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Article

Diurnal timing of nonmigratory movement by birds: the importance of foraging spatial scales

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Timing of activity can reveal an organism's efforts to optimize foraging either by minimizing energy loss through passive movement or by maximizing energetic gain through foraging. Here, we assess whether signals of either of these strategies are detectable in the timing of activity of daily, local movements by birds. We compare the similarities of timing of movement activity among species using six temporal variables: start of activity relative to sunrise, end of activity relative to sunset, relative speed at midday, number of movement bouts, bout duration and proportion of active daytime hours. We test for the influence of flight mode and foraging habitat on the timing of movement activity across avian guilds. We used 64 570 days of GPS movement data collected between 2002 and 2019 for local (non-migratory) movements of 991 birds from 49 species, representing 14 orders. Dissimilarity among daily activity patterns was best explained by flight mode. Terrestrial soaring birds began activity later and stopped activity earlier than pelagic soaring or flapping birds. Broad-scale foraging habitat explained less of the clustering patterns because of divergent timing of active periods of pelagic surface and diving foragers. Among pelagic birds, surface foragers were active throughout all 24 hrs of the day while diving foragers matched their active hours more closely to daylight hours. Pelagic surface foragers also had the greatest daily foraging distances, which was consistent with their daytime activity patterns. This study demonstrates that flight mode and foraging habitat influence temporal patterns of daily movement activity of birds.

Keywords: flight mode, foraging, movement ecology, multispecies, nonmigratory, temporal

Introduction

An animal's movement behavior is heavily influenced by its evolutionary history, which affects movement capacity and behavior (Norberg and Norberg 1988, Tobalske 2001). An animal's movement path is based, in part, on the distribution of resources (Fryxell et al. 2004), which is determined by their environment. These interact when animals forage, as they need to traverse the landscape according to their movement capacities to locate resources distributed non-randomly in the environment (Suryan et al. 2008). To maximize energetic gains from foraging, the timing of an animal's foraging movements is expected to correspond to either the temporal availability of its resources (Rydell et al. 1996, Lang et al. 2018) or the quantity and quality of resources required (Jetz et al. 2004, Ramesh et al. 2015, Cid et al. 2020). Alternatively, animals can reduce their energy expenditure by timing their foraging activity when their movements are most energetically efficient (Chapman et al. 2011, Shepard et al. 2013) via behavioral thermoregulation (Matern et al. 2000) and passive movement (Krupczynski and Schuster 2008). Both strategies are used by animals to forage optimally (Stephens and Krebs 1986), but these strategies have yet to be evaluated together within any group of animals.

Birds are distinct from other vertebrates because most are volant and fly actively (i.e. by flapping) while a smaller number fly passively (i.e. by soaring). Soaring birds save energy by using updrafts (Baudinette and Schmidt-Nielsen 1974) to move across the landscape. One tradeoff faced by terrestrial soaring birds is that the availability of updrafts is skewed towards daylight hours (Pennycuick 1978). Switching to flapping flight can further extend the activity of soaring birds (Stark and Liechti 1993, Harel et al. 2016) as flapping flight is self-powered and can therefore be used in a broader suite of conditions.

When animals can be flexible in the timing of their movements, their activity is expected to be driven more by ecological interactions and the need to acquire resources. These needs can manifest as temporal matching between consumers and their resources. For example, black-legged kittiwakes *Rissa tridactyla* time their foraging concurrently with tidal cycles, when prey are most accessible (Irons 1998). Alternatively, the amount of movement activity may be due to resource quality. When high quality food items are available, animals can spend more time resting as their energetic needs are met more quickly (Saj et al. 1999, Fleischer Jr. et al. 2003, Ménard et al. 2013). Despite long lasting interest in the factors that shape animal activity times, it is still poorly understood how internal traits and external conditions jointly shape the timing of movement across avian species.

Using daily movement activity data from a wide range of avian species, we tested for broad-scale differences in the temporal patterns by flight mode and foraging habitat. Temporal patterns do not only describe when individuals are moving, but they also convey information about the behaviors driving those movements (Pasquaretta et al. 2020). Therefore, temporal patterns of movement activity are best described using a suite of variables. First, we evaluated the similarity of temporal patterns among species using multivariate analyses and test for signals of foraging habitat and flight mode among clusters of species in ordinal space. Due to geographic and dietary segregation, we expected to find the greatest differences in multivariate space to be between birds from terrestrial and pelagic foraging habitats.

Second, we hypothesized that the timing of daily movement activity is more restricted for species that soar, because the flight performance of soaring birds varies within a day (Mellone et al. 2012) due to temporal variation in availability of environmentally derived updrafts (Spiegel et al. 2013). We predicted start and end times of movement activities would differ between flight modes. Flapping birds are unrestricted in their capacity to move and therefore can be active before sunrise and after sunset; in contrast, we expected terrestrial soaring birds to be limited to daylight hours. Soaring flight is most beneficial for large-bodied birds (Hedenström 1993), which are often raptorial (Schoener 1968); consequently, the use of soaring flight covaries with trophic level and morphology (Viscor and Fuster 1987, Baliga et al. 2019). We also predicted that pelagic soaring birds would be less temporally restricted than non-soaring birds as dynamic soaring is not driven directly by solar energy but by wind and wave energy (Pennycuick 1982).

Material and methods

Data

We compiled GPS tracking data for 49 bird species whose movements were studied between 2002 and 2019. We obtained data from Movebank (<www.movebank.org>; Wikelski and Kays 2018) or through direct contributions by co-authors (Supplementary information). For quality control, we removed anomalous locations with speeds > 80 km h^{-1} for flapping species and locations with speeds > 100 km h^{-1} for soaring species. All speeds were calculated as the speed between points. We calculated UTM zones from coordinates. To evaluate the timing of movement relative to local sunrise and sunset, all timestamps were converted from GMT to local time.

Our dataset included movements from 49 species (Supplementary information). These species represent 14 orders: Accipitriformes, Anseriformes, Bucerotiformes, Charadriiformes, Ciconiiformes, Falconiformes, Gruiformes, Otidiformes, Passeriformes, Pelecaniformes, Phaethontiformes, Phoenicopteriformes, Procellariiformes and Suliformes. Most (n = 46) species were non-Passeriformes, and all Passeriformes were from the genus *Corvus*.

We analyzed movement data at the daily scale. Most of the data were sampled at hourly time intervals, so we subsampled high resolution data to an hourly scale with location intervals ≥ 57 min (mean time between locations: 79.5 ± 31.1 min). To accurately assess active and inactive states while maximizing number of sampling days, we excluded sampling intervals ≥ 180 min. We did not interpolate missing points.

Days included in the analysis had a minimum of eight locations. We selected 8-h minimum time periods to represent the daily scale because many telemetry units do not sample continuously and, instead, cycle on and off to save battery life. To avoid any potential bias in movements due to handling during tagging, we excluded the first day of tracking for all studies. We included species with at least 20 days of data. Full sampling information is provided in Supplementary information.

Due to known intra-specific differences that occur in association with migration (Cagnacci et al. 2016), our analyses explore non-migratory daily foraging movements. To compare local foraging movements of birds, we standardized the data to include only non-migratory movements by excluding migrations from individuals with range shifts > 500 km.

Table 1. Temporal variables and their definitions.

Variable	Definition
Sunrise activity	The time difference between first activity and sunrise
Sunset activity	The time difference between last activity and sunset
Relative speed at midday	Speed at solar noon relative to mean speed
Number of movement bouts	Number of groups with 1+ consecutive, active hours
Activity duration	The length of time between non-active locations
Proportion of daytime activity	Number of daytime active locations/total number of daytime locations

We intentionally selected a high threshold to avoid removing exploratory and foraging movements by individuals that did not migrate in partially migratory populations.

Movement characteristics

Measurement errors due to error in calculations of latitude and longitude by global positioning system (GPS) are inherent in movement tracking studies (Frair et al. 2010) and can inflate estimates of movement activity. After comparing the distributions of location errors across species, we characterized locations as either 'active' or 'inactive' according to their mean speed. Species with a mean speed < 9 km h^{-1} had an activity threshold of 50 m h^{-1}. This threshold was conservative relative to the distributions of mean location errors across most of the species (Supplementary information). Species with a mean speed > 9 km h^{-1} had an activity threshold of 300 m h^{-1}.

These different thresholds allowed us to identify active versus inactive periods for terrestrial and pelagic birds, which forage at different spatial scales (Schoener 1968, Oppel et al. 2018). To confirm our results were not sensitive to spatial scale, we compared our results using a smaller threshold (25 m h^{-1}) and found no difference in the change in activity levels. To determine if the sampling frequency affected the activity patterns of any groups of species, we compared our results to a 20 min sampling scheme. The differences between these two sampling schemes were linear; our results are therefore robust to temporal sampling (Supplementary information).

Based on these daily, active hours, we summarized temporal characteristics of daily movements using six variables, defined in Table 1. The objective of these measures was not to reliably estimate species averages for these temporal variables, but to provide standard, relative measures that could allow for multispecies comparisons. We included the timing of activity relative to sunrise and sunset to understand the relationship between activity and light availability, while accounting for variation in latitudes and time of year across datasets. Several sampling regimes were set to collect data between sunrise and sunset, which limit our interpretations. However, these intervals were selected by experts on the focal species' biology, so we do not expect that the true mean start and end times of activity would differ strongly from our results. We list species with limited sampling periods (i.e. mean start or end of sampling time were within the hour of local sunrise and sunset), as well as the distributions of the timing of movement activity for each species, in the Supplementary information.

To determine if movements were clustered in time or dispersed throughout the day, we defined number of movement bouts as the number of groups of consecutive active hours. We used the duration of these movement bouts to represent activity duration. To determine how active species are at midday, for each day we calculated relative speed, which is the speed at solar noon divided by their speed averaged across all active bouts. Last, to compare activity among species, we calculated the proportion of time birds were active during the day, which was the proportion of hours between sunrise and sunset where the individual exceeded the speed threshold. We calculated this metric using the number of daylight hours, rather than the full 24-h, because species with limited sampling periods would have artificially high activity levels. We first calculated each temporal variable at the daily scale and then found the mean of each temporal variable at the species level (Supplementary information).

Morphological and ecological characteristics

Ecological characteristic data were taken from the Elton 1.0 database (Wilman et al. 2016), which broadly describes the feeding ecology of all extant bird species in terms of the percent contribution of diet items and of different foraging habitats. We combined variables that were redundant for the species in our dataset; Table 2 lists the variables used and how they were derived.

Foraging habitats were collapsed to five levels: above ground, ground, freshwater, pelagic surface and pelagic diver.

Table 2. Ecological variables used in analysis. Data sourced from Elton database (Wilman et al. 2016). Where variables are combined, sample sizes are indicated in parentheses. Final sample size used in analyses are in column n.

Variable	Category	n	Definition
Foraging habitat	Above ground	7	Midcanopy (6) + canopy (3) + aerial (6)
	Ground	34	Ground (34) + understory (5)
	Water (other)	29	Freshwater or non-obligate pelagic species that forage below (4) + around surface (18)
	Pelagic surface	7	Pelagic specialists that forage around surface
	Pelagic diver	8	Pelagic specialists that forage below surface
Diet	Herbivore	17	Plant (17) + seed (14)
	Frugivore	6	Fruit
	Carnivore	33	Endotherms (18) + ectotherms (14) + unknown (4)
	Piscivore	25	Fish
	Invertivore	32	Invertebrates
	Scavenger	20	Carrion
Flight mode	Pelagic soaring	7	Pelagic birds that soar > 20% of the time
	Obligate soaring	8	Terrestrial birds that cannot sustain flapping flight
	Facultative soaring	14	Terrestrial birds that soar > 20% of the time
	Flapping	20	Birds that flap > 80% of the time

Similarly, several diet variables were collapsed to six levels: herbivore, frugivore, carnivore, piscivore, invertivore and scavenger.

Flight mode was described as either flapping or soaring. Although many species may occasionally be observed soaring, we included only species that soar regularly. We further subdivided soaring into obligate, facultative and pelagic soaring. All other species were categorized as flapping.

We gathered morphometric data for three variables: body mass (kg), wing span (m) and wing area (m^2). Where wing area values were missing, but wing span was known, we calculated wing area using aspect ratio (wing $span^2$/wing area) from a closely related species. Then, using known wingspan and estimated aspect ratio, we were able to derive wing area and relative wing loading (Pennycuick 2008). Wing spans were unknown for two species (*Anas poecilorhyncha* and *Grus nigricollis*), which we excluded from the analyses of morphological characteristics. We controlled for the effect of body size by using relative wing loading (body $mass^{2/3}$/wingarea; Norberg and Norberg 1988). We used only relative wing loading and aspect ratio in our analyses. All species' morphological data and sources, as well as ecological character data, are provided in the Supplementary information.

Analysis

To determine which guilds were most similar in the timing of movement activity, we quantified dissimilarity across the suite of temporal variables (Table 1) using non-metric multidimensional scaling (NMDS). NMDS is a distance-based ordination that maximizes rank order correlation, which is suitable for non-parametric data. Accipitriformes and Anseriformes were over-represented in our dataset, making our dataset phylogenetically uneven.

To correct for this, we bootstrapped our NMDS analysis by randomly subsampling four species (the median size of other orders with multiple individuals) within each order, iterated 100 times. For each iteration, we then tested for any significant diet, foraging, flight and morphological correlates of the NMDS (Table 2). Our final analysis included only variables that were significant predictors for at least 20% of subsampled datasets. This allowed us to exclude any predictors that would have been significant only due to the skewedness of our dataset. As many behaviors and adaptations have coevolved, we also report any highly correlated predictors.

To test our flight mode hypothesis, we used one-way ANOVAs followed by TukeyHSD post hoc tests. We excluded one species that was an outlier with regards to daytime movement activity, Cory's shearwater *Calonectris diomedea*, as our estimates of activity duration exceeded those of known activity budgets (Ramos et al. 2019). To explore the drivers of clustering among foraging habitats in ordinal space, we compared the distributions of active hours among foraging groups. To assess if the differences in activity level are due to physiological limitations of flight speed, we included a post hoc analysis of the mean daily net squared displacement, a measurement of daily foraging distance, according to foraging habitat. Due to insufficient sample size, terrestrial above ground foragers were excluded from this analysis. We report summary statistics as mean and standard deviation. We performed analyses using R ver. 3.6.3 (2020-02-29) (<www.r-project.org>); a list of R packages used can be found in the Supplementary information.

Results

We summarized 64 570 days of movement data for 991 birds. For three species, movement data came from fewer than three individuals (Supplementary information). Wing spans ranged from 0.71 to 2.81 m and body mass ranged from 0.44 to 9.87 kg, a range that includes the body masses of 28% of all volant non-Passeriformes.

We found several continuous covariates related to the clustering of species according to the suite of temporal variables. Variation along NMDS1 was largely attributed to terrestrial ground foragers and pelagic surface foragers (Fig. 1a). Terrestrial ground foragers were largely comprised of Accipitriformes and were therefore correlated with obligate and facultative soaring birds, scavenging ($r = 0.63$) and carnivorous diets ($r = 0.71$). Pelagic surface foragers were comprised of Procellariiformes and some Suliformes (i.e. Frigatebirds), which were positively correlated with high aspect ratio wings ($r = 0.76$), pelagic soaring and invertivores. However, there was no separation between terrestrial and pelagic foragers in ordinal space. The greatest separation between foraging groups was between pelagic diving and pelagic surface foragers (Fig. 1b). Variation along NMDS2 was largely attributed to flapping versus soaring flight (Fig. 1c). In our dataset, body size was related to flight mode (soaring 3.65 ± 2.76 kg, flapping 1.20 ± 0.60 kg).

Soaring birds had higher relative speeds than flapping birds at midday (soaring: $0.901 \pm 0.232\ ms^{-1}$; flapping: $0.568 \pm 0.211\ ms^{-1}$; $F = 26.28$, $df = 1$, $p < 0.001$). Obligate soaring birds began activity later than flapping birds (obligate soaring: 3.250 ± 1.035 h; flapping: 0.750 ± 1.943 h; $F = 14.542$, $df = 3$, $p < 0.001$; TukeyHSD $p = 0.017$; Fig. 2a). Similarly, obligate soaring birds stopped activity earlier than did flapping birds (obligate soaring: −1.286 ± 0.881 h; flapping: 0.850 ± 1.755 h; $F = 6.777$, $df = 3$, $p < 0.001$; TukeyHSD $p = 0.018$; Fig. 2b). The same pattern was observed for pelagic soaring birds. Obligate soaring birds began activity later than pelagic soaring birds (pelagic soaring: −3.143 ± 3.532 h; TukeyHSD $p < 0.001$; Fig. 2a) and obligate soaring birds stopped activity earlier than pelagic soaring birds (pelagic soaring: 2.429 ± 2.37 h; TukeyHSD $p < 0.001$; Fig. 2b). Post hoc tests did not reveal significant differences in the start or end times between obligate and facultative soaring birds (sunrise $p = 0.159$, sunset $p = 0.224$), but obligate soaring birds were active for a shorter range of hours in the day (Fig. 2).

Activity distributions differed by foraging habitats (Fig. 3a). Pelagic surface foragers were active most continuously throughout the day and terrestrial ground foragers had

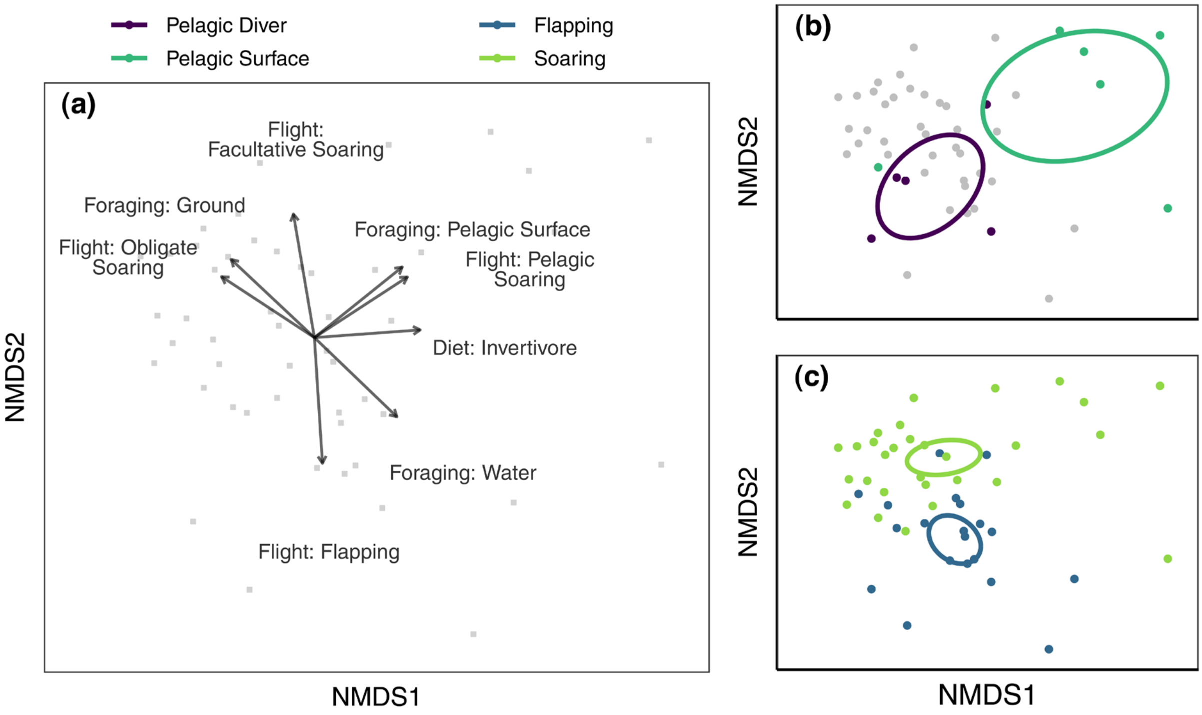

Figure 1. The NMDS ordination indicates inter-specific similarities within temporal activity patterns, among all 49 species. (a) NMDS annotated with environmental fit loadings (included if significant at p-value < 0.05). Environmental fit loadings were bootstrapped to correct for an uneven sample across phylogeny. Ground foragers were correlated with carnivorous diets (r = 0.71) and scavenging diets (r = 0.63) and both were omitted from the environmental loadings for clarity. Pelagic surface foragers were correlated with high aspect ratio wings (r = 0.76), which was removed for clarity. NMDS annotated by (b) pelagic foraging habitats and (c) flight mode. Ellipses represent 90% confidence interval around the centroid of each group. (b) There is little overlap between the pelagic foraging groups, indicating that pelagic divers (purple) have different activity patterns than pelagic surface foragers (green). Terrestrial foragers (grey) had high overlap with pelagic foragers, indicating little differences between terrestrial and pelagic foragers, overall. (c) There is little overlap between flight modes, indicating that soaring species (light green) have different activity patterns than flapping species (blue). Stress value is 0.15.

the narrowest range of active hours. Differences in the activity patterns of pelagic surface foragers and diving foragers corresponded to differences in daily foraging distances (Fig. 3c). Daily maximum net squared displacement was greatest among pelagic surface foragers, indicating they travelled the furthest within a day of any foraging group (F = 3.373, df = 3, p = 0.027). These differences were not due to differences in mean flight speed (Fig. 3b). Pelagic foragers had greater mean flight speeds than terrestrial foragers, but this was partially an artifact of our methods requiring different activity thresholds.

Discussion

In this study we have combined a rich GPS tracking data set, spanning over several species and guilds, and used a multi-species comparative approach to test for intrinsic factors that shape the timing of activity by birds. We found broad-scale differences in the timing of avian daily movement activity between flight modes, supporting our hypothesis. Movements of Accipitriformes, which represent the largest proportion of soaring birds in our broad dataset, were largely restricted to daytime hours. This effect was even stronger among obligate soaring birds (i.e. Old World and New World vultures). Soaring species were further differentiated from flapping species by higher relative speeds at midday. These findings were not surprising as updrafts are stronger around midday than in the morning or late afternoon, supporting previous research suggesting their activity is more strongly linked to the temporal availability of updrafts (Mandel and Bildstein 2007, Bildstein et al. 2009, Nathan et al. 2012, Sur et al. 2017) than to their spatial availability (Mallon et al. 2015).

Flapping species were characterized by a lower percent of activity during the day. This suggests either flapping species are less active than soaring species, or they are similarly active, but on different spatial scales. Flapping species were largely represented by Anseriformes (i.e. ducks and geese) and Pelecaniformes (i.e. herons), which forage locally (e.g. < 1 km) by walking, stalking, dabbling or grazing. These species generally feed on abundant or localized resources (i.e. herbivores and granivores), and therefore spend greater amounts of time foraging within a given area (Mueller and Fagan 2008).

Other species either face less temporal predictability of resources or have greater spatial heterogeneity of resources and are more mobile as a consequence (Mueller and Fagan 2008). This is true of soaring species, many of which use a fly-and-forage strategy where birds spend substantial time in flight searching for food over large spatial scales (e.g. 10s

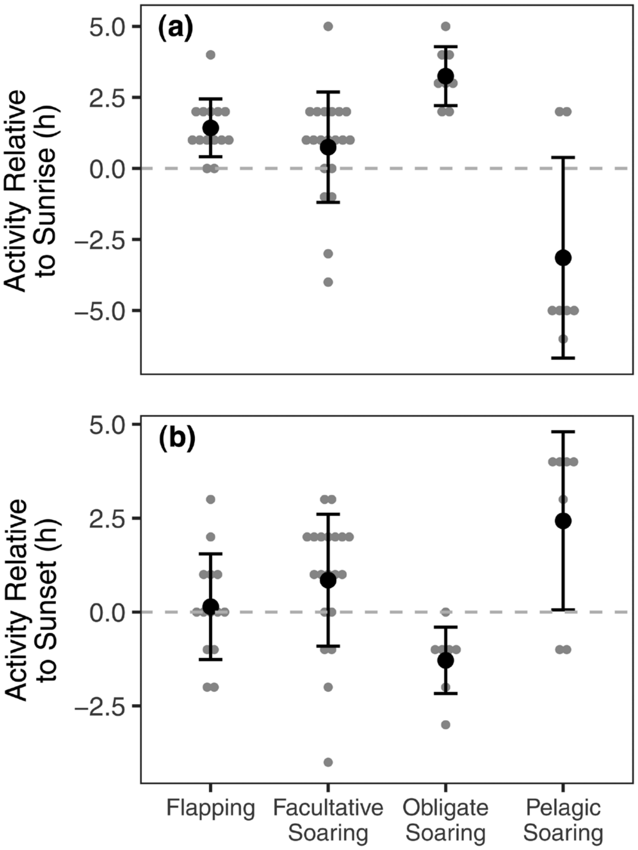

Figure 2. Dot plots of flapping, terrestrial soaring (obligate and facultative) and pelagic soaring birds by (a) start of activity relative to sunrise and (b) end of activity relative to sunset, with units in hours. (a) Terrestrial soaring birds began activity after sunrise, with obligate soaring birds beginning activity later than facultative soaring birds. (b) Terrestrial soaring birds ceased activity before or at sunset, with obligate soaring birds stopping activity earlier than facultative soaring birds. Sunrise and sunset times were similar for facultative soaring and flapping birds.

of km; Ruxton and Houston 2004). This is consistent with other findings concerning foraging space use: large-bodied birds, which tend to feed on high-quality resources and forage over large spatial scales (Schoener 1968), travel farther in homogeneous environments than heterogeneous environments (Tucker et al. 2019). Among mammals, trophic level is correlated with home range size (Jetz et al. 2004), which is positively correlated with activity levels (Cid et al. 2020), suggesting a positive relationship between space use and activity levels over large scales.

Like our results for terrestrial species, the temporal patterns we observed of pelagic species are a consequence of the spatial scale they forage over. While flight mode is related to the same morphological adaptations that allow pelagic species to specialize as surface or diving foragers (Ashmole 1971), we argue instead that the differences in timing among pelagic birds are not due to flight mode but to foraging behavior. In our dataset, pelagic surface foragers were comprised of Suliformes (i.e. boobies and frigatebirds) and Procellariiformes (i.e. albatrosses and shearwaters), which forage over different spatial scales (Oppel et al. 2018). Although in some colonies, Suliformes respond to intraspecific competition by traveling further from the colony to forage (Oppel et al. 2015), Suliformes in our dataset forage closer to their colonies relative to the Procellariiformes, which frequently forage in open ocean. This difference in space use also likely drives the observed differences in the temporal patterns of their movement activity. To travel further, but at similar flight speeds, Procellariiformes have longer foraging trips that often extend overnight. This resulted in Suliformes appearing to be relatively less active, as their foraging trips in our dataset were always < 24 h. The predominantly diurnal activities of Suliformes contributed greatly to the overlap in temporal activity patterns between pelagic and terrestrial foragers. There was better contrast among pelagic birds when comparing foraging groups, as frigatebirds are not diving foragers like other Suliformes, but are surface foragers that behave more like Procellariiformes. Frigatebirds in our dataset did move at night but are diurnal foragers that sleep on the wing (Rattenborg et al. 2016). This, in part, explains why the differences in start times between pelagic surface and diving foragers were more distinct than between Procellariiformes and Suliformes alone.

At least for some species, the relative significance of flight mode and foraging habitat may not be clear cut. The timing of their movements may not be driven by food availability, but instead by foraging restrictions. For example, in arid climates, some birds reduce their activity during midday as a means of behavioral thermoregulation (Silva et al. 2015, Gudka et al. 2019). Likewise, visually orienting species are limited by the availability of light. As such, although fruits and seeds are available at all hours, Passerines begin activity at dawn when there is sufficient light to detect their food resources (Roth and Lima 2007). Temporal segregation of foraging can also be driven by pressures to avoid predators or kleptoparasites (Baglione and Canestrari 2009), such as frigatebirds. Such adaptive behavior is thought to have contributed to the evolution of nocturnal foraging behavior by some pelagic species (Hailman 1964).

Interpretation of our results is influenced by the fact that we compiled our dataset from several different studies, which were biased towards larger, data-rich species that can support the weight of telemetry units. Also, sampling schemes across studies were uneven in terms of inter-location frequency and effort; this required us to use data averaged at the species level. If our data could be resolved on the scales specific to each guild, rather than standardized across species, we might have identified other ecological variables, such as diet, as important drivers of movement activity. Nevertheless, our approach provided standardized activity metrics for 49 bird species, which allowed us to compare intrinsic drivers of movement activity across a diversity of avian guilds.

Although our analyses were restricted to temporal attributes of movement, the relationship between physiological limitations on flight speed and activity duration lead us to hypothesize that the spatial scales animals forage over is an

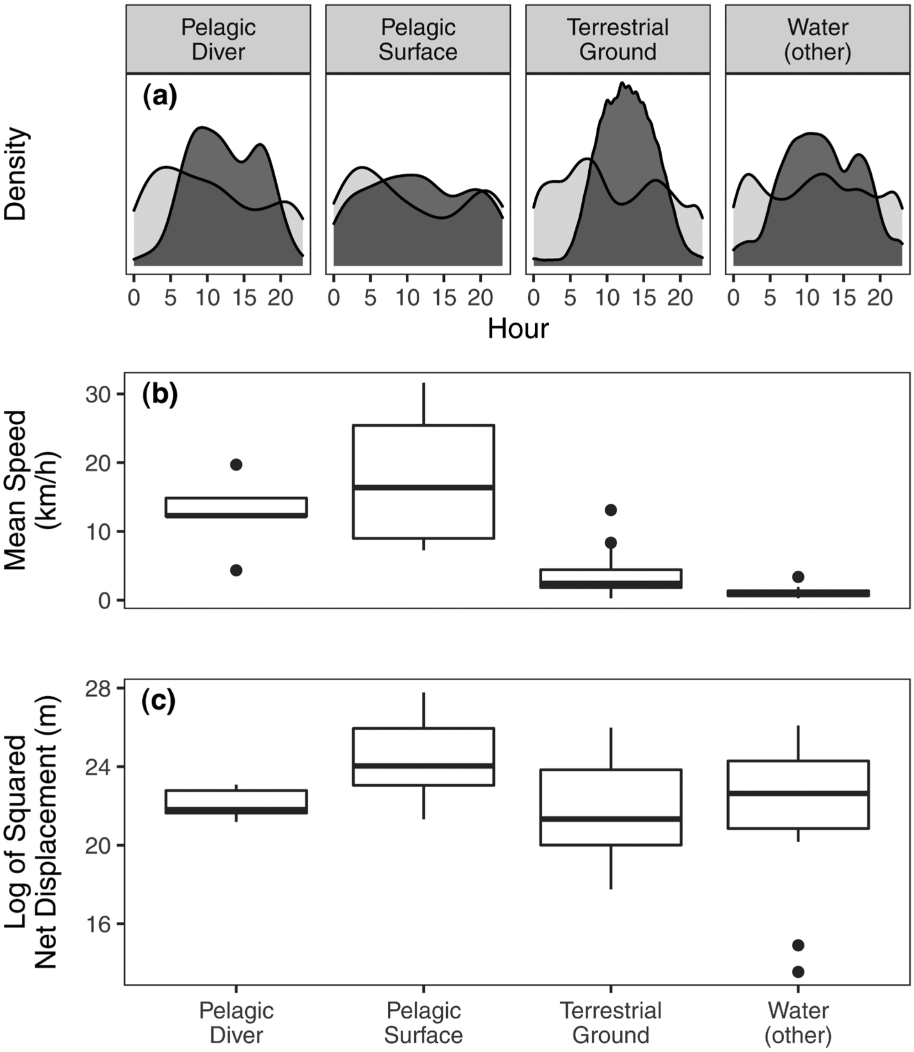

Figure 3. Foraging habitats by (a) active time, (b) mean speed and (c) distance. For all plots, terrestrial above ground foragers were excluded due to small sample size (n = 2). (a) Distributions of active (black) and inactive (grey) hours by foraging habitat. Pelagic surface foragers were active a greater proportion of the day than pelagic diving and terrestrial foragers, whose activity was more clustered during midday. (b) Mean speed between points. There is no difference in maximum speeds among pelagic foraging habitats. (c) Post hoc analyses of log-transformed squared net displacement (in meters) of daily foraging trips according to foraging habitat. Pelagic surface foragers travel farther than pelagic divers on daily foraging trips, suggesting differences in their activity levels is driven by their respective foraging distances.

important driver of the timing of movement activity. Our results show that animals have predictable, intrinsic patterns to the timing of local movements that make up the large-scale behaviors we are interested in studying. Recognizing that spatial scale indirectly influences the timing of movement activity, future studies that focus on the spatial attributes of animal movement should consider the temporal attributes of movement as well. For example, studying spatial and temporal patterns in concert may reveal intraspecific differences due to personality influences on movement behavior (Spiegel et al. 2017, Hertel et al. 2019). With the development of smaller, high-resolution tracking devices, future research may apply analyses such as ours to the full diversity of birds, filling gaps of our knowledge on granivorous, frugivorous and insectivorous species (e.g. passerines, shorebirds, swifts, etc.), which may reveal interesting new phylogenetic or allometric predictors of movement.

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Data availability statement

R code used in analyses can be accessed at datadryad.com (<http://dx.doi.org/10.5061/dryad.0p2ngf1zz). Most of the data used are publicly available at <www.movebank.org>.

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