude of this increase varied between the different species (Table 3). The activity of buzzards and geese increased 1.32 and 1.43 times, respectively, when migrating from wintering to breeding grounds. The activity of storks and vultures increased 1.89 and 1.36 times, respectively (Figure 2b; Table 3).

3.2 | Daily activity pattern

We discovered that daytime activity levels of all study species depended strongly on the locally experienced light conditions, measured as sun elevation (Figure 3a; Tables 4 and 5; Tables S5 and S6). However, the relationships between daily activity and sun elevation revealed two distinct daily activity patterns (Figure 3b). Daytime activities of buzzards and vultures (flying foragers) changed uniformly together with the sun's movement, thereby exhibiting a season-specific *activity slope*. This can be described as an *increasing activity pattern* (Figure 3b). In contrast, storks and geese (ground foragers) showed a *constant activity pattern*, in which they increased their activity in the morning up to an *activity level* that they kept until sunset (Figure 3b). Simultaneously, irrespective of location, species or time of the year, animals started and stopped to be active during twilight (hereafter 'activity sun angle', Figure 3b). While the activity patterns remained stable, parameters of these two patterns (e.g. activity slope and activity level) varied throughout the year (Figure S1). Activity slopes of buzzards and vultures reached their minimum in summer (June/July) and their maximum in autumn (October/November; Figure S1a,b). The model with the sun angle and the month as fixed factors and interactions between them received higher support from the likelihood ratio test ($p < 0.001$, Table 4; Table S5). However, geese and storks varied in their maximum activity level that peaked during the migration seasons (Figure S1c,d). The model with the month as a fixed factor received more support from the likelihood ratio test ($p < 0.001$, Table 5; Table S6).

4 | DISCUSSION

Here we examined the impact of long days on birds' activity patterns, arising from migration to higher latitudes. All four long-distance

TABLE 4 The daily activity pattern of Rough-legged buzzards and Himalayan vultures. The relationship between activity and sun elevation. The likelihood ratio test to compare four candidate models: with the sun angle as a fixed factor ('~sun angle'), with the month as a fixed factor ('~month'), and with the sun angle and the month as fixed factors: with ('~sun angle × month') and without interaction ('~sun angle + month') between them. For the plot of the model, see Figure 3; Figures S1 and S2. For the fixed and random effects of the best model, see Table S5

Species	Model	*df*	AIC	BIC	Deviance	χ^2	*p*-value
Rough-legged buzzard	~sun angle	4	−7,095	−7,073	−7,103		
	~month	14	−7,322	−7,243	−7,350	247.1	<0.001
	~sun angle + month	15	−8,524	−8,439	−8,554	1,203.5	<0.001
	~sun angle × month	26	−8,903	−8,755	−8,955	400.7	<0.001
Himalayan vultures	~sun angle	4	−12,749	−12,725	−12,757		
	~month	14	−9,741	−9,658	−9,769	0	1
	~sun angle + month	15	−13,225	−13,136	−13,255	3,485.2	<0.001
	~sun angle × month	26	−13,671	−13,517	−13,723	468.4	<0.001

TABLE 5 The daily activity pattern of White storks and Greater white-fronted geese. The relationship between activity and sun elevation. The likelihood ratio test to compare two candidate models: with ('~month') and without the month ('~1') as a fixed factor. For the plot of the model, see Figure 3; Figures S1 and S2. For the fixed and random effects of the best model, see Table S6

Species	Model	*df*	AIC	BIC	L. Ratio	*p* value
White storks	~month	16	−8,219	−8,128		
	~1	5	−7,748	−7,719	493.2	<0.001
Greater white-fronted geese	~month	16	−5,588	−5,498		
	~1	5	−5,272	−5,244	338.2	<0.001

migrants exhibited longer activity periods during days with more daylight hours (Figure 2a), showing a strong positive relationship between total daily activity and day length (Figure 2b). At the same time, the underlying mechanisms of these relationships reveal two distinct patterns of daily activity (Figure 3). Therefore, we prove that the assumption of the 'daylight availability hypotheses' (Sockman & Hurlbert, 2020) is valid by showing that long days allow prolonged activity which, in turn, results in higher total daily activity. However, the increase in total daily activity is far more expressed in Arctic migrants than mid-latitude migrants. Thus, the prediction that daylight availability could be an additional ultimate cause of bird migration and act as a selective agent for migration evolution should be considered based on species-specific migration traits (see Section 4.3 for details).

4.1 | Daily dynamic of activity

The primary physiological constraint of an individual's energy budget is its energy assimilation. Given that foraging rates may exceed digestion rates strongly (Weiner, 1992), we conclude that birds distribute their activity across the available daylight period to maximise foraging time and, with it, energy assimilation (Figure 3a). Species-specific foraging behaviours determined the shape and dynamics of these activities, resulting in two distinct activity patterns (Figure 3b). The form of locomotion while searching for food seemed to strongly influence these activity patterns, especially for the species with increasing activities (e.g. buzzards and vultures). As large soaring birds, these birds rely on thermal uplift to minimise their movement costs while foraging. Thermal occurrences and strengths vary throughout the day and year and reflect the daily and yearly variation in the birds' activity patterns. Especially the arctic migrant (buzzards) that experienced large differences in day length exhibited strong annual variation. Based on the activity patterns, we excluded prey availability or activity as influential factors on the different activity patterns as they do not correspond to the birds' periods of high activities. Buzzards forage on rodents which are active during dusk and dawn, while vultures search for carrion that has no daily dynamics. The ground foragers (i.e. geese and storks) that do not depend on thermals for foraging exhibited constant activity patterns: activity levels rose quickly in the morning and remained constant throughout the day. High activity peaks shortly after twilight (that geese exhibited only outside their nesting period) may be caused by flights from and to the roosting sites. Geese, contrary to the three other species, showed additional low levels of activity during nighttime. As herbivores, they can forage during nighttime with minimal light coming from the moon or stars (McNeil et al., 1992; Ydenberg et al., 1984).

Although all our study species exhibited an all-day-active pattern, other species (1) may experience additional ecological constraints (such as tidal regimes, Klaassen et al., 2010) that limit their foraging time, (2) use other foraging strategies (e.g. aerial, diving or nocturnal foragers), (3) and use night time not only for foraging (Liechti et al., 2013). When examing passerines, we would, for example, expect a different daily activity pattern, as those species are known to show a two—peak daily activity pattern (Aschoff, 1966). The diversity of these patterns, as well as their seasonal change, remain to be explored. Our findings, however, allow us to state general rules on the dynamic of daily activity patterns: First, the shape and dynamics of daily activity pattern depend strongly on the daylight availability (notably light intensity as opposed to fixed celestial time marks) and are determined by foraging behaviour and locomotion features. Second, different ecological constraints can add a specific feature to the patterns but not change their entire shape or dynamic. Third, the shape of the patterns remains stable throughout the life cycle, but parameters of the patterns (as *activity slope* and *activity level* for the studied species) can change with the seasons due to differences in daylight availability.

4.2 | Seasonal dynamic of activity

In all four species, longer daylight hours led to increased total daily activity (Figure 2b). This is consistent with data obtained on captive animals (Daan & Aschoff, 1975), which described the relationship between day length and activity duration as an S-shaped curve. However, this study tested migratory species during the polar night, although migratory species travel south under natural conditions and do not experience the constant darkness. The measurements during the low day length conditions caused the lower asymptote of the S-shaped curve. Given that our study examined animals under natural conditions, our results were qualitatively the same but quantitively different.

While birds can spend more time foraging during these long days, an increase in total daily activity may also be harmful to individuals. Artificially increased brood sizes in European kestrels *Falco tinnunculus* led to an increase in the birds' daily energy expenditure and resulted in higher mortality rates of the parents (Daan et al., 1996). Although the exact mechanisms underlying this relationship are unclear, one hypothesis states that high energy turnover (or rate of energy expenditure) could be linked to more rapid ageing (Sacher, 1978). However, most studies linking increased daily energy expenditure to higher mortality were conducted under constant light conditions. This also comprises that larger daily energy expenditure equals higher rates of energy expenditure. Yet, by increasing the length of the activity period (i.e. day length), daily energy expenditure can also rise without a simultaneous increase in the rate of energy expenditure. During longer days, the higher total daily activity could result in similar or even lower (as for buzzards in our study) rates of energy expenditure. Thus, when migrating towards longer days, increasing total daily activity may not necessarily induce rapid ageing. Therefore, the advantages ascending from rising total daily activity (i.e. longer foraging periods and the possibility to raise more offspring) persist while the disadvantages (i.e. rapid ageing) disappear when moving to areas with longer days.

It has often been assumed that the upper limit of an animal's daily energy budget depends only on its metabolic rate or could be determined by allometric relationships (Kirkwood, 1983). Previous studies found that this limit can be higher for animals experiencing longer days. They suggested that animals could surpass the predicted ceiling because they experienced high-energy demands (e.g. migration; Klaassen et al., 2010; Kvist & Lindström, 2000, 2003). Here we showed that total daily activity and maybe even the entire daily energy budget were correlated with day length. Exceeding the predicted ceiling may not (only) be linked to high-energy demands but could also be a consequence of the increase in day length. Therefore, an increase in total daily activity on longer days may be a benefit for birds rather than a disadvantage. However, this may be reversed for nocturnal animals breeding at high latitudes, as their foraging times during the reproductive period are constrained due to the shorter nights (Zárybnická et al., 2012).

We quantified the relationship between day length and activity for migrating birds. These estimates could be used to understand changes in animal migration patterns and predict the consequences of human activities on them. Global changes in climate and habitat induce warmer temperatures. This is especially rapid in the Arctic (Gilg et al., 2012; Post et al., 2009). Forecasts predict an increase in food abundance in the Arctic, making it more attractive for different species. However, even if the Arctic climate was mild and food abundance high, birds would still leave the Arctic during winter due to the polar night and their inability to forage there during this period.

When simply taking day length as a frame of reference for possible activity levels, we can hypothesise that Arctic species (buzzards and geese) would lose approximately 30% of the total daily activity if they did not migrate to the Arctic during spring. Similarly, if they did not perform fall migration, they would experience polar nights in the Arctic during winter and lose almost all of their total daily activity (Figure 1b). Another example arises from human-related food sources (e.g. landfills on the Iberian peninsula or abandoned fish farms in Uzbekistan) impacting white storks' migratory behaviour. These anthropogenic effects may alter the migration (and thus distribution) of storks. According to our results, the benefit of migration for mid-latitude migrants in terms of daily activity is low (from 2% to 9%) because of the lower difference in day length between breeding and wintering grounds (Figure 1b). Thus, we can assume that the food supply will play a more prominent role than this slight gain in daylight and has the potential to alter migration. In fact, we already begin to see changes (Flack et al., 2016).

4.3 | Could daylight availability be an additional ultimate cause of bird migration

Here we showed that migration to the regions with longer days is beneficial for birds. Long days enable higher activity levels, allowing birds to achieve this activity with lower energy expenditure rates. However, quantitative estimations of this benefit let us conclude that because the amplitude of the annual changes in daylight is more pronounced at high latitudes, the role of daylight availability as an ultimate factor of migration is higher for Arctic than for mid-latitude migrants. Many other factors further constrain and regulate migration and species distributions (Alerstam et al., 2003; Laird, 1961; McKinnon et al., 2010; Schekkerman et al., 2003). Besides extrinsic factors, there are intrinsic factors—photoperiodism regulates the annual reproductive cycle and could constrain migration and the distribution of birds (Sockman & Hurlbert, 2020). Therefore, day length could be considered as an additional ultimate case of bird migration, which varies for different species. To predict the consequences of future global change on bird migration, we should take into account all of these factors.

5 | CONCLUSIONS

To conclude, our results suggest that year-round patterns of activity of avian migrants with contrasting latitudinal ranges and foraging modes depended strongly on day length. When examining single species for short periods, the dependence on this primary factor may not be detectable, as it could be hidden by the species' dependence on other extrinsic factors that constrain its lifetime paths like local weather conditions or food availability. Considering day length as one of the essential (but not unique) determinants of migration becomes highly relevant when exploring species' life-history decisions in a rapidly changing world (Steffen et al., 2018) because, even under vastly different environmental conditions, the available hours of sunlight will remain stable. Thus, a thorough understanding of this primary, unifying concept of day length dependency will help scientists and conservationists predict future changes caused by the Anthropocene. This is of utmost importance for vulnerable ecosystems, such as the Arctic, where the role of day length is high, and rapid warming is already affecting terrestrial tundra ecosystems (Post et al., 2009; Terraube et al., 2015).

ACKNOWLEDGEMENTS

We are very grateful to all the people who helped us to collect these data in the field: Helmut Kruckenberg, Gerard Müskens, Gerhard Nikolaus, Alexander Dmitriev, Heidi Schmid, Rolf Weinzierl and Liya Pokrovskaya. This study was funded by the Max-Planck Institute of Animal Behavior, and the German Air and Space Administration (DLR). Peter Glazov was funded by the Russian Ministry of Science and Higher Education (project no. AAAA-A19-119022190168-8) and by the Russian Foundation for Basic Research (grant 18-428 05-60057 Arctic). Open Access funding enabled and organized by Projekt DEAL; WOA Institution: Max-Planck-Gesellschaft; Blended DEAL: Projekt DEAL.

AUTHORS' CONTRIBUTIONS

I.P. conceived of the presented idea, developed the theory and performed the computations; I.P., A.F., A.K. and M.W. prepared the database and taking responsibility for logical interpretation and presentation of the results; I.P., A.F., A.K., S.S., W.F., P.G., O.K. and M.W. conducted fieldwork; M.W. obtained funding. All authors took part in the preparation of the manuscript.

DATA AVAILABILITY STATEMENT

The datasets generated during and/or analysed during the current study are available in the Movebank Data Repository (Fiedler, Flack, Schäfle, et al., 2019; Fiedler et al., 2019; Kölzsch et al., 2021; Pokrovsky et al., 2021; Sherub & Wikelski, 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Pokrovsky I, Kölzsch A, Sherub S, et al. Longer days enable higher diurnal activity for migratory birds. *J Anim Ecol*. 2021;90:2161–2171. https://doi.org/10.1111/1365-2656.13484