

## LETTER

# Efficient movement strategies mitigate the energetic cost of dispersal

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## INTRODUCTION

Dispersal is a key life history process comprised of three stages: departure, transience and settlement (Bowler & Benton, 2005; Clobert et al., 2009). Competition for resources (Clobert et al., 2001; Hamilton & May, 1977) and avoidance of inbreeding (Gandon, 1999; Matthysen, 2012) drive individuals to leave their natal range. The potential benefits of dispersing are generally offset by substantial costs. During the active phase

**Abstract**

Dispersal is a critical, but costly, stage of life. During the active phase of dispersal—called transience—individuals face many costs, from increased mortality to reduced foraging opportunities. One cost that is often assumed, but rarely explicitly tested, is the energy expended in making large dispersal movements. However, this cost is not only determined by the distance individual's move, but also how they move. Using high-resolution GPS tracking of dispersing and resident vulturine guineafowl (*Acryllium vulturinum*), we show that transient individuals exhibit distinct movement behaviours—travelling farther, faster and straighter—that result in a significant reduction in the energetic costs of making large displacements. This strategy allows dispersing birds to travel, on average, 33.8% farther each day with only a 4.1% cost increase and without spending more time moving. Our study suggests that adaptive movement strategies can largely mitigate movement costs during dispersal, and that such strategies may be common.

**KEY WORDS**

adaptive strategies, animal behaviour, biologging, dispersal, ecophysiology, energetic costs, GPS tracking, movement ecology, terrestrial ecology, vulturine guineafowl

of dispersal—transience—individuals can suffer from increased mortality (Alberts & Altmann, 1995; Isbell et al., 1993; Yoder et al., 2004) and missed reproductive or foraging opportunities (Alberts & Altmann, 1995; Zollner & Lima, 2005), compared to resident individuals. Furthermore, animals often have to make extraordinarily large displacements during transience (Elliot et al., 2014; Killeen et al., 2014; Woollard & Harris, 1990), in some cases achieving several times the daily net displacement of non-transient individuals (Delgado et al., 2009).

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Observations of such large-scale displacements have led to the suggestion that dispersal must incur a substantial energetic cost arising from movement (Bonte et al., 2012; Van Dyck & Baguette, 2005). However, what has largely been overlooked is that this cost may not only be a function of how far an individual travels, but also how it moves when making large displacements. For example, moving straighter should minimize the costs of making net displacements relative to moving in a more tortuous manner. Further, because the relationship between walking speed and metabolic rate in terrestrial animals is linear (Chassin et al., 1976; Taylor et al., 1982), it results in a non-linear decrease in the gross cost of transport—the total amount of energy consumed to move a unit of body mass a given distance—with increasing speeds. Thus, moving faster could allow animals to make larger displacements for a given energetic cost. These fundamental relationships could underpin the evolution of adaptive movement strategies that can mitigate movement costs when dispersing.

There is increasing evidence that dispersal behaviour is shaped by the costs encountered after departure. Examples include dispersing meerkats (*Suricata suricatta*) moving along territory boundaries to avoid conflicts with residents (Cozzi et al., 2018) or changes in the timing of dispersal allowing individuals to maximize the chances of integration into new social groups (Armansin et al., 2020; Cheney & Seyfarth, 1983). However, it still remains unclear whether movement behaviour during dispersal is shaped by the energetic costs of making large-scale displacements. A study focused on energetic expenditure of dispersing roe deer (*Capreolus capreolus*) found that dispersers travelled 63% farther per day, expending an estimated 22% more energy than non-dispersers (Benoit et al., 2020). While these results indicate an additional net cost to making large displacements, they also suggest that movement costs may not scale equally with the displacements achieved. How might this happen? Several studies, in a range of terrestrial mammals (Elliot et al., 2014; Killeen et al., 2014; Woollard & Harris, 1990), have found that individuals express different movement behaviours during transience, specifically moving straighter and faster. The results from these studies suggest that dispersers may be exhibiting cost-mitigating movement behaviours. However, to date, studies have been limited in their ability to link the movements behaviours of dispersers to the actual costs incurred, as they have relied on either indirect measures of activity (e.g. accelerometers) without capturing data on movement or sparse GPS sampling [e.g. 1 point per hour (Elliot et al., 2014)] that cannot capture the fine-scale moment-by-moment movement behaviour of individuals (Kays et al., 2015).

In this study, we use simultaneous high-resolution (1 Hz) GPS tracking of dispersing and resident vulturine guinea fowl (*Acryllium vulturinum*)—comprising 1367 bird-days (where one bird-day represents one day of tracking for one individual)—to test two key hypotheses.

First, we test whether individuals exhibit distinct changes in how they move during each stage of dispersal (pre-departure, during transience and post-settlement). Second, we quantify the energetic costs of moving during transience relative to pre-departure and post-settlement to test whether these changes in movement correspond to a cost-mitigating strategy for achieving the large-scale displacements typical of dispersal. Because vulturine guinea fowl live in stable groups (Papageorgiou et al., 2019), our data collection allows us to test these hypotheses by employing a powerful two-step comparative approach: first making within-individual comparisons of movement behaviours of dispersers across stages, and second by making comparisons between dispersers and residents from their natal group (at each stage) to discard the potential contribution of daily variation in environmental conditions. By integrating fine-scale tracking of individual movements over long time periods with robust data on the energetic costs of moving, we reveal that animals exhibit an adaptive strategy during transience that largely mitigates the costs of dispersing.

## METHODS

### Study system

We collected our data in a population of vulturine guinea fowl, which are a largely-terrestrial bird species, at the Mpala Research Centre in Laikipia, Kenya (0.292120, 36.898670). Since 2016, field observations have confirmed that, like most other bird species (Greenwood, 1980), dispersal in vulturine guinea fowl is heavily sex-biased towards females. We used data from 35 individuals, comprising 20 dispersing subadult females—approximately 18 months old at the time of dispersal—and 15 non-dispersing residents (four subadult males, five adult males, six adult females) from six social groups. Birds were captured as whole groups using walk-in traps, and each individual was marked with an individually numbered stainless steel ring, a unique combination of four plastic colour bands, and was fitted with a 15 g Bird Solar GPS tag (e-obs GmbH) using a backpack-style Teflon harness and a neoprene pad to elevate solar panels above body feathers (Papageorgiou et al., 2019). The total weight of backpacks and tags combined was approximately 20.5 g, well below the suggested 3% of birds' body weight (Kenward, 2000). Data were recorded across two dispersal seasons in 2019 (See Table S1).

### Research permits

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 Authorisation and a Capture Permit issued by the Kenyan Wildlife Service, and in affiliation with the National Museums of Kenya.

## GPS tracking

Each GPS device was programmed to record data during daylight hours, from 06:00 to 19:00. Data points (date, time and location) were recorded continuously at 1 Hz (i.e. one fix per second) when the tags' battery had a high charge (approximately every second to third day, 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 two days using a BaseStation II (e-obs Digital Telemetry, Grünwald, Germany). For the purposes of our analyses, we separated the data into two resolutions: high-resolution data, comprising all continuous periods of 1Hz data; and 5-min data, comprising data from the tenth second of every fifth minute of the day. The latter was collected from both the low-resolution dataset and by sub-sampling the 1Hz

data, thereby reliably providing data every 5 min for every bird on every day it was tracked. For logistical reasons the accelerometer function of our GPS tags was disabled, as the increased amount of data would have greatly hindered our ability to reliably track, and download data from, birds dispersing over large distances. 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., 2020).

## Dispersal

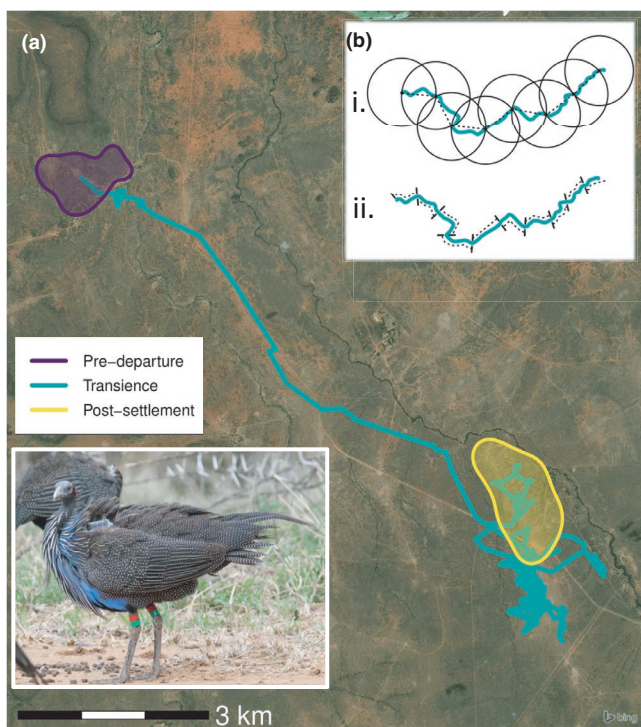
We divided each disperser's dataset into three stages (Figure 1a)—pre-departure (7 days when dispersers were still moving with their natal group), transience (mean of 16.8 days when birds were actively dispersing), and post-settlement (7 days when individuals were moving with their post-dispersal group). Birds were considered to have dispersed—i.e. to have started transience—on the first date when they were observed to be 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 then considered settled from the first day in which they spent the entire day within their eventual post-settlement group (based on field observations over the following months). In three instances, this included birds who failed to successfully find a new group and ultimately returned to their natal group. These three individuals attempted to disperse again in a subsequent season, resulting in 23 recorded dispersal events. For birds that dispersed into groups outside of our study population, settlement was determined from field observations and dated based on the first instance of repeated use of the same roost site that ultimately would represent their post-dispersal home range. For 8 of the 23 recorded dispersal events, we were unable to record settlement, owing to either: predation during transience (1 individual); a failure of the Teflon ribbon causing the tag to fall off (one individual which was later visually confirmed to have survived based on colour bands); or because the dispersing bird moved sufficiently far from our study area that we were not able to relocate the tag for download (six individuals). These birds were excluded from analyses of post-settlement movement.

## Analyses

All analyses were performed in R version 4.0 (R Core Team, 2020).

## Defining movement states

We implemented an unsupervised Hidden Markov Model (HMM) to delineate the different movement



**FIGURE 1** Tracking vulturine guineafowl across three stages of dispersal: pre-departure (purple), transience (green) and post-settlement (yellow). (a) Full dispersal track of one individual with transience movements (line) between pre-departure and post-settlement home ranges (polygons). (b) Illustration of how 50 m segments of net (i) or cumulative (ii) displacement were derived from movement tracks



states exhibited by vulturine guineafowl. Because a 1Hz 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 dataset, using the R package *depmixS4* (Visser & Speekenbrink, 2010). We selected a 4-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). The choice of a 4-state model was also critical for isolating a clear “stationary” state for the purposes of calculating metabolic expenditure. We then assigned the state of each 10-s burst to all of the 1Hz data points which contributed to it. Birds were considered to be moving when a GPS point was assigned to any of states 2–4.

### Characterizing how dispersers move across stages of dispersal

We extracted five key measures to characterize birds' movement behaviours: daily track length (km), speed while moving ( $\text{m s}^{-1}$ ), straightness of movement (a straightness index, Batschelet, 1981), the percent of overall time spent moving, and the duration of each burst of movement. Daily track lengths were measured from the sum of displacements 5-min data, in order to control for variation in the amount of high-resolution data collected each day. Speed was calculated from the per-second displacement when an animal was moving (i.e. assigned to states 2–4), summarized for each 5-min window of high-resolution data available. In order to reduce the effect of small GPS errors on calculated velocities, individuals' speeds at each second were derived from the mean velocity over a rolling 5-s window within the high-resolution data (i.e. at each second, we averaged the animals speed with the 2 s which preceded and followed it). Straightness of movement was characterized using the straightness index (Batschelet, 1981) calculated over each available 5-min window of 1Hz data, dividing the net displacement achieved over the 5 min by the summed cumulative displacement therein. The percent 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 divided by the total number of seconds to which any state was assigned (only hours with 95% or greater, i.e. 57 min or more, of high-resolution coverage were used). Finally, duration of movements was defined as the number of consecutive seconds in which an animal was moving without stopping, summarized for each distinct bout of movement.

To test how individuals' movement behaviours changed across stages, we first fit linear mixed models (LMM), using the package *lmerTest* (Kuznetsova et al., 2017), to each movement measure. For analyses of daily

track length, we included one measure per individual per day. For speed while moving and straightness index, we included one observation from each available 5-min period of continuous high-resolution data (mean = 54.0, range = 2 to 140 observations per individual per day). For the percentage of time spent moving, we included data for each distinct hour of the day that collected sufficient high-resolution data (mean = 5.3, range = 1 to 11 observations per individual per day). Finally, for the durations of movements, we fit the length of each continuous burst of movement that was detected. Because movement duration is left-truncated, forming a long-tailed distribution, we square-root-transformed durations to aid with model fitting. In each model, we included stage (pre-departure, transience, post-settlement) as a predictor. We considered two factors as random effects—individual identity and natal group—in one of three configurations: individual identity as random intercept, individual identity and group as crossed random effects, or individual identity as crossed random effects where individuals were allowed to have random slopes. We then selected the best random effect structure in each model using Akaike's Information Criterion (AIC). AIC values for all models of individual behaviours can be found in Table S2, and specific equations for all LMMs can be found in the corresponding table in the supporting information. Model selection was performed without restricted maximum likelihoods (REML) for all random effect structures tested, as this could affect AIC values, although final models were fit using REML. For all models, the pre-departure stage was used as the reference category, as these movements were interpreted to be typical of daily behaviours for both subadults and resident adults.

To perform the comparison between dispersers and residents, we fit LMMs of movement as a function of the stage a given disperser was in, this time using the difference between the disperser's and its corresponding resident group members' measures of movement as the response variable and individual (disperser) as a random effect. We were limited to this model structure because multiple dispersing individuals from the same group could be at different stages, making it difficult to fit resident individuals independently into the model for the purpose of making the comparison. For daily track length, we calculated the difference between each disperser and the mean of the residents from its natal group on the same day. For speed while moving and straightness index, we calculated the difference in each unique 5-min window of each day in which both the disperser and at least one of the resident individuals collected high-resolution data. Similarly, we calculated the difference in percentage of time spent moving for each hour of the day in which both the disperser and at least one of corresponding resident individuals collected high-resolution data. Finally, we calculated the difference in movement duration as daily measures, based on the differences in mean duration of all bouts of continuous movement in

a given day for both dispersers and their corresponding residents. To avoid over-representing days with fewer high-resolution data, we excluded any day containing less than 2 hours of high-resolution data (for both the disperser and the residents of its natal group) from analyses of movement duration. For all movement variables, we calculated the mean value across all members of the group when simultaneous measures were available within a group of residents.

## Calculating the energetic costs of movement

To quantify how movement at each stage of dispersal translate to metabolic costs, we used published data (Ellerby et al., 2003) on the relationship between metabolic costs ( $\text{mL O}_2 \text{ kg}^{-1} \text{ s}^{-1}$ ) and movement speed ( $\text{m s}^{-1}$ ) in the morphologically similar, and closely-related, helmeted guineafowl (*Numida meleagris*). Specifically, we used two formulas to calculate the costs incurred for each second of high-resolution data, corresponding to when birds were either stationary (state 1) or moving (states 2–4). When moving (i.e. velocity  $v > 0$ ), guineafowl exhibit a linear relationship between speed and oxygen consumption, given by  $\text{VO}_2 = (24.0v + 27.2)$ , where  $\text{VO}_2$  is the per-minute volume of oxygen consumed in  $\text{mL O}_2$  per kilogram of body mass. The formula for when birds were stationary is a fixed consumption of  $19.1 \text{ mL O}_2 \text{ kg}^{-1} \text{ min}^{-1}$ , corresponding to the oxygen consumption rate when not moving, as described in the literature (Ellerby et al., 2003). These per-second measures of metabolic oxygen consumption were then transformed into units of Joules  $\text{kg}^{-1} \text{ s}^{-1}$  using a conversion factor of  $20.1 \text{ J mL}^{-1} \text{ O}_2$  (per Marsh et al., 2006; Ellerby et al., 2003).

## Calculating the energetic costs of displacements

We used the high-resolution GPS data from each individual to partition movement tracks into fixed segments representing 50 m of net or cumulative displacement (Figure 1b). Net displacement is the absolute movement in space between two points in time, while cumulative displacement is the sum of the individual step distances travelled. We segmented tracks starting from the first second of high-resolution data available (i.e. after the GPS switched on or switched from low-resolution to high-resolution) until the 50 m net displacement threshold was crossed. The first GPS point to fall on or outside of the given radius then represented the first point for the next segment. Using the same high-resolution data, we also calculated the corresponding cumulative displacements by summing each consecutive step length in a track until it reached a sum of 50 m, at which point we started a new segment. The total energetic expenditure for each

segment was calculated by summing the per-second costs for each detection which contributed to that segment, and translated into the energetic cost of transport (in  $\text{J kg}^{-1} \text{ m}^{-1}$ ) for each type of displacement by dividing by the distance travelled (either net or cumulative).

For each displacement type, we then fit an LMM with the cost of transport associated with each segment as the response variable, stage of dispersal as a predictor, and individual and natal group as crossed random effects, where individuals were allowed to have random slopes (see Table S2 for AIC values of alternate random effect structures). To generate a comparison between dispersers and residents, we calculated the mean cost for each disperser to achieve a given displacement within each hour of each day, and subtracted the mean cost of all residents from the same group to achieve the same given displacement within the same time window. We then fit an LMM with the difference in cost as the response variable, stage of dispersal as a predictor and individual (disperser) as a random effect.

## Calculating the total energetic costs of dispersing

We calculated the total energetic expenditure over each 13-h day for each bird by summing all of the per-second costs from each unique day of tracking for each individual into a single measure of daily energetic expenditure (i.e.  $\text{J kg}^{-1} \text{ day}^{-1}$ ). Because not all days contained an equal amount of high-resolution data, we standardized the cost value for each day by multiplying the mean cost within the day by 46,800 s. To avoid over-representing days with fewer high-resolution data, we excluded any day containing less than 2 h of high-resolution data.

To estimate the change in energy use across stages, we fit an LMM of daily energetic expenditure as the response variable, with stage of dispersal as the predictor variable individual identity as a random intercept (see Table S2 for AIC values of alternate random effect structures). To make the comparison to residents from the same group, we calculated the difference in daily energetic expenditure between dispersers and residents on matched days. When multiple resident measures were available for the same date, we opted to use the value from whichever individual collected the most high-resolution data for comparison. We then fit an LMM of the difference in energetic expenditure as the response variable, with stage as the predictor and individual (disperser) as a random effect.

## RESULTS

We collected over 13 million GPS fixes, constituting 158 bird-days pre-departure, 382 bird-days of transience, 105 bird-days post-settlement from subadults, and 722 corresponding bird-days of data from resident adults (see Table S1 for a summary of each dispersal event). In

total, 85.7% of fixes—comprising 17.5% of total tracking time—were collected at high resolution (continuous 1 Hz), with the remainder collected in 10-s bursts every fifth minute of daylight hours.

### Dispersers move farther, faster and straighter during transience

Individuals' daily cumulative track lengths confirm that dispersers travelled significantly farther during the transience stage relative to both pre-departure and post-settlement (Figure 2ai). The difference in daily distances between dispersers and residents was also greatest during the transience stage relative to other stages (Figure 2a(ii)). These results indicate that increased distances travelled during transience were attributable to individuals' dispersal stage and not underlying environmental conditions.

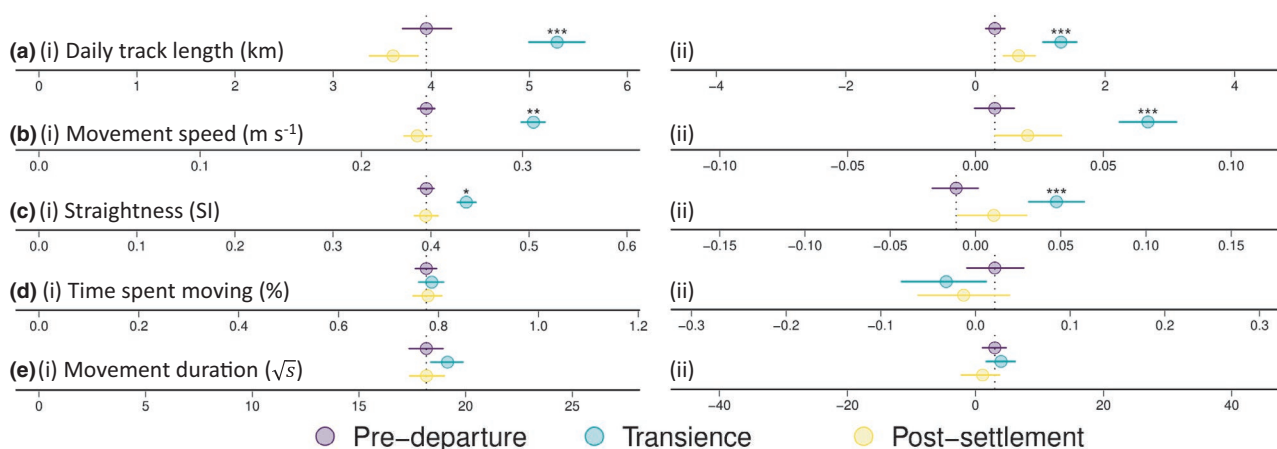
Birds exhibited distinct movement behaviours during transience. Transient birds were significantly faster in their moving speed when compared to other stages (Figure 2bi), and when compared to residents (Figure 2b(ii)). Transient also made significantly straighter movements when compared to other stages (Figure 2ci) and when compared to residents (Figure 2c(ii)). Despite moving over much larger distances, transient birds did not spend a greater amount of time moving relative to pre-departure and post-settlement (Figure 2di), or when compared to residents (Figure 2d(ii)). Dispersing birds also showed no difference in the duration of their

movements across stages (Figure 1ei), or when compared to residents (Figure 1eii).

Overall, transient birds moved farther, faster and straighter. Relative to their pre-departure movements, changes in movement corresponded to an average 33.8% greater daily travel distance, which they achieved by moving, on average, 27.7% faster and 10.3% straighter. However, they did not increase the overall time spent moving. The differences in movement behaviours were also captured by the raw HMM state assignments (Figure 3), which detected a similar expression of the stationary state (state 1) across all stages, but revealed that the slow tortuous state (state 2, which we hypothesize corresponds to foraging) was underrepresented during transience (35.8% vs 43.9% pre-departure and 41.0% post-settlement), while the expression of fast, directed movements (state 4) increased during transience (15.3% vs 10.1% pre-departure and 10.0% post-settlement).

### Dispersers make more efficient displacements

Transient birds' movements translated to a significant decrease in the energetic cost of transport. Dispersers spent an average of 23.6% less energy to achieve a 50 m net displacement during transience relative to pre-departure (Figure 4ai), and were similarly more efficient than residents (Figure 4a(ii)). Birds also used an average 17.2% less energy per cumulative displacement during transience relative to pre-departure (Figure 4bi), a pattern that also held when compared to resident birds (Figure 4bii).



**FIGURE 2** Dispersing birds move farther, faster and straighter during the transience stage (green) than pre-departure (purple) or post-settlement (yellow). (a–e) Summary of linear mixed-effect models (LMMs) characterizing movement behaviours across stages (coefficient  $\pm$  95% confidence intervals), with significance (stars: \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ ) estimated using pre-departure as the reference category (the dotted vertical lines, corresponding to model intercepts). (a) Dispersers had longer daily track lengths when transient than during other stages (i); a pattern which held when comparing dispersers to natal group residents on the same days (ii). (b) Transient birds exhibited higher movement velocities compared to other stages (i), and when compared to residents (ii). (c) Transient birds moved straighter, exhibiting a higher ratio between net and cumulative displacement, when compared to other stages (i) and when compared to residents (ii). (d) Dispersing birds showed no change in the total amount of time spent moving at different stages (i), or when compared to natal group residents (ii). (e) Dispersing birds did not express a significant change in the average duration of each burst of movement during transience (i), or when compared to natal group residents (ii). Full model results are available in Tables S3-S12

## Dispersers achieve substantial displacements with relatively small movement costs

Our data revealed that dispersers did pay a higher total daily energetic cost during the transience stage than during the pre-departure and post-settlement stages (Figure 5a). However, the scale of this increase—on average 4.1% more over the course of a day—is substantially lower than the corresponding increase (33.8%) in displacement achieved. As with our other estimates, the comparison between dispersing individuals and resident members of their groups was consistent with the differences observed within individuals across stages (Figure 5b).

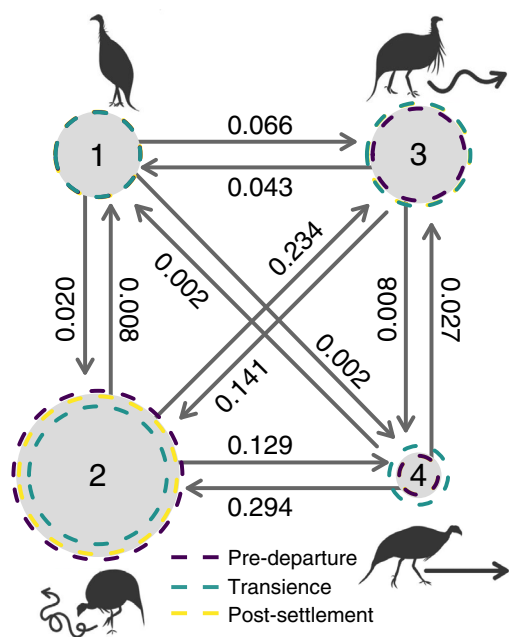
## DISCUSSION

We show that dispersers express distinct movement behaviours during transience that can mitigate the energetic costs of achieving the large displacements necessary for dispersal. Our results bring together previously

disparate findings showing that animals exhibit different movement behaviours during transience (Elliot et al., 2014; Killeen et al., 2014; Woollard & Harris, 1990) and that the energetic costs incurred when making dispersal movements do not scale equally with the displacements these movements achieve (Benoit et al., 2020). Furthermore, we are able to go beyond these previous studies by showing that transient animals are able to achieve such large displacements by specifically changing how they move, and not by simply moving more. Our results demonstrate how both increases in straightness (efficiency in space) and speed (efficiency over time) contribute towards reducing the cost of transport when making net displacements, with the increased efficiency in achieving cumulative displacements demonstrating the specific savings made by moving faster. By aligning with previously disparate findings, our study reveals what is likely to be a taxonomically widespread set of efficient movement strategies that animals employ when dispersing. In doing so, our work suggests that the assumed movement costs of dispersing (reviewed in Bonte et al., 2012) may have been over-stated.

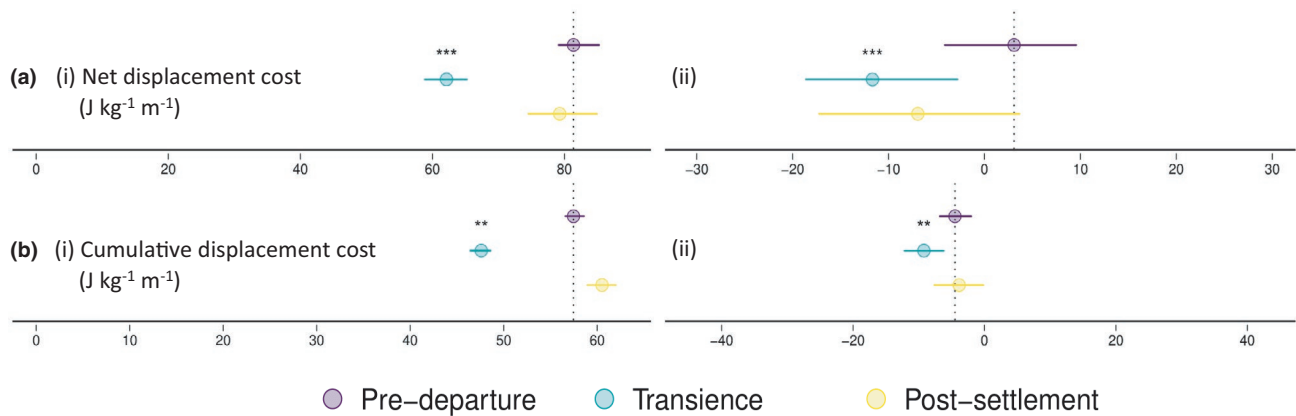
Our results show that dispersers can mitigate the energetic costs of movement by changing how they move. However, the overall energetics of dispersal are also influenced by trade-offs between foraging and moving (Zollner & Lima, 2005). Vulturine guinea-fowl exhibit reduced foraging-type movements (state 2) and an increase in fast, directed movements (state 4) when transient (Figure 3). Reduced foraging movements could indicate an additional cost beyond the mechanical costs of displacement, but these costs could be further offset by the timing of dispersal. We found that vulturine guinea-fowl disperse following periods of increased rainfall that correspond to periods of resource abundance (e.g. the emergence of termite alates, Darlington, 1985), which have been shown to allow substantially greater foraging efficiency in savannah-dwelling species (Owen-Smith, 1979; Wronski, 2002), including guinea-fowl (Kumssa & Bekele, 2013). Thus, dispersal could coincide with periods of relaxed constraints on foraging time for transient animals. Further evidence for this comes from our data showing that some individuals are capable of making large, continuous movements over 10 or more consecutive days (see Figure S1), suggesting that dispersers may not be fully depleting their energy reserves if they can continue moving for days at a time. However, during the transience period, birds occasionally spent entire days moving in a foraging-like manner, which from anecdotal observations seem to also involve prospecting within non-natal groups. How these days of reduced displacement serve to inform settlement and/or replenish birds' energy reserves warrants further investigation.

Although we show that vulturine guinea-fowl follow a cost-mitigating strategy which reduces their total cost of transport, they still often move slower than speeds which

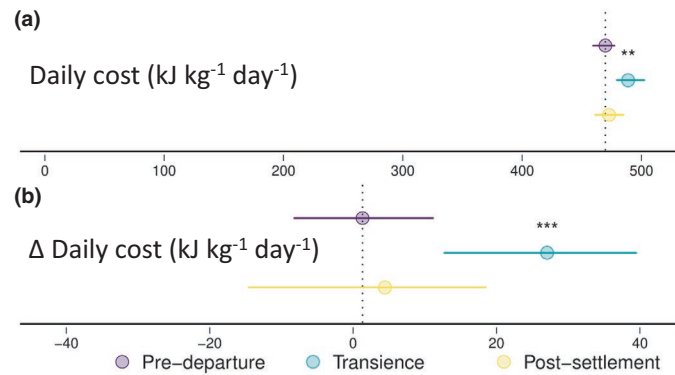


**FIGURE 3** Dispersing birds exhibit less slow, tortuous movements and more fast, directed movements during transience. A hidden Markov model (HMM) was used to identify four behavioural states, representing animals: not moving (state 1), making slow and tortuous foraging movements (state 2), making medium-speed movements with some changes in direction (state 3), or moving quickly in a directed manner (state 4). Grey circles show the representation of each state and arrows transition probabilities between states in the entire dataset; coloured dotted lines (pre-departure—purple; transience—green; post-settlement—yellow) show representation of each state at each stage of dispersal (e.g. during transience, state 2 is expressed less and state 4 is expressed more). Full details of HMM outputs available in Table S13 while the summary of the proportion of time birds spent in each state, according to dispersal stage, are available in Table S14





**FIGURE 4** Dispersers make more efficient displacements during transience (green) than during the pre-departure (purple) or post-settlement (yellow) stages. Plots show the summary of linear mixed-effect models (LMMs) of the total cost of transport associated with making either a 50 m net (a) or cumulative (b) displacement across stages (coefficient $\pm$ 95% confidence intervals), with significance (stars: \*\* $p \leq 0.01$ , \*\*\* $p \leq 0.001$ ) estimated using pre-departure as the reference category (the dotted vertical lines, corresponding to model intercepts). (a) Transient birds paid a lower energetic cost to achieve a fixed-distance net displacement than they did pre-departure or post-settlement (i), which also held true when comparing the average cost paid by dispersers in a given hour to the average paid by residents of their natal group in the same hour (ii). (b) Transient birds were also more efficient when measured in terms of cumulative displacements (i), and when compared to residents (ii). Full model results are available in Tables S15-S18



**FIGURE 5** Dispersing birds pay a relatively small increased daily cost of moving during transience. Plots show the summary of linear mixed-effect models (LMMs) of daily energetic expenditure across stages (coefficient $\pm$ 95% confidence intervals), with significance (stars: \*\* $p \leq 0.01$ , \*\*\* $p \leq 0.001$ ) estimated using pre-departure as the reference category (the dotted vertical lines, corresponding to model intercepts). (a) Dispersers paid a significant, but relatively small (4.1% higher) daily movement cost during transience relative to pre-departure. (b) This pattern also held when comparing dispersers to resident adults from their natal groups on the same days. Full model results are available in Tables S19-S20

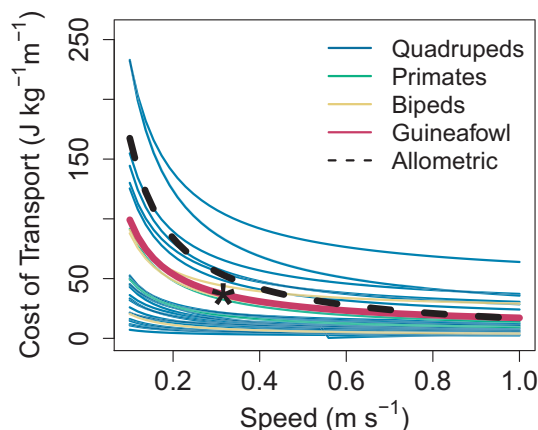
would maximally reduce these costs. Animals only approach their minimal cost of transport when running at their aerobic maximum (Taylor et al., 1970). In guinea-fowl, this speed should be approximately  $2.78 \text{ m s}^{-1}$  (Ellerby et al., 2003), which is much higher than the estimated average speed of  $0.307 \text{ m s}^{-1}$  exhibited by transient birds in our study (Figure 2b, Table S5). However, the average speed we observed closely matches what might be an alternative optimal point along the speed-cost curve: the point of maximal curvature (here  $0.316 \text{ m s}^{-1}$ ; Figure 6), where the benefits of increased efficiency with increasing speeds taper-off the fastest. Several factors can shape what optimality criterion applies to animal movements (Pyke, 1981), with higher speeds imposing greater costs arising from diminished spatial information processing (Chittka et al., 2009), increased risk of

predation (Kramer & McLaughlin, 2001) and the potential for injury (Wheatley et al., 2021). The diminishing per-unit savings in the costs of transport at very high movement speeds are therefore likely to become negligible relative to the increase in other, related costs. Thus, it may be that the critical speed as described under laboratory conditions may not accurately reflect an optimal strategy for cost-reduction in wild animals which have evolved to balance multiple constraints as they move through their environments. Our results suggest that, while dispersing animals are capable of travelling at highly-efficient speeds, other contextual factors—such as increased risk from moving alone, navigational challenges or reduced foraging constraints—are likely to determine the optimal movement strategy at any given point in time or space.



We also note that, while birds averaged a speed near the point of maximum curvature in the speed-to-metabolic-cost relationship, they often moved at speeds that were above or below this asymptotic point (95% range of velocities during transience: 0.094–0.792 m s<sup>-1</sup>), meaning that their energy use was greater than it would have been had they moved at their average speed (0.307 m s<sup>-1</sup>) throughout (due to Jensen's inequality, *sensu* Denny, 2017). The difference in interpretation when using average speed values versus the second-by-second speeds highlights the importance of collecting high-resolution movement data for generating insights about the drivers of animal movement. Such fine-scale data should allow for a bottom-up approach when modelling energy landscapes (Shepard et al., 2013) or resistance surfaces (Zeller et al., 2012). How landscape features facilitate or restrict movement speed, straightness or continuity—as measured by deviations from the most-efficient movement behaviours—could be used to predict where animals should move and subsequent landscape connectivity (Diniz et al., 2020). Thus, landscape-level tools combined with high-resolution movement tracks could help to identify the factors that shape individuals' decision-making on the go.

Whether to avoid in-breeding (Gandon, 1999; Matthysen, 2012) or social conflicts (Christian, 1970; Cozzi et al., 2018), individuals depart their natal environment in search of new places to settle (Clobert et al., 2001; Hamilton & May, 1977). For dispersal to be adaptive, selection should favour strategies that mitigate the costs of dispersing. Such strategies include not only when (Tarwater & Brawn, 2010) and where (Cox & Kesler, 2012; Cozzi et al., 2018) animals move, but also



**FIGURE 6** The energetic cost of transport decreases non-linearly with speed. The relationship between movement speed and the energy needed to move a given distance is conserved across terrestrial taxa and gait types. Formulas for cost of movement as a function of speed were taken from laboratory studies of oxygen consumption (Chassin et al., 1976; Taylor et al., 1982), including a generalized allometric equation (dashed line). The cost of transport for helmeted guineafowl (Ellerby et al., 2003), which we used in this study, is plotted in red, with the black star marking the asymptote of the curve

how they move. Our study reveals distinct movement behaviours during transience that are consistent with those from other species. Specifically, dispersers across a range of terrestrial species, including foxes (*Vulpes vulpes*) (Woollard & Harris, 1990), lions (*Panthera leo*) (Elliot et al., 2014) and elk (*Cervus canadensis*) (Killeen et al., 2014), exhibit distinctly faster and straighter movements during transience. These results lead to a potentially general insight into terrestrial dispersal and how animals can reduce the cost of transport over large distances to offset the energetic costs of dispersing. Further, the relationship between movement speed and the cost of transport is likely to be highly conserved across species, with the relationship in guineafowl being consistent with the allometric relationship derived from many terrestrial species and gait types (Figure 6). Thus, the seemingly adaptive movement strategies we report are likely to be common across species. Our results are also consistent with how migrating insects (Wikelski et al., 2006), birds (Wikelski et al., 2003), bats (O'Mara et al., 2019) and ungulates (Sawyer & Kauffman, 2011) move. All express straighter long-distance movements that are distinct from tortuous foraging movements, suggesting a general selective pressure for movement efficiency arising from a range of social and ecological drivers.

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#### AUTHOR CONTRIBUTION

J.A.K., M.W and D.R.F. conceived the study, J.A.K and D.R.F. collected the data, J.A.K. and D.R.F. performed the analyses, J.A.K. and D.R.F. wrote the manuscript; all authors contributed to the final manuscript.

## PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ele.13763>.

## DATA AVAILABILITY STATEMENT

The datasets used in our analyses and all code required to replicate the present study is available via the Figshare repository at <https://doi.org/10.6084/m9.figshare.14363600.v1>.

## REFERENCES

- Alberts, S.C. & Altmann, J. (1995) Balancing costs and opportunities: Dispersal in male baboons. *American Naturalist*, 145, 279–306.
- Armansin, N.C., Stow, A.J., Cantor, M., Leu, S.T., Klarevas-Irby, J.A., Chariton, A.A. & et al. (2020) Social barriers in ecological landscapes: The social resistance hypothesis. *Trends in Ecology & Evolution*, 35(2), 137–148. <https://doi.org/10.1016/j.tree.2019.10.001>
- Batschelet, E. (1981) *Circular statistics in biology*. New York, NY: Academic Press.
- Benoit, L., Hewison, A.J.M., Coulon, A., Debeffe, L., Grémillet, D., Ducros, D. et al. (2020) Accelerating across the landscape: The energetic costs of natal dispersal in a large herbivore. *Journal of Animal Ecology*, 89, 173–185.
- Bonte, D., Van Dyck, H., Bullock, J.M., Coulon, A., Delgado, M., Gibbs, M. et al. (2012) Costs of dispersal. *Biological Reviews*, 87, 290–312.
- Bowler, D.E. & Benton, T.G. (2005) Causes and consequences of animal dispersal strategies: Relating individual behaviour to spatial dynamics. *Biological Reviews*, 80, 205–225.
- Chassin, P.S., Taylor, C.R., Heglund, N.C. & Seeherman, H.J. (1976) Locomotion in lions: Energetic cost and maximum aerobic capacity. *Physiological Zoology*, 49, 1–10.
- Cheney, D.L. & Seyfarth, R.M. (1983) Nonrandom dispersal in free-ranging vervet monkeys: social and genetic consequences. *The American Naturalist*, 122, 392–412.
- Chittka, L., Skorupski, P. & Raine, N.E. (2009) Speed-accuracy tradeoffs in animal decision making. *Trends in Ecology & Evolution*, 24, 400–407.
- Christian, J.J. (1970) Social subordination, population density, and mammalian evolution. *Science*, 168, 84–90.
- Clobert, J., Danchin, E., Dhondt, A.A. & Nichols, J.D. (2001) *Dispersal*. Oxford: Oxford University Press.
- Clobert, J., Le Galliard, J.F., Cote, J., Meylan, S. & Massot, M. (2009) Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecology Letters*, 12, 197–209.
- Cox, A.S. & Kesler, D.C. (2012) Prospecting behavior and the influence of forest cover on natal dispersal in a resident bird. *Behavioral Ecology*, 23, 1068–1077.
- Cozzi, G., Maag, N., Börger, L., Clutton-Brock, T.H. & Ozgul, A. (2018) Socially informed dispersal in a territorial cooperative breeder. *Journal of Animal Ecology*, 87, 838–849.
- Darlington, J.P.E.C. (1985) Lenticular soil mounds in the Kenya highlands. *Oecologia*, 66, 116–121.
- del Delgado, M.M., Penteriani, V., Nams, V.O. & Campioni, L. (2009) Changes of movement patterns from early dispersal to settlement. *Behavioral Ecology and Sociobiology*, 64, 35–43.
- Denny, M. (2017) The fallacy of the average: On the ubiquity, utility and continuing novelty of Jensen's inequality. *J. Experimental Biology*, 220, 139–146.
- Diniz, M.F., Cushman, S.A., Machado, R.B. & De Marco Júnior, P. (2020) Landscape connectivity modeling from the perspective of animal dispersal. *Landscape Ecology*, 35, 41–58.
- Ellerby, D.J., Cleary, M.E., Marsh, R.L. & Buchanan, C.I. (2003) Measurement of maximum oxygen consumption in guinea fowl *numida meleagris* indicates that birds and mammals display a similar diversity of aerobic scopes during running. *Physiological and Biochemical Zoology*, 76, 695–703.
- Elliot, N.B., Cushman, S.A., Loveridge, A.J., Mtare, G. & Macdonald, D.W. (2014) Movements vary according to dispersal stage, group size, and rainfall: The case of the African lion. *Ecology*, 95, 2860–2869.
- Gandon, S. (1999) Kin competition, the cost of inbreeding and the evolution of dispersal. *Journal of Theoretical Biology*, 200, 345–364.
- Greenwood, P.J. (1980) Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour*, 28, 1140–1162.
- Hamilton, W.D. & May, R.M. (1977) Dispersal in stable habitats. *Nature*, 269, 578–581.
- Isbell, L.A., Cheney, D.L. & Seyfarth, R.M. (1993) Are immigrant vervet monkeys, *Cercopithecus aethiops*, at greater risk of mortality than residents? *Animal Behaviour*, 45, 729–734.
- Kays, R., Crofoot, M.C., Jetz, W. & Wikelski, M. (2015) Terrestrial animal tracking as an eye on life and planet. *Science*, 348(6240), aaa2478.
- Kenward, R.E. (2000) *A manual for wildlife radio tagging*. London, UK: Academic press.
- Killeen, J., Thurfjell, H., Ciuti, S., Paton, D., Musiani, M. & Boyce, M.S. (2014) Habitat selection during ungulate dispersal and exploratory movement at broad and fine scale with implications for conservation management. *Movement Ecology*, 2, 1–13.
- Kramer, D.L. & McLaughlin, R.L. (2001) The behavioral ecology of intermittent locomotion. *American Zoologist*, 41, 137–153.
- Kranstauber, B., Smolla, M. & Scharf, A.K. (2020). move: Visualizing and Analyzing Animal Track Data.
- Kumssa, T. & Bekele, A. (2013) Population status, feeding ecology and activity pattern of helmeted guinea fowl [*Numidia meleagris*] in Abijata-Shalla Lakes National Park. *African Journal of Environmental Science and Technology*, 7, 49–55.
- Kuznetsova, A., Brockhoff, P.B. & Christensen, R.H.B. (2017) lmerTest package: Tests in linear mixed effects models. *The Journal of Statistical Software*, 82, 1–26.
- Marsh, R.L., Ellerby, D.J., Henry, H.T. & Rubenson, J. (2006) The energetic costs of trunk and distal-limb loading during walking and running in guinea fowl *Numida meleagris*: I. Organismal metabolism and biomechanics. *Journal of Experimental Biology*, 209, 2050–2063.
- Matthysen, E. (2012) Multicausality of dispersal: A review. *Dispersal Ecology and Evolution*, 27, 3–18.
- O'Mara, M.T., Wikelski, M., Kranstauber, B. & Dechmann, D.K.N. (2019) First three-dimensional tracks of bat migration reveal large amounts of individual behavioral flexibility. *Ecology*, 100, 1–4.
- Owen-Smith, N. (1979) Assessing the foraging efficiency of a large herbivore, the kudu. *African Journal of Wildlife Research*, 9, 102–110.
- Papageorgiou, D., Christensen, C., Gall, G.E.C., Klarevas-Irby, J.A., Nyaguthii, B., Couzin, I.D. et al. (2019) The multilevel society of a small-brained bird. *Current Biology*, 29(21), R1120–R1121. <https://doi.org/10.1016/j.cub.2019.09.072>.
- Pyke, G.H. (1981) Optimal travel speeds of animals. *The American Naturalist*, 118, 475–487.
- R Core Team (2020) *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.
- Sawyer, H. & Kauffman, M.J. (2011) Stopover ecology of a migratory ungulate. *Journal of Animal Ecology*, 80, 1078–1087.
- Shepard, E.L.C., Wilson, R.P., Rees, W.G., Grundy, E., Lambertucci, S.A. & Vosper, S.B. (2013) Energy landscapes shape animal movement ecology. *The American Naturalist*, 182, 298–312.
- Tarwater, C.E. & Brawn, J.D. (2010) Family living in a Neotropical bird: Variation in timing of dispersal and higher survival for delayed dispersers. *Animal Behaviour*, 80, 535–542.
- Taylor, C.R., Heglund, N.C. & Maloiy, G.M. (1982) Energetics and mechanics of terrestrial locomotion. I. Metabolic energy consumption as a function of speed and body size in birds and mammals. *Journal of Experimental Biology*, 97, 1–21.

- Taylor, C.R., Schmidt-Nielsen, K. & Raab, J.L. (1970) Scaling of energetic cost of running to body size in mammals. *American Journal of Physiology-Legacy Content*, 219, 1104–1107.
- Van Dyck, H. & Baguette, M. (2005) Dispersal behaviour in fragmented landscapes: Routine or special movements? *Basic and Applied Ecology*, 6, 535–545.
- Visser, I. & Speekenbrink, M. (2010) depmixS4: An R Package for Hidden Markov Models. *Journal of Statistical Software*, 36, 1–21.
- Wheatley, R., Buettel, J.C., Brook, B.W., Johnson, C.N. & Wilson, R.P. (2021) Accidents alter animal fitness landscapes. *Ecology Letters*.
- Wikelski, M., Moskowicz, D., Adelman, J.S., Cochran, J., Wilcove, D.S. & May, M.L. (2006) Simple rules guide dragonfly migration. *Biology Letters*, 2, 325–329.
- Wikelski, M., Tarlow, E.M., Raim, A., Diehl, R.H., Larkin, R.P. & Visser, G.H. (2003) Costs of migration in free-flying songbirds. *Nature*, 423, 704.
- Woollard, T. & Harris, S. (1990) A behavioural comparison of dispersing and non-dispersing foxes (*Vulpes vulpes*) and an evaluation of some dispersal hypotheses. *Journal of Animal Ecology*, 59, 709.
- Wronski, T. (2002) Feeding ecology and foraging behaviour of impala *Aepyceros melampus* in Lake Mburo National Park, Uganda. *The African Journal of Ecology*, 40, 205–211.
- Yoder, J.M., Marschall, E.A. & Swanson, D.A. (2004) The cost of dispersal: Predation as a function of movement and site familiarity in ruffed grouse. *Behavioral Ecology*, 15, 469–476.
- Zeller, K.A., McGarigal, K. & Whiteley, A.R. (2012) Estimating landscape resistance to movement: A review. *Landscape Ecology*, 27, 777–797.
- Zollner, P.A. & Lima, S.L. (2005) Behavioral tradeoffs when dispersing across a patchy landscape. *Oikos*, 108, 219–230.

## SUPPORTING INFORMATION

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

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