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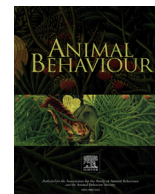
Diel patterns of movement reveal temporal strategies during dispersal

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ARTICLE INFO

Movement is a key part of life for many animals. However, a number of temporal constraints, from changes in light and temperature to varying risks of predation, limit not only where animals can move, but also when. Such constraints are likely to be most pronounced when animals must make large displacements, as is the case when individuals disperse. However, little is known about how dispersers overcome temporal constraints on movement, despite significant implications for the success of dispersal. We outline a general framework for identifying the strategies animals use to achieve large displacements in the face of constraints on when and how to move, which we predict should follow one of three patterns: increasing their movements during those times when they typically move more, uniformly across the day, or when they previously moved least. Using high-resolution GPS tracking of dispersing and resident vulturine guineafowl, *Acryllium vulturinum*, we show that dispersers expressed the greatest increases in movement at the same times of day that they moved most prior to dispersing. Our results suggest that individuals face the same ecological constraints during dispersal as they do in daily life and achieve large displacements by maximizing movement when conditions are most favourable.

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Dispersal is a fundamental part of many species' life histories. Comprising three main phases, departure, transience and settlement (Bowler & Benton, 2005), dispersal is typically the result of individuals needing to escape unfavourable conditions in their natal environment, such as inbreeding (Gandon, 1999; Matthysen, 2013) or kin competition (Cote & Clobert, 2010; Hamilton & May, 1977), or to secure access to new reproductive opportunities (Alberts & Altmann, 1995). To effectively reap these benefits, individuals often move over great distances (Delgado et al., 2009; Elliot et al., 2014; Killeen et al., 2014; Klarevas-Irby et al., 2021; Woollard & Harris, 1990). This increase in movement can result in increased costs or constraints, such as greater energy expenditure (Bonte et al., 2012; Maag et al., 2019). These can, in turn, drive the evolution of dispersal strategies to mitigate or overcome some of these costs or constraints (Cozzi et al., 2018; Klarevas-Irby et al., 2021). For example, delaying departure can reduce the risk of mortality until breeding territories become available (Tarwater & Brawn, 2010), and transient animals can change their movement behaviours in ways that reduce the energetic costs of movement over large distances (Klarevas-Irby et al., 2021). Moving larger distances also involves overcoming constraints on the timing of movement. However, while numerous studies have looked at where animals go during transience (e.g. how to effectively search for new habitats; Zollner & Lima, 1999) or how they move (e.g. how movement speed or straightness influences risk avoidance or energy use; Klarevas-Irby et al., 2021; Zollner & Lima, 2005), much less is known about whether dispersers face ecological constraints on when during the day they can move, and what strategies they employ to overcome these constraints. Understanding diel patterns of movements during dispersal has the potential to generate new insights into the persistence of ecological constraints that limit when animals can move, and how these shape movement during this key stage of life.

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Animals face temporal constraints on movement at multiple scales. On the one hand, large-scale factors, such as weather conditions, can impact what days are suitable for moving versus not. For example, soaring birds are more likely to initiate dispersal movements on days with strong, directional wind support (Walls et al., 2005). At much finer scales, animals also face changing conditions over the course of each single day, for example because predators are more or less active at certain times of day (Lang et al., 2019; Mugerwa et al., 2017; Veldhuis et al., 2020), because of higher temperatures during the middle hours of the day (Carroll et al., 2015; Rocha et al., 2022), or because they face trade-offs between information and starvation as the night approaches (Farine & Lang, 2013). These diel-level constraints often produce distinct patterns of activity by animals over the course of the day, for example with greater activity early in the morning and late at night (Rocha et al., 2022). Such patterns have also been observed with movement behaviours, with peaks and valleys in movement in the morning, midday and/or evening (Owen-Smith & Goodall, 2014). In extreme cases, when making large displacements, diel-level constraints on individuals can drive strategies that involve moving in periods when individuals would otherwise move very little, such as in species that migrate at night to take advantage of cooler temperatures (Kerlinger & Moore, 1989) and to maximize refuelling efficiency during the day (Alerstam, 2009). A question is, therefore, whether dispersers face similar constraints on when they can move and how they overcome these during transience, or whether they time their dispersal movements to coincide with periods in which those constraints are relaxed allowing them to move for more of the day.

In many species, dispersal movements are linked to changes in seasonal conditions which are thought to reflect periods of reduced constraints on movement (Shaw, 2020; Studds et al., 2008). For example, warmer temperatures (Haughland & Larsen, 2004), stronger winds (Walls et al., 2005) and more abundant food sources (Kojola et al., 2006) have all been linked to increased departure rates and dispersal distances. Individuals can also time their dispersal departures with periods where spatial barriers are removed, such as when otherwise disconnected waterbodies become connected by seasonal flooding (Smith et al., 2019). However, many constraints can continue to persist across life history stages, even in seasonally dispersing species. For example, a recent study of brown bears, *Ursus arctos*, found both adults and subadult males express movement peaks in net displacement at similar times of day, despite the latter moving more (Bogdanović et al., 2021). Thus, dispersing animals could face persistent constraints on the diel timing of movements (e.g. hotter midday temperatures, greater predation risk during the middle of the day), even if larger-scale constraints on movement (e.g. spatial barriers, food resources) are relaxed. In such cases, it is unclear what strategies they employ to overcome these constraints in order to achieve the large displacements they express during transience.

Quantifying the contribution of environmental constraints in shaping the dispersal movements of animals is challenging, as movement can be affected by many factors (or combinations of factors) and it is typically difficult to measure how individuals experience these. One approach is to compare the diel patterns of movement by dispersing individuals to their movement patterns prior to dispersal and/or to the movements of nondispersing individuals at the same time. Broadly, we can predict that increases in movement during transience should manifest following one of three patterns (Fig. 1), with each providing insights into the temporal constraints (or changes in constraints) faced by dispersers. In
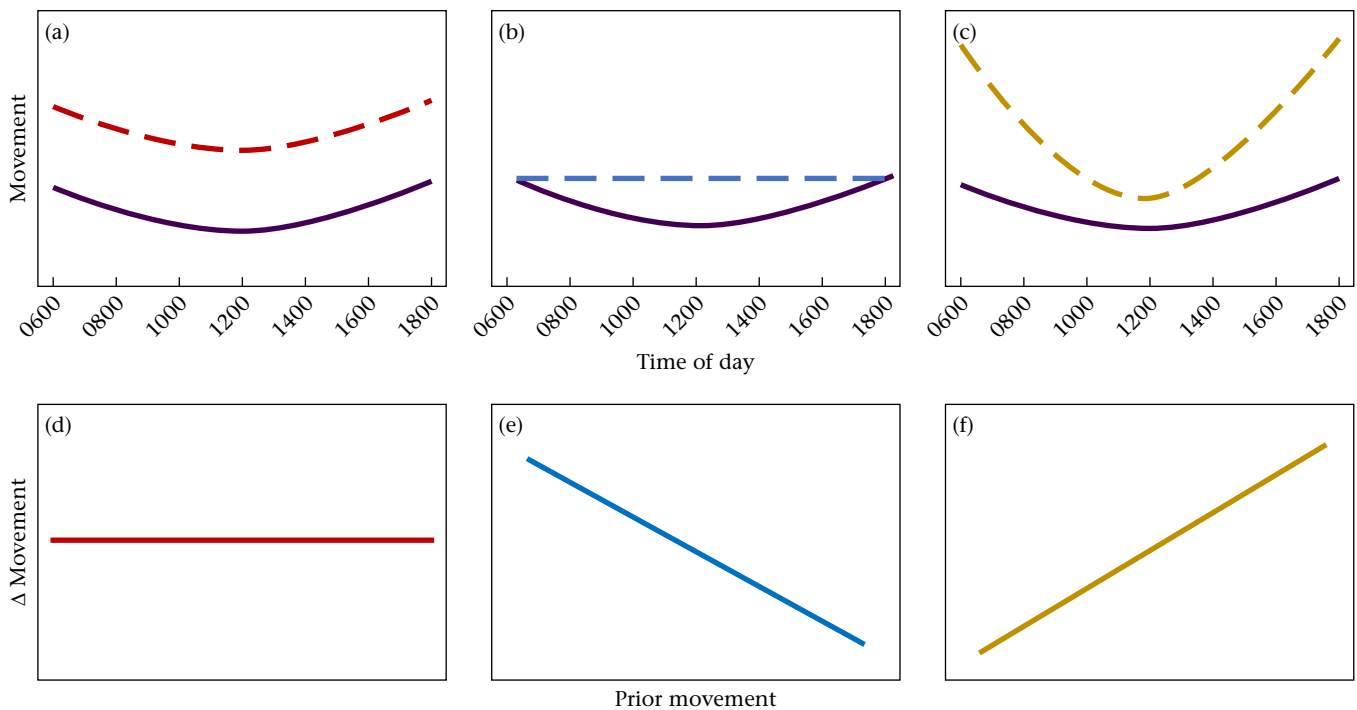
Figure 1. Three predicted patterns of change in diel movements during dispersal. In general, transience (a–c, dashed lines) should be characterized by an increase in individuals' movements, such as an increase in the distances displaced, relative to their nondispersal movements (a–c, solid line). These increases can follow one of three general patterns, each generating a distinct predicted correlation between the change in movement at a given time of day and the corresponding amount of movement at the same times prior to dispersing. (a) A uniform increase in the level of movement at all times of day results in (d) no correlation between the level of prior movement and the change in movement. (b) Increasing movement at those times when the baseline levels of movement were previously lower (for example if previous high movement corresponded to a physiological maximum) results in (e) a negative correlation between prior movement and change in movement during transience. (c) An increase in movement at times when dispersers were previously moving the most (e.g. because these periods have the least constraints) results in (f) a positive correlation between the baseline movement and the change in movement that is expressed.

the first pattern, dispersers could increase their movements in a uniform fashion throughout the day (Fig. 1a). This strategy would represent a general increase in movement irrespective of any constraints faced by individuals. Such a pattern would produce no correlation between the change in movement and the individuals' baseline levels (Fig. 1d). In the second pattern, dispersers could exhibit an increase at times that previously corresponded with less movement (Fig. 1b). This scenario might arise if, for example, the animals' prior maximum levels are indicative of some physiological ceiling, or if they choose to disperse when conditions (e.g. seasons or weather conditions) free them from prior constraints on when during the day they can move. In extreme cases, this could even result in a complete inversion of the diel timings of movement, such as in migrating birds which make large flights at night (Kranstauber et al., 2023). Such a scenario would produce a negative correlation between the change in movements and the individuals' baseline levels (Fig. 1e). Finally, in the third pattern, dispersers could exhibit an increase in movement at times corresponding to previous high levels of movement (Fig. 1c). Such a pattern could indicate the persistence of environmental constraints on movement during transience. For example, if temperature constrains movement during the middle of the day, dispersers should disproportionately increase their movements during periods of the day when movement is already least restricted (e.g. at the coolest times of day). Such a pattern would result in a positive correlation between the change in movement and their baseline levels (Fig. 1f). This simple test, correlating nondispersal diel patterns of movement with those made during transience, requires no data on ecological conditions either before or during dispersal. While simple and relatively crude, it can be applied post hoc to any movement data set, and thereby provide broad insights on dispersal strategies.

In this study, we used simultaneous high-resolution (1 Hz) GPS tracking data from resident and actively dispersing vulturine guineafowl, *Acryllium vulturinum*, to determine whether the timing of dispersal corresponds to a reduction in the constraints on movement. We started by first demonstrating that nondispersing birds varied in terms of the times of day when they moved most. We then tested for, and quantified the timing of, increased movements made by birds during transience For this study, we used a two-step comparative approach, first comparing transient individuals to their own predispersal movements and then comparing them to residents from their natal groups on the same days (as a further test for changing environmental conditions). Our analyses confirm that dispersing vulturine guineafowl continue facing persistent diel constraints during transience, and therefore that the timing of when they disperse is unlikely to coincide with temporal relaxation of ecological constraints on when in the day they can move.

METHODS

Study System

We conducted our study in a population of vulturine guineafowl, which are a terrestrial gallinaceous bird species, located at the Mpala Research Centre in Laikipia, Kenya (0.29120 N, 36.898670 E). Vulturine guineafowl live in large stable groups comprising 13–65 individuals; groups contain multiple family units and interact regularly with other groups (Papageorgiou et al., 2019). While vulturine guineafowl can fly, their flight is limited to very short (tens of metres) displacements (e.g. crossing rivers, flying to the top of a roosting tree or escaping from a predator); large displacements are almost exclusively made terrestrially. Birds in our study population are captured as whole groups using baited walk-in traps, and

each individual is marked with an individually numbered stainless-steel ring plus a unique combination of four plastic colour bands. Selected individuals in each group are also fitted with a 15 g Bird Solar GPS tag (e-obs GmbH, Grünwald, Germany). Tags were fitted using a 'backpack-style' harness, using a neoprene pad to elevate tags above body feathers, 6.5 mm Teflon tubing which looped around each wing, and a break-away connection point at the keel made from a 25 mm length of 6.5 mm heat-shrink tubing. Full details of the strategy by which tags were distributed across our study population can be found in He et al. (2022). For this study, we used data from 35 individuals, comprising 21 subadult females fitted with GPS tags prior to dispersing and 14 adult (non-dispersing) members of the four natal groups from which GPS-tracked subadults dispersed (five females, nine males; one to five residents per group). While our study involved comparisons with resident males, we note that groups of vulturine guineafowl are highly cohesive, meaning that all residents of a given group make largely the same movements. Data were recorded predominantly from two dispersal seasons in 2019 but include a further two dispersal events from 2020 to 2021 (Table A1).

Ethical Note

All work was conducted under research permits from the Max Planck Society Ethikrat Committee (2016_13/1), the National Commission for Science, Technology and Innovation of Kenya (NACOSTI/P/16/3706/6465), the National Environment Management Authority (NEMA/AGR/68/2017), under a Research Authorization (KWS-0016-01-21) and a Capture Permit issued by the Kenyan Wildlife Service, and in affiliation with the National Museums of Kenya. Capture and handling of birds were performed by trained personnel, following methods approved by the Kenyan Wildlife Service. The total weight of backpacks and tags combined is approximately 20.5 g, well below 3% of birds' body weight (Kenward, 2000). Birds were released in groups of four to eight at a time (including tagged and untagged individuals) to avoid isolation and increased risks of postcapture exposure to predators. Follow-up observations confirmed that tagging had no adverse impact on birds' ability to forage, move or maintain cohesion with their social group. Tagged individuals typically carried their tags for 18 months before either being recaptured for tag removal or tags falling off due to degradation of the break-away material.

GPS Data

Each device was programmed to record data during daylight hours, from 0600 to 1900. Data points (date, time and location) were recorded continuously at 1 Hz (i.e. 1 fix/s) when the tag's battery had a high charge (every 2–3 days, for up to 4.5 h continuously). When the battery was below the high-resolution charge threshold, we set tags to record 10 GPS points in the first 10 s of every fifth minute. If battery charge was at the lowest threshold, tags were set to record one point every 15 min (this threshold was not crossed during this study). Data were remotely downloaded every 2 days using a BaseStation II (e-obs Digital Telemetry, Grünwald, Germany). For our analyses, we separated the data into two resolutions: high-resolution data, comprising all continuous periods of 1 Hz data; and 5 min data, comprising data from the 10th second of every fifth minute of the day. The latter were collected from both the low-resolution data set and by subsampling the 1 Hz data, thereby reliably providing data every 5 min for every bird on every day it was tracked. GPS data were uploaded to Movebank (https://www.movebank.org/) and retrieved and prepared for analysis in R using the move package (Kranstauber et al., 2023).

Dispersal

We divided each dispersing bird's data set into two phases: predispersal (7 days when dispersers were still moving with their natal group) and transience (mean of 19.5 days when birds were actively dispersing; Table A1). Birds were considered to have started transience on the first date when we observed them moving separately from their natal group, based on field observations and confirmed via visual observation of the GPS tracks of dispersers and residents. Birds were considered settled, i.e. to no longer be transient, from the first day in which they spent the entire day within their eventual postsettlement group (based on field observations over the following months). Three birds failed to successfully find a new group, and transience was considered to finish on the day that they returned to their natal group. Two such individuals attempted to disperse again in a subsequent season, and two individuals that had previously settled into new groups dispersed a second time in the following season, resulting in a total of 25 recorded dispersal events. For eight of these 25 events, we were unable to record settlement, owing to either predation during transience (one individual), early failure of the GPS backpack failure point causing the tag to fall off during transience (one individual which was later visually confirmed to have survived based on colour bands) or the dispersing bird moving sufficiently far from our study area that we were not able to relocate the tag for download (six individuals). However, in each of these cases the GPS data that we collected finished during transience, and thus we used these data as such.

While transience generally involves the process of relocating in space, in many social species it also involves periods in which individuals attempt to join new social groups (Armansin et al., 2020). In vulturine guineafowl, this is expressed as two distinct types of days: those in which the birds make large roost-to-roost displacements (from our field observations, this generally involved moving alone) and those in which birds moved together with, and attempted to join, new social groups (resulting in short or no roost-to-roost displacements). Birds often failed to integrate into groups, or opted to keep searching, by resuming making large movements after several (range 1–27; Fig. A1) days of local movements. To study constraints on large-scale movements, we divided the data from transient birds into two daily categories based on the types of movements exhibited on a given day: 'big days', during which transient birds made large displacements that are typical of active dispersal, and days of 'local movements', during which transient birds exhibited highly tortuous paths and typically did not change roost locations from morning to evening. Thus, big days of movement were defined as days in which the roost-to-roost distance was greater than 1500 m, or if the roost distance was greater than 1200 m and the ratio of the distance between roosts and their total daily track length (i.e. a measure of the straightness of their daily path) was greater than 0.3. All big day assignments were confirmed by visual observation of daily paths. As our focus in this study is on increases in movement that resulted in large displacements, and because local movements are shaped by the movement characteristics of unknown groups, we focused our analyses on data from big days.

Data from resident (i.e. nondispersing) birds were taken from GPS-tracked adult members of each dispersing bird's natal group. Data from each resident were recorded for all unique dates on which a dispersing bird from that resident's group was represented (i.e. for all days of predispersal and transience from matched dispersers). Where possible, multiple residents were included for each group. In two instances, dispersers departed from groups with no GPS-tracked adults, and so these dispersal events were excluded from comparisons with residents.

Analyses

All analyses were performed in R version 4.0 (R Core Team, 2022).

Defining movement states

We implemented an unsupervised hidden Markov model (HMM) to delineate the different movement states exhibited by vulturine guineafowl. Because a 1 Hz resolution violates the Markov assumption, we first summed the distance moved and absolute turning angles for every 10 s in the high-resolution data. We searched for four movement states across the entire high-resolution data set, using the R package depmixS4 (Visser & Speekenbrink, 2010). We selected a four-state model based on field observations that individuals spend time not moving (state 1), making slow, tortuous foraging movements (state 2), walking at a medium speed (state 3), and moving quickly in a directed manner (state 4). We then assigned the state of each 10 s burst to all the 1 Hz data points that contributed to it. When considering how birds budgeted their time, we considered birds to be moving for displacement in states 3 and 4 (as opposed to the small, localized movements associated with foraging, state 2).

Calculating temporal movement measures

We extracted two key measures to characterize birds' movement behaviours throughout the day: total displacement, which was calculated in 15 min intervals, and the proportion of time spent moving, which was calculated for each hour that the birds were active (i.e. all daylight hours 0600 to 1900). Total displacement was calculated as the sum of all step distances from the 5 min data for each 15 min segment of each day. We avoided using 1 Hz data for this measure as this would result in only partial daily tracks. The proportion of overall time spent moving was calculated for each hour of the day, as the number of seconds the animal was in a moving state (states 3 and 4, as assigned by the HMM) divided by the total number of seconds to which any state was assigned. We used only hours with 95% or greater (i.e. 57 min or more) of high-resolution coverage. Measures of proportion of time moving were calculated at hourly scales due the relative scarcity of 1 Hz data in any given 15 min window, unlike the 5 min data that were present for every 15 min window throughout the study period. For both measures, we (post hoc) discarded data from the last hour of daylight (1800–1900) because birds would roost at variable times during this hour, with roosting introducing large periods of nonmovement.

Characterizing baseline diel patterns of movement

We first characterized the baseline level of movement (15 min displacements and hourly proportion of time spent moving) using data from subadults during the 7 days prior to dispersing. To evaluate significant within-day variation in each movement variable, we performed 1000 permutations of the time of day labels for each observation (within individuals and within days) and evaluated whether the observed mean at each time step day fell within the 95% distribution of permuted mean values. This permutation test relates our observed hourly movement values to the expected levels of hourly movement if birds moved randomly with respect to time of day, all the while controlling for any structure of our observed data set. If the mean at a given time was greater than the 97.5% quantile or less than the 2.5% quantile of the permutation distribution, birds were considered to be moving significantly more or less, respectively, at those specific times (15 min periods) of the day.

Testing for an increase in movement during dispersal

We next investigated the extent to which dispersing birds changed their behaviours when transient (Fig. 1a–c). For each 15 min period of the day, we calculated the difference in the movement behaviours of actively dispersing birds relative (1) to their predispersal movements (mean movement for transient birds − mean movement for the same birds during the predeparture period) and (2) to those of resident birds from natal groups during the same time period (mean movement for transient birds − mean movement for nondispersing birds). To determine the times of day in which transient birds expressed significant changes in movement, i.e. increased or decreased relative to nondispersal movements in (1) and (2), we randomly permuted two categorical labels: (1) transient versus predispersal or (2) transient versus resident for each observation. We also restricted permutations to only make biologically meaningful comparisons. Specifically, for (1) we only permuted labels (transient versus predispersal) within individuals, and for (2) we only permuted labels within a given date and within individuals from the same natal groups. We conducted 1000 permutations for each test and compared the differences in the observed data with the distribution of differences in permuted data. We considered the changes in movement to be significant when the observed difference fell outside the 95% distribution of the permuted differences as described above.

*Characterizing the temporal pattern of changes in movement*

After identifying potential changes in movement behaviours exhibited by actively dispersing birds within each time step, we examined the overall correlation between the dispersers' movements and baseline levels (i.e. which pattern is produced from Fig. 1d–f). To calculate the significance of our observed correlations, we bootstrapped our test data set (i.e. the observed data from transience movements) 1000 times. Each bootstrap consisted of randomly resampling the observations (with replacement), recalculating the changes in movement levels at each 15 min period (per the previous section) and recalculating the correlation. We used this approach to quantify uncertainty in our data set while avoiding altering the distributions of the data set. From the distribution of correlation values, we performed a two-tailed test where correlations were considered significantly positive (or negative) if 97.5% of the distribution of bootstrapped correlation values was greater than (or less than) zero.

RESULTS

We collected a total of 1281 bird-days of GPS data (where 1 bird-day is a day of data from a given individual), comprising 25 dispersal events by 21 individuals, and from 14 residents on matched days (i.e. the same dates as the big days made by dispersers, from individuals in the same natal group). Of all bird-days, 172 were recorded from predispersal movements (mean 39.5 per group, range 7–53), 410 from transience (mean 89.5 per group, range 31–138) and 699 were from matched resident birds (mean 174.75 per group, range 38–320). Of the transience data, we recorded a total of 94 unique instances in which dispersers engaged in 'big days' of movement (Fig. A1). In total, our data were divided into 13 947 hourly measures of movement, or over 54 000 15 min measures.

Baseline Diel Patterns of Movement

Guineafowl expressed significant within-day variation in their movement when not dispersing (Fig. 2). Prior to dispersing, subadults (and other members of their groups) moved most in the mornings and evening, with significantly greater travel distances
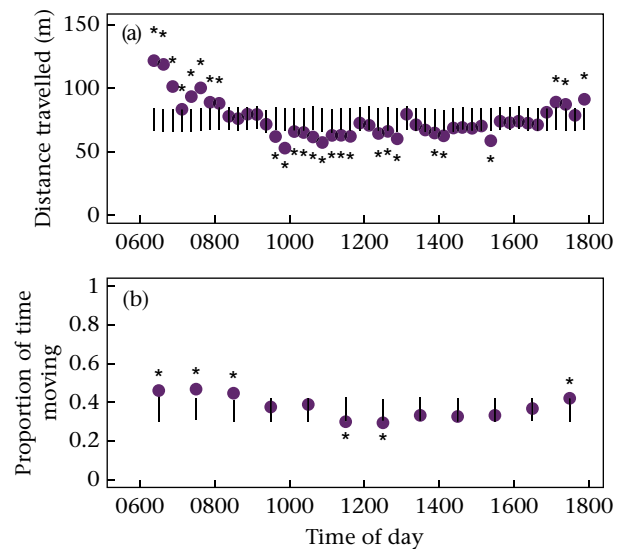

Figure 2. Within-day variation in baseline movements by subadults prior to dispersing. Circles represent the mean of observed values at each time step (e.g. from 0615 to 0630, or from 0600 to 0700) of (a) distance travelled, in 15 min periods, and (b) proportion of each hourly interval spent moving by subadults for each hour of the day during the predispersal period. Vertical lines show 95% range of random permutations in which time step labels were reassigned 1000 times, and stars mark time steps in which the observed movements fall either above or below the 95% range of permuted values. Corresponding data from resident adult members of the same groups (on the same days) are shown in Fig. A2.

during the first 2 h of the day (0615–0815) and for much of the last hour of the day (1700–1730, 1745–1800; Fig. 2a). They also significantly increased the proportion of time they dedicated to movement (i.e. bouts of movements assigned to states 3–4 by an unsupervised four-state HMM) in the morning (0600–0900) and evening (1700–1800), with particularly strong patterns in the morning (Fig. 2b). The increase in movement activity late in the day was borderline significant (over several runs, permutations were sometimes just above and sometimes just below $P = 0.05$). Birds also significantly reduced levels of movement in the middle of the day, including shorter travel distances (0930–1145, 1215–1300, 1345–1415, 1515–1530) and less time spent moving (1100–1300). These results also held true for the movements of resident birds on the same days (Fig. A2), with significantly greater levels of movement in the mornings and evenings, and reduced movements in the middle of the day.

Actively Dispersing Birds Move More Throughout the Day

When making big days of dispersal, individuals expressed an overall increase in both the displacements they achieved and the proportion of time they spent moving. Relative to their own baseline movements (prior to dispersing), dispersers significantly increased their travel distances at nearly every 15 min period, with the exception of six time steps near the middle of the day (1015–1030, 1115–1215 and 1230–1245), where the increase was not significant (Figs. 3a, A3a). There was also a significant increase in the proportion of time that individuals dedicated to movement early in the morning (0700–0800) and from the afternoon to the evening (1400–1800; Figs. 3b, A3b). Relative to the movements of nondispersing residents during the same dates, actively dispersing birds travelled significantly further in the morning (0615–0900), at midday (1145–1215, 1300–1345) and for most of the afternoon and evening (1400–1630, 1645–1800; Figs. A4a, A5a). They also spent a significantly greater proportion of time on the move in the first and
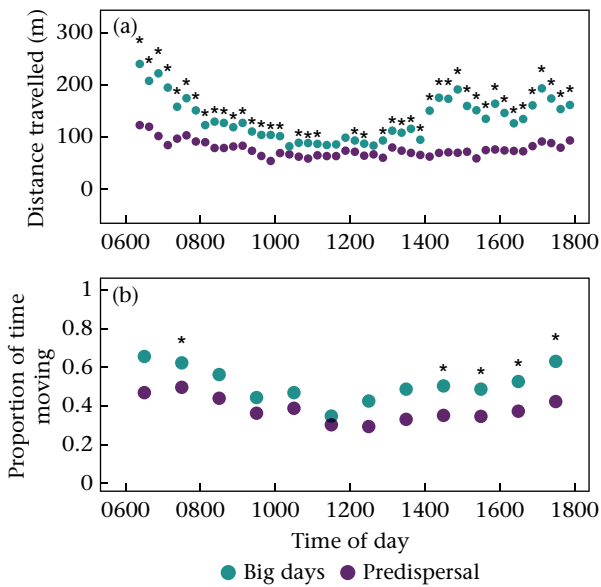
Figure 3. Movements of actively dispersing individuals relative to their predispersal movements. (a) Distances travelled and (b) proportion of time spent moving. Circles show mean values of each movement variable at each time step. 'Big days' are days during which transient birds made large displacements that are typical of active dispersal. Stars mark observed mean differences that fell outside the 95% range of calculated differences from random permutations in which categorical labels (e.g. 'big day' or 'predispersal') were randomized within each time step 1000 times (see Fig. A3 for difference values relative to permutation ranges).

last hour of the day and for 2 h shortly after midday (0600–0700, 1300–1500 and 1700–1800; Figs. A4b, A5b). These increases in movement resulted in an overall increase in the total daily distance travelled by actively dispersing birds: 6.45 km per-big-day, on average, compared to 3.67 km predispersal and 3.64 km by residents.

Changes in Movement are Positively Correlated with Baseline Levels of Movement

We found positive correlations between the diel timing of predispersal movements and the timing of increases in movement during dispersal (Fig. 4). Increases in 15 min travel distances during big days were significantly and positively correlated with predispersal travel distances ($r = 0.454$, $P < 0.001$; Fig. 4a) in the same time period. In terms of the proportion of time spent moving on big days, actively dispersing birds expressed a positive, but not significant, correlation between the increased proportion of time they spent moving on big days compared to predispersal movements from the same time period ($r = 0.289$, $P = 0.22$; Fig. 4b).

DISCUSSION

Our results show that nondispersing vulturine guineafowl move more, and further, during the mornings and evenings, with an even greater increase in movement during these same times when actively dispersing. These results are consistent with a pattern of positively correlated increases in movement (Fig. 1c, f), suggesting that individuals face, and respond to, the same set of general constraints on their movements during dispersal as they do during other stages of life. Our hypotheses and findings are likely to be applicable to other terrestrially dispersing species. We demonstrate this by applying our approach to data from a recent study of dispersal movements in adult and subadult male brown bears (Bogdanović et al., 2021). These data corroborated our results, with

the subadult males increasing movement more during times when nondispersing adult males moved most (see Appendix and Fig. A6). Given similar movements described recently in migrating deer (Jakopak et al., 2022), the patterns we observed in vulturine guineafowl likely apply to other large movements beyond just dispersal. Thus, our study is part of an emerging body of evidence that the timing of large-scale movements is not always linked to a relaxation of ecological constraints that shape when animals can move.

Many studies have focused on the various ecological conditions that lead dispersers to depart from their natal environment (e.g. Pasinelli & Walters, 2002; Studds et al., 2008; Walls et al., 2005). Our results provide some insights into the drivers of the timing of departure. Vulturine guineafowl, as with many species (Gaines & McClenaghan, 1980; Glenn & Miller, 1980; Keppie, 2004; Kojola et al., 2006; Nixon, 1994), appear to tie the timing of their departures to changes in seasonal conditions (here, increased rainfall and the onset of wet seasons; Fig. A1). One prediction is that individuals could match the timing of their departures to periods when ecological conditions are most suitable for movement (Shaw, 2020; Studds et al., 2008), such as if changes in temperature facilitate increased movement activity (Pärn & Sæther, 2013; Walls et al., 2005). In vulturine guineafowl, at least, our results suggest that the timing of dispersal does not appear to correspond to a relaxation in the constraints on movements that dispersers have to contend with, as both residents and dispersers had similarly constrained diel patterns of movement during the time when subadults were actively dispersing. Departures by subadult vulturine guineafowl could instead be tied to social drivers, although our field observations suggest that such drivers may not be as clear as in other species (e.g. social evictions in meerkats, *Suricata suricatta*; Cozzi et al., 2018).

While the maintenance of the diel patterns of movement that we observed could suggest persistence of ecological constraints, they may also capture a possible interplay between where these constraints are expressed most strongly and where dispersers move during transience. We previously (Klarevas-Irby et al., 2021) found that vulturine guineafowl can overcome energetic constraints to movement by moving more efficiently, that is, faster, straighter and more continuously. One way that they could achieve this could be by moving through more open habitats (J. A. Klarevas-Irby, personal observation). However, these habitats also expose dispersers to greater predation risk during the day (e.g. from martial eagles, *Polemaetus bellicosus;* Naude et al., 2019) and higher operative temperatures(van Beest et al., 2012). Thus, while some constraints may be relaxed (e.g. more food or denser cover during rainy seasons), the need for greater efficiency could mean that diel patterns of constrained movement could persist during transience due to spatial factors (i.e. the habitat that they choose to disperse through). Future studies that investigate this spatiodiel pattern in more detail could reveal some important new dimensions across which dispersers face trade-offs during transience.

The presence of persistent ecological constraints on movements can drive the evolution of distinct movement strategies (Alerstam et al., 2003; Chapman et al., 2011). Despite the sizeable increases in travel distances achieved by dispersing birds on big days, these increases in distance were not always accompanied by a corresponding increase in the proportion of time that dispersers spent moving, at least not during the middle of the day. Subadult brown bears also show a disproportionate increase in the distance covered relative to the probability of moving during mating seasons (Bogdanović et al., 2021). This disconnect between the amount of time that individuals spend moving and the large displacements they achieve is likely a product of other changes in behaviour during transience, that is, increased speed and straightness of movement (Benoit et al., 2020; Elliot et al., 2014; Killeen et al., 2014;
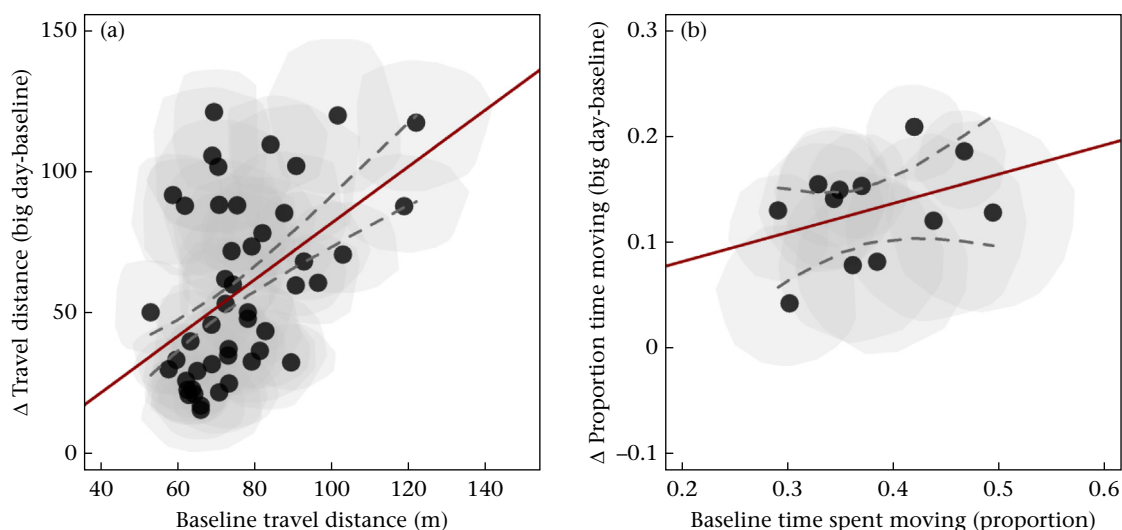
Figure 4. Movement distances during dispersal in relation to baseline (predispersal) movements. (a) Travel distances and (b) the proportion of time spent moving for each time period on big days relative to predispersal levels for the same time period. 'Big days' are days during which transient birds made large displacements that are typical of active dispersal. Polygons show the 75th percentile distributions of the estimated differences in movement, relative to baseline values, for each period (from 1000 bootstraps). Solid lines illustrate the linear relationship between the observed points, with dashed lines illustrating the 95% distribution of these linear relationships estimated using the bootstrapping procedure.

Woollard & Harris, 1990) that result in greater energetic efficiency over large distances (Klarevas-Irby et al., 2021). However, this raises a further question: if individuals have more energy available for movement, then why not spend more time moving? Our results suggest that, at least in part, this is likely to be because the constraints on individuals' movements are acting primarily by limiting the time that they can dedicate to these behaviours, more than the specific mechanics of their movements at these times. However, while transient birds showed relatively constrained patterns in terms of when they moved, they expressed relatively high day-to-day variation in how they moved.

While the primary focus of our analyses was on big days of active movements, these were often interspersed with days of local movements (Fig. A1). This raises the question of whether the energetic costs of dispersal (e.g. trade-offs between moving and foraging; Bonte et al., 2012; Zollner & Lima, 2005) or some ecological constraints might be preventing birds from moving on certain days. In terms of the latter, beyond the larger, seasonal connection between rainfall and the onset of dispersal, there does not seem to be a consistent pattern as to when a given individual will commit to a big day of movement. In terms of the former, while most individuals engaged in only one or two consecutive big days at a time, we also observed some individuals moving for many days at a time, up to 11 consecutive days in one case, suggesting that it is unlikely that energetic costs are the predominant driver of individuals opting to engage in more local movements. Instead, it may be that the big day patterns we observed arise from different selective pressures acting on searching and social evaluation behaviours. For example, as well as decreasing energetic costs, straight-line paths (such as those exhibited on big days) are also thought to be more effective for sampling settleable habitats (Zollner & Lima, 1999). Moving in straight lines, however, prevents individuals from evaluating and trying to join new social groups, as these make shorter and more tortuous movements. Thus, transient individuals appear to be switching between days of displacements (moving to areas with new sets of groups) and days in which they engage in social behaviours (evaluating and/or attempting to join new groups). But, as the process of becoming integrated into a new group is challenging (sensu Armansin et al., 2020), individuals often fail (as noted by a number of birds in our study eventually

reintegrating into their natal group to reattempt dispersal again in a later season), potentially driving them to engage in further cycles of periodic, large displacements.

Overall, our study adds a new dimension to the study of dispersal by predicting different strategies that individuals might use to achieve the large displacements needed to escape their natal environment. Although we did not set out to identify any specific ecological constraints limiting the movements of dispersers, we have none the less identified that these are likely to shape dispersal in the same way that they shape movements during other life history stages. In response to these consistent constraints, vulturine guineafowl achieve larger daily displacements by moving further and for a larger proportion of time during the times of day when they naturally (i.e. outside of dispersal) express greater movements. This strategy, combined with more efficient movement strategies (Klarevas-Irby et al., 2021), allows individuals to achieve much greater daily displacements on big days (on average, a 75.6% increase relative to predispersal movements) while spending relatively little extra time moving on big days (average increase of 34.7%). These types of long displacements and seasonal timing are core components of successful dispersal in many species, even if the specific ecological drivers leading individuals to depart one area or settle in another, or to conduct a big day versus a day of local movements, are different. Given vulturine guineafowl's terrestrial habits, and the common patterns of diel variation in activity among terrestrial animals, our findings may capture a general phenomenon. Whether other terrestrial animals exhibit the same positive correlation (i.e. Fig. 1f) as expressed by dispersing vulturine guineafowl, or whether some species show reversed patterns (e.g. Fig. 1e), warrants further empirical investigation. Regardless of the patterns, future studies testing our predictions will help to build a broader picture of whether the timing of dispersal is linked to relaxations in movement constraints or not.

Author Contributions

J.A.K. and D.R.F. conceived the study, collected the data, performed the analyses and wrote the manuscript; both authors gave final approval for publication.

Data Availability

Declaration of Interest

We declare that neither author is subject to any conflicts of interest.

Acknowledgments

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Appendix

*Diel Movements of Adult and Subadult Brown Bears*

We tested for the correlation between the hourly distances moved by adult and subadult male brown bears during the mating seasons, using data from Bogdanović et al. (2021). This data set included hourly net displacement data from seven male bears, of which two were tracked as subadults, four as adults and one during both life history stages. In total, these data comprised 8919 measurements of travel distances across 206 unique days of tracking. We summarized the hourly mean distance moved within each class of bear ('adult' or 'subadult'), and calculated the differences between these hourly means. To test for a correlation between this difference and the baseline (adult) movements, we bootstrapped the data set 1000 times, first resampling observations within category (i.e. 'adult' or 'subadult') before recombining them and recalculating the hourly mean travel distances and differences between the bootstrapped movements of subadults and the observed baseline movements of adults. For each iteration, we recorded the correlation between the bootstrapped difference values and the observed baseline values at the same time stamps. To test for the overall direction and significance of the correlation between baseline movement levels and changes in movement, we performed a two-tailed test where correlations were considered positive or negative if 97.5% of the distribution of bootstrapped correlation values was greater or less than zero, respectively. The resulting correlation was strongly and significantly positive ($r = 0.676$, $P < 0.001$).

Table A1
Summary of each dispersing GPS-tagged subadult female

| ID	Mass (kg)	Start of transience	End of transience	Natal group	Dispersal outcome
WT00392	1.30	27 Apr 2019	28 Apr 2019	Mpala[1]	Settled
WT00400	1.40	27 Apr 2019	01 May 2019	Mpala[1]	Returned to natal group
WT00009	1.34	27 Apr 2019	11 May 2019	Mpala[1]	Returned to natal group
WT00394	1.40	27 Apr 2019	27 May 2019	Mpala[1]	Settled
WT00400	1.50	14 Sep 2019	–	Mpala[2]	Tag fell off 23 Sep 2019
WT00391	1.48	26 Sep 2019	–	Mpala[2]	Last seen 15 Oct 2019
WT00009	1.34	22 Sep 2019	26 Oct 2019	Mpala[2]	Predated 26 Oct 2019
WT00394	1.40	20 Oct 2019	19 Nov 2019	Unmarked group	Settled
WT00395	1.34	03 Oct 2019	25 Oct 2019	Mpala[2]	Settled
WT00474	1.18	21 Oct 2019	20 Nov 2019	RR Upper	Settled
WT00567	1.24	14 Oct 2019	–	RR Main	Last seen 26 Nov 2019
WT00617	1.38	14 Oct 2019	–	Dump site[1]	Last seen 27 Oct 2019
WT00041	1.32	06 Oct 2019	03 Nov 2019	RR Main	Settled
WT00025	1.28	19 Oct 2019	30 Oct 2019	Dump site[1]	Returned to natal group
WT00027	1.36	11 Oct 2019	25 Oct 2019	Dump site[1]	Settled
WT00568	1.38	19 Oct 2019	29 Oct 2019	RR Main	Settled
WT00575	1.18	19 Oct 2019	–	RR Main	Last seen 19 Oct 2019
WT00570	1.28	14 Oct 2019	22 Oct 2019	RR Main	Settled
WT00577	1.34	18 Oct 2019	25 Oct 2019	RR Main	Settled
WT00038	1.22	13 Oct 2019	24 Oct 2019	Dump site[1]	Settled
WT00046	1.26	06 Oct 2019	–	RR Main	Last seen 19 Oct 2019
WT00031	1.22	18 Oct 2019	29 Oct 2019	Dump site[1]	Settled
WT00523	1.26	18 Oct 2019	–	Dump site[1]	Last seen 19 Oct 2019
WT00577	1.34	21 Oct 2020	10 Nov 2020	Unmarked group	Settled
WT00542	1.24	21 Mar 2021	27 Mar 2021	Dump site[2]	Settled; Predated 13 Apr 2021

Start of dispersal corresponds to date of departure from the natal group and end of dispersal marks dates when settlement occurred. In some cases, dispersers failed to find a new group and returned to the natal group. In instances where we tracked dispersers from the same group in multiple seasons, superscript numbers for groups denote the season, as the composition of GPS-tagged residents was subject to slight changes.
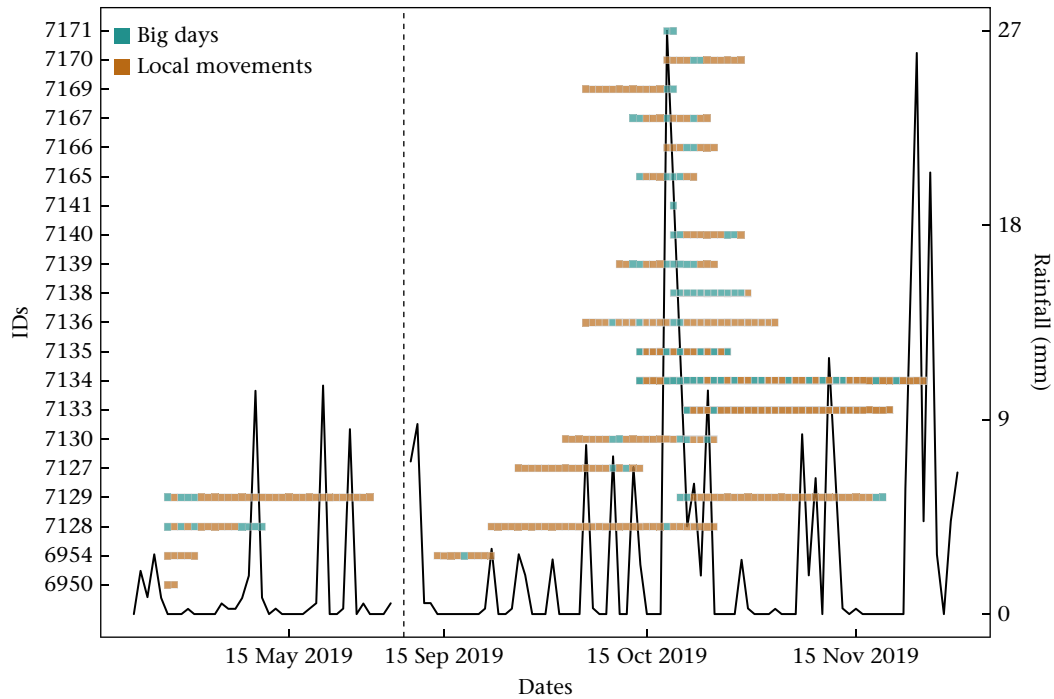
Figure A1. Daily movement classifications of transient dispersers and daily rainfall totals. Dispersing birds typically alternated between periods of dedicated, long-distance movement behaviours ('big days') and periods of local movements. Black lines indicate daily rainfall (mm); median daily rainfall across all seasons was 0 mm. Dotted vertical line marks the jump in dates between study seasons, from 1 June to 10 September 2019.
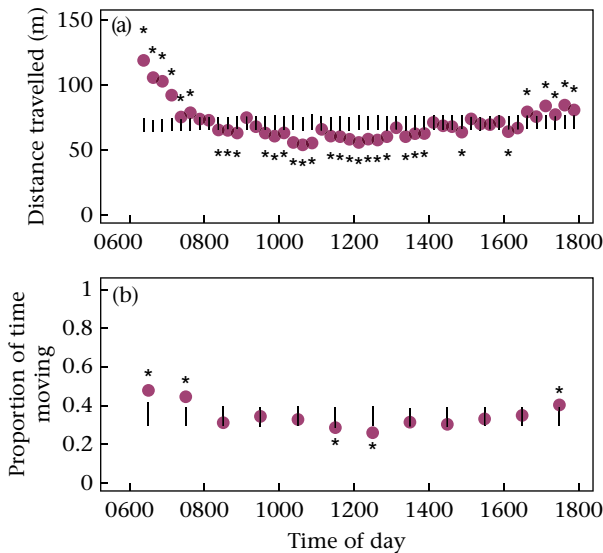

Figure A2. Within-day variation in movements by nondispersing residents during the same period that subadults from their group were in the active phase of dispersal. Circles show the mean of observed values of (a) distance travelled (15 min time steps) and (b) proportion of time spent moving (hourly) over the course of a day (e.g. from 0600 to 0615, or from 0600 to 0700) vertical lines show 95% range of random permutations in which hourly labels were reassigned 1000 times, and stars mark hours in which the observed movements fell either above or below the 95% range of permuted values.
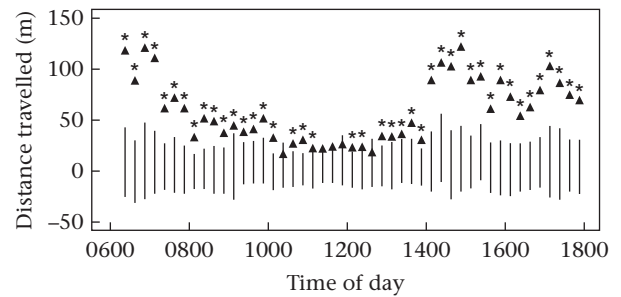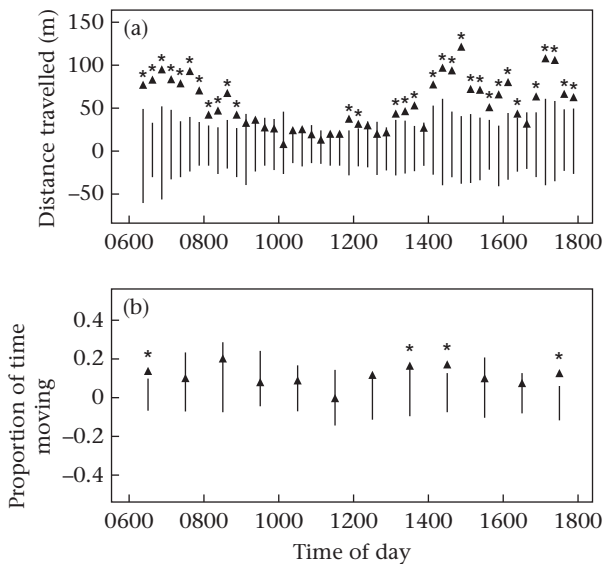

Figure A3. Differences in movements between actively dispersing birds and their baseline predispersal movements, for (a) distances travelled and (b) proportion of time spent moving. Triangles show the mean within-individual difference in movement activity at each time step. Vertical lines show the 95% range of calculated differences from random permutations in which categorical labels were randomized within each time step 1000 times. Stars mark observed mean differences that fell outside this range, denoting significance. All significant differences occurred where the difference was greater than expected by chance.
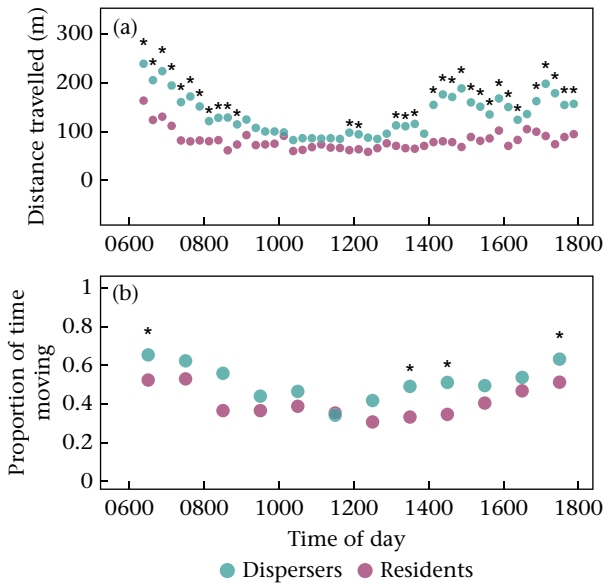
Figure A4. Differences in movement by actively dispersing birds relative to the movements of nondispersing residents, for (a) distances travelled and (b) proportion of time spent moving. Circles show mean values of each movement variable at each time step. Stars mark observed mean differences that fell outside the 95% range of calculated differences from random permutations in which categorical labels were randomized within each time step 1000 times.
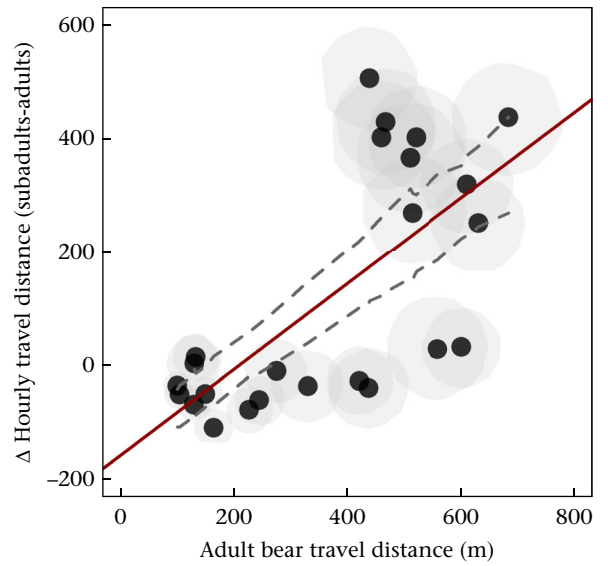
Figure A6. Hourly movement by subadult male brown bears in relation to baseline (adult male) movements. Black dots show observed changes in hourly travel distances for each hour of movement, relative to baseline (adult) levels. Light grey polygons show the 75th percentile distributions of the estimated differences in movement, relative to baseline values, from 1000 bootstraps. Solid red line illustrates the linear relationship between the observed points, with dashed grey lines illustrating the 95% distribution of these linear relationships from the bootstrapped differences in movement.

Figure A5. Differences in movements between actively dispersing birds and the movements of nondispersing residents on the same dates, for (a) distances travelled and (b) proportion of time spent moving. Triangles show the mean difference in movement activity at each time step. Vertical lines show the 95% range of calculated differences from random permutations in which categorical labels were randomized within each time step 1000 times. Stars mark observed mean differences that fell outside this range, denoting significance. All significant differences occurred where the difference was greater than expected by chance.