Habitat selection during dispersal reduces the energetic cost of transport when making large displacements

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Abstract

When dispersing, individuals typically have to make large displacements. While previously thought to be costly, recent work has suggested that individuals can largely mitigate these costs by expressing distinct movement strategies—moving faster and straighter—during dispersal. Several studies have also found that individuals express differences in their habitat preferences during dispersal. These preferences often involve an increased use of open habitats relative to their non-dispersing habitat selection, within which individuals typically achieve larger displacements per unit of time. As a result, it has been suggested, but never explicitly tested, that changes in habitat selection could reflect an increased preference for habitats that facilitate greater energetic efficiency in terms of movement. Here, we combine

step-selection analysis with models of the energetics of movement to determine whether actively dispersing vulturine guineafowl (*Acryllium vulturinum*) select different habitats relative to their non-dispersing counterparts, and whether their habitat preferences correspond to a decrease in the cost of transport. Our results confirm that fine-scale differences in habitat preferences expressed when making large displacements during the transient stage of dispersal correspond with an increase in the energetic efficiency of movement. These findings highlight the ability for animals to exhibit adaptive movement strategies across different axes of decision-making (e.g., where and how to move) to overcome different ecological challenges.

Introduction

Dispersal is a complex, and often costly process. In order to disperse successfully, individuals must navigate through complex and heterogeneous habitats, both in terms of locating suitable habitats to settle into (Reed et al., 1999; Stamps, 2001) and also when traversing environments between their departure and settlement points (Clobert et al., 2009; Zollner & Lima, 1999). A growing body of literature has investigated the question of how habitat preferences differ during the active phase of dispersal (transience). For example, individuals disproportionately select habitats during dispersal based on factors such as risk (Scrafford et al., 2018; Theuerkauf & Rouys, 2008) or resource availability (Killeen et al., 2014; Ward, 2005). It has also been hypothesized that transient individuals select habitats based on differing costs in terms of time or energy, in particular prioritising low cost and high gain habitats during dispersal (Long et al., 2016).

For most species, dispersing requires individuals to make large displacements. However, while it was long assumed that making these large displacements necessarily invokes an increase in energetic expenditure (Bonte et al., 2012; Van Dyck & Baguette, 2005), recent work has shown that distinct movement strategies can largely mitigate increases in the energetic cost of transport—i.e., the energy consumed to move a given distance—during dispersal. Specifically, by moving faster and straighter, dispersing individuals can achieve much greater displacements with only minimal increases in the total cost of transport relative to their daily ranging movements when not dispersing (Klarevas-Irby et al., 2021). While movement speed and path

directedness can be shaped by the movement decisions of individuals, characteristics of the habitat, such as vegetation density, are also likely to determine the ability for individuals to express these movement characteristics (Gallagher et al., 2017; Shepard et al., 2013). For example, dispersing African wild dogs (*Lycaon pictus*) typically make larger 'steps' or more directed movements in open (e.g., grassland) versus closed (e.g., woodland) habitats (Hofmann et al., 2023), a pattern that is mirrored in several other species (e.g., elk *Cervus elaphus,* Killeen et al., 2014, and red squirrels *Sciurus vulgaris,* Hämäläinen et al., 2019). However, while habitat preferences expressed during transience may allow individuals to mitigate increased costs of transport associated with making large displacements, the link between habitat selection and cost of transport remains to be explicitly tested.

Here we use high-resolution GPS tracking in a wild population of vulturine guineafowl (*Acryllium vulturinum*) to assess (i) the habitat preferences by dispersing individuals, and (ii) quantify how these preferences correspond to the cost of transport associated with making large displacements. Vulturine guineafowl live in large groups varying in size from 13 to 65 individuals. Being almost exclusively terrestrial, vulturine guineafowl disperse by walking up to 15 km per day, doing so mostly alone (Klarevas-Irby et al., 2021). When dispersing, individuals traverse a mixture of savannah scrub, open grassy areas, and roads, all habitat features that are similar to those present in the home range of their natal group. Dispersal in vulturine guineafowl is therefore ideal for analysing habitat selection when dispersing as we can draw direct comparisons to their preferences when not dispersing. Guineafowl are also a model system for physiology, with detailed data available on their energetic expenditure when walking at different speeds (Ellerby et al., 2003). Previous work combining physiological models with second-by-second movement data has revealed that, when dispersing, individuals experienced only an average 4.1% increase in the daily cost of transport relative to their normal daily ranging behaviours, despite achieving an 33.8% increase in displacement (Klarevas-Irby et al., 2021). This leads us to our two key questions, whether (i) vulturine guineafowl express distinct preferences for specific habitat features when dispersing, and (ii) whether these features correspond to a lower energetic cost when traversing them. We predict that vulturine guineafowl should show a disproportionate preference for open habitats (e.g., grassy areas, bare soil, and roads) during dispersal relative to making non-dispersal movements, and that these habitats will correspond to a lower average cost of transport.

Methods

Overview

Our study consists of four components.

1. We fitted GPS tags to subadult vulturine guineafowl and to adults from their natal group, from which we extracted periods of high-resolution (1 Hz) GPS data on the position of each bird.
2. We used remote sensing to extract features of habitats through which both resident and dispersing individuals moved.
3. We used a step-selection analysis (SSA) (Avgar et al., 2016) framework to infer the habitat preferences of individuals, which we split across three categories: transience, non-transience, and resident adults (time-matched to the periods of transience).
4. We combined information on energy expenditure as a function of movement with the high-resolution GPS data of individuals moving through each habitat type to quantify the average efficiency (the cost of transport for a given displacement) of the habitat types.

We performed all analyses in R version 4.3.1 (R Core Team, 2022).

Study System

This study was conducted at the Mpala Research Centre in Laikipia county, central Kenya (0.29120 N, 36.898670 E). The research centre is part of the Mpala Conservancy, covers an area of roughly 200 km^2 in size and is part of the Greater Ewaso Ecosystem (Winowiecki et al., 2018). However, because vulturine guineafowl disperse outside of Mpala, our study extends beyond these boundaries to cover approximately 769 km^2. Within this broader study area, the landscape contains a heterogeneous mix of habitat, which can broadly be divided into three major types. In the more elevated areas, we find a type of clay vertisol commonly known as "black cotton" soil (Young et al., 1998) and its dominant tree species the whistling thorn (*Acacia drepanolobium*). On the lower part of the escarpment typical "red soils" which contain a mixture of denser Acacia scrub and open glades as well as riverine habitats with fever trees (*Vachellia xanthophloea*) are present (Young et al., 1995). Both major habitat types are crossed by numerous roads and smaller vehicular tracks.

Our study on vulturine guineafowl has been running since 2016 (Papageorgiou et al., 2019). The present study, however, relies on a shorter, more focused, period— September 7th to November 25th, 2019—during which we had fitted GPS tags (see below) to female vulturine guineafowl that were still in their natal group. Previous work using this GPS-tagged cohort, together with field observations, has suggested that dispersal is exclusively done by females, is typically solitary, and occurs around two years of age (Klarevas-Irby et al., 2021). However, because dispersing guineafowl do not form new groups but disperse between existing groups (Papageorgiou et al., 2019), they often fail to settle into a new group (due to social resistance, *sensu* Armansin et al., 2020) and return to their natal group. They can remain in their natal group for several months before trying again. There are typically two dispersal seasons per year, corresponding to the major and minor wet seasons, of which our study fell into the minor wet season of 2019. As the study cohort is part of a larger, GPS-tracked population, we studied the movements of both dispersing individuals and non-dispersing resident members of their natal group during the same time period. In doing so, we can compare movements under the same environmental conditions and assess whether there are differences in the types of habitats selected.

Research permits

Work was conducted under a Research Authorisation (KWS-0016-01-21) and a Capture Permit issued by the Kenyan Wildlife Service, research authorisations from the Wildlife Research and Training Institute, and in affiliation with the National Museums of Kenya. Further research permits were granted by the Max Planck Society Ethikrat Committee (2016_13/1), the National Environment Management Authority (NEMA/AGR/68/2017) and the National Commission for Science, Technology and Innovation of Kenya (NACOSTI/P/16/3706/6465, NACOSTI/P/21/8699).

<u>Field data collection</u>

As part of the long-term study, birds are captured using baited walk-in traps, allowing us to trap the entire group at once. All individuals are subsequently marked on their legs with a uniquely numbered stainless-steel ring and a distinct combination of four plastic colour bands, allowing individual identification in the field. Within each group, we also select individuals (typically 2-4 resident adults of both sexes) to be fit with a 15g Bird Solar GPS tag from e-obs

GmbH using a backpack-type harness (see Papageorgiou et al., 2019 for more details). For the purpose of studying dispersal, an additional 18 dispersal age females were fitted with GPS tags, from four social groups, which were complemented by 13 resident GPS-tagged adults (9 males, 4 females). The combined weight of backpacks, tags, and leg markings is less than 3% of birds' body weight.

Tags are programmed to record fixes from 06:00 to 19:00 local time (corresponding to daylight hours when the birds are active). Fix data (date, time, and location) are recorded at two resolutions: continuous high-resolution (i.e., 1Hz) data is recorded when tag batteries have a high level of charge (up to 4.5h continuous recording, approximately every second to third day), and at a lower resolution—collecting a 10-second burst of 10 fixes every five minutes—when battery levels fall below the high-resolution threshold. He et al., (2023) provides further details on the strategy behind this sampling design. GPS data are uploaded to the Movebank repository (https://www.movebank.org) for remote storage and retrieved and prepared for analysis in R through the move package (Kranstauber et al., 2023). For the purposes of this study, we use only the high-resolution data for the analysis of habitat selection and to quantify the cost of transport in each habitat type.

Dispersal

For this study, we defined three stages of dispersal (departure, transience, and settlement) in the GPS tracking data based on several key features. Birds were considered to have departed (i.e., to have started dispersing) on the first date when their GPS tracks diverged from those of the resident adults in their natal group. Dispersers were subsequently considered to have settled in a new area following a period of two weeks in which they consistently used the same roosting site (at which point settlement was back-dated to the first date in which they entered the new roost). Where possible, all departure and settlement events were confirmed by both visual observation of the GPS tracks as well as field observations of guineafowl groups. All GPS data between the departure and settlement dates for each individual were then treated as transience. In 11 cases, we were unable to record settlement—either due to dispersers failing to settle a new group and returning to the natal group after a period of several weeks (3 events), due to instances of predation during transience (1 event), because the dispersing individual moved far enough from the study area that the tag could not be relocated for downloading data (6 events), or due to the harness failing and the tag falling off during

transience (1 event). In these cases, all transience data up to the available end point were used. As this study focused on the habitat selection behaviours of actively dispersing birds, all pre-departure and post-settlement GPS data were excluded from our analyses. In order to facilitate comparisons to non-dispersing residents, we included date-matched GPS data for each transient individual from all available resident adults of each dispersers' natal group.

From our field observations, we noted that transience movements are not uniform over time, but differentiated into two distinct daily patterns. The first category involves birds making large roost-to-roost displacements, which reflects the typical movements of active dispersal that is characterized by extended periods of long, straight movements across the landscape. The second involves movements that take place over much smaller local scales (often without changing roosts from morning to evening) and typically consists of more tortuous paths. Field observations suggested that these local movements are the result of dispersers temporarily joining and moving with groups other than their natal group for one or more days before resuming making large displacements (first category). As a result, we split the daily data during the transience period of each bird into the two categories based on the straightness and the length of each day's movement path. Specifically, an individual was considered to have engaged in large, active dispersal movements if the distance between their morning and evening roost exceeded 1500m, or else if the roost-to-roost distance was greater than 1200m and the ratio of this distance to their total daily track length (i.e., a straightness index, Batschelet, 1981) was greater than 0.3 (Klarevas-Irby & Farine, 2023). Sub-categorizing the movements of transient individuals in this way allows us to better disentangle the habitat preferences of actively dispersing birds from the overall effect of being transient, and compare each to the preferences of non-dispersing residents.

Environmental Data Collection

To measure and define the overall habitat composition of our study area, we downloaded satellite imagery from the Planet Explorer by Planet Labs (Planet Team, 2017). The boundary of our satellite data was selected such that all GPS tracking data fell inside a bounding box, which was then used to build the base geometry for the search and download of suitable satellite imagery. We selected the PlanetScope Scene imagery from the 3rd of November 2019 (resolution: 3 m, area coverage: 94%), as it best satisfied our criteria (maximum area coverage,

no cloud coverage) within the period when we recorded the majority of our recorded dispersal events. Satellite imagery was then prepared and processed for analysis in ArcGIS' ArcMap 10.6.1. (ESRI, 2011). The satellite images were georeferenced and the created habitat layers were projected to WGS84 UTM Zone 37N (EPSG: 32637). We also used a digital elevation model (DEM) from the Open Data Site of the Regional Centre for Mapping of Resource for Development (opendata.rcmrd.org) with a spatial resolution of 30m to calculate a Terrain Ruggedness Index (TRI) which quantifies topographic heterogeneity (Riley et al., 1999).

Defining Environmental Categories

We represented the landscape of the study system using four categories: roads, water bodies, elevation difference and cover type. Roads and water bodies are both binary variables, meaning for these two categories that all classified pixels contained either presence (1) or absence (0) for every pixel. Elevation difference (continuous) was represented by a digital elevation model (DEM) and a terrain ruggedness index (TRI). TRI values were calculated by taking the DEM values from a centre cell and the differences to its surrounding eight neighbour cells (we ground-truthed the DEM by measuring elevation at 24 locations in the study area). The differing values to each of the eight neighbour cells were then squared, summed up and subsequently square rooted (Riley et al., 1999). Cover types include five different habitats (see below).

As no road network layer was available for our study area, we manually marked roads as polylines. With our spatial resolution of 3 m it was not always easy to distinguish between smaller or older/abandoned roads and animal paths. Thus, we opted for including roads that were distinguishable through visual inspection of our satellite data and Google Earth. As most roads are between 4 and 10 m wide, we defined roads as polygons which extended 15m to either side of the center of each polyline (thus allowing for GPS positional errors when capturing movement along roads). All of the roads are gravel rural roads, with no heavy-use roads present in the area.

For the water bodies, we proceeded in the same way as for the roads to obtain the rivers (also buffering 15 m on each side). Ponds, dams and small lakes were drawn as polygons and merged with the river features. Water pixels could be distinguished from other landscape features based on their reflection in false colour infrared or in the NDVI. The main component for the water bodies layer in our study area is the Ewaso Ng'iro river and some of its side channels.

There can also be found a few ponds, small lakes and dams, the largest being a dam on the nearby Ol Jogi reserve with an area of 0.3 km^2.

Utilizing the satellite data's cover layer, we categorized all remaining habitats into five different cover types. Categorization was done using the false colour infrared band combination and was then compared to Google Earth scenes with higher spatial resolution and true colour. black cotton soils, due to their dark colour, were easily detectable as dark tones in the false colour infrared spectral combination. Glades (open grassy areas) appeared in vivid red in the same band combination, which is due to the higher chlorophyll content found in the plant species on open glades (given that green reflectance shows as red in false colour infrared) compared to surrounding vegetation. Bare soil represents sandy patches with little to no vegetation and was distinguishable through its white pixel colouring. The largest habitat proportion in our study area is dense acacia scrub on red soil. This acacia scrub mainly appears in a dark reddish colour, indicating its lower chlorophyll content compared to glades. Finally, Riverine Habitat consists of a 50m buffer zone along the rivers.

Step Selection Analysis

We used a step selection analysis (SSA) to assess how landscape features influence movements of dispersing and resident vulturine guineafowl. This type of analysis uses positional data, and movements from one location to another, to generate movement steps. Each of these observed step (two consecutive relocations) is then matched with a chosen number of alternative steps (Avgar et al., 2016) that represent plausible alternative locations in which the individual could have moved (given the properties of its movements). The environmental features are then compared between the observed and alternative steps to identify which are over-represented in the observed steps. Step selection analysis has been proposed to be the most suitable method when trying to infer habitat selection from animal tracking data (Avgar et al., 2016; Mercker et al., 2021). We used of the 'amt' package (Signer et al., 2019) in R to conduct our step selection analysis.

Spatial Discretization of Steps

Working within our high-resolution (i.e., periods of continuous 1Hz data) GPS dataset (for both dispersers and residents), we divided each continuous track into spatially-discretized steps.

While temporal discretization is often used for analyses of habitat use (Thurfjell et al., 2014), spatial discretization records locations in a constant spatial rate, facilitating our focus on where an animal moved rather than on the timing of movement (Strandburg-Peshkin et al., 2017). In this way, the resulting step selection model is less affected by periods of no to very little movement. To get spatially discretized movement data, we used the first location from each GPS track and set it as starting point of the trajectory. For each successive time point (current location of the bird) we calculated the net displacement (or Euclidian) distance to the first location, until reaching a threshold radius of 50 meters was reached, which we marked as the end of the step. We then marked the next time point as the start of a new step, and repeated the process for the rest of the track. The product is a dataset containing relocations approximately every 50 meters which also contains data on the movements between each relocation. Although our threshold was set at 50m, the true length of a step often slightly exceeded this (owing to the temporally discrete sampling of our tags), and so we took the distribution of true step lengths into account when generating alternate steps for our analyses. In total, our spatial discretization resulted in a dataset of 3,473 observed steps. However, because multiple consecutive steps are required to assign a turning angle to a given step, our final observed step dataset consisted of 2,034 observed steps for which we had information on both step length and turning angle.

Generating Alternate Steps

For each observed step, we recorded the true step length (in meters) as well as the turning angle between consecutive steps (in radians) and the duration (in seconds) between the first and last fix of that step. The distributions of these values (Figure S1) were subsequently used to generate a series of randomized alternative steps for our SSA. We subset all observed 50 m steps belonging to the same continuous high-resolution burst and then for each subset, fit a uniform distribution to the observed turning angles and step lengths (Fieberg et al., 2021). For each observed step, we generated 20 alternative steps based on the resulting distributions of step lengths and turning angles (for our observed steps).

Linking Steps to Habitat Features

Using the ‘raster’ package (Hijmans, 2022) in R, we combined our dataset of observed and alternate steps with our environmental covariates. We first imported all our environmental raster layers which we prepared above and then projected our step locations onto them. For

each step, we extracted the relevant environmental covariates from the raster cell which contained the endpoint of that step. The one exception to this rule was for measuring elevation, where we extracted the absolute difference in elevation between the start and endpoint of each step. From each elevation change measure, we then derived a gradient measure which indicated whether a step moved "uphill" or "downhill" (depending on whether the change in elevation was positive or negative). For each step in our dataset, time of day was also included as a covariate as a factor with three levels (morning, day, and evening, corresponding to 06:00-09:00, 09:00-16:00 and 16:00-19:00, respectively).

Fitting a Step Selection Function

Using the R package 'amt', we fit a wrapper function of a conditional (fixed-effects) logistic regression for matched case-control (observed vs. alternative step) data using the R package 'survival' (Therneau, 2020). We fit the conditional logistic regression using the same routine as a Cox Proportional Hazards model (Signer et al., 2019). Each observed step and its matching 20 alternatives formed a stratum together. Our main effects in the model were the environmental covariates: water bodies, roads, cover type, and terrain ruggedness. We included all these environmental covariates as interactions with a three-level factor—actively-dispersing transient, local transient, and resident. We included these interactions to test for whether habitat selection differs between resident and transient birds, and between the two observed transient movement patterns within transient birds.

<u>Estimating Energetic Cost of Transport per Habitat and 50m Step</u>

We quantified differences in the energetic cost of transport as a means of assessing the energetic efficiency of movement within each of our defined habitat types and landscape features. First, we sub-sampled our dataset of observed steps for all instances in which the start and endpoint of a given step were within the same habitat or landscape feature, operating under the assumption that individuals moved through continuous habitat between the two points. If the step took place on a road, we defined the category as "road" for this analysis, independent of the habitat cover type that the road crossed. For all other categories, the cover type of the step was used as the categorical label. For each high-resolution fix within a given step, we first derived the metabolic cost of movement (in mL O2 kg^{-1} s^{-1}) at each second based on the relationship between the speed (m s^{-1}) and metabolic costs of movement in the

morphologically similar and closely related helmeted guineafowl (*Numida meleagris*) (Ellerby et al., 2003). Metabolic costs were assigned at each second according to two formulas, depending on whether or not the individual was actively moving (movement was assigned according to the outputs of a 4-state Hidden Markov Model parameterized on 10-second step lengths and turning angles, which was first derived as part of Klarevas-Irby et al., 2021). When stationary, birds were assigned a flat rate of oxygen consumption of 19.1 mL O2 kg^{-1} min^{-1} and, when moving, the rate of oxygen consumption followed the formula VO2 = 24.0v + 27.2, where VO2 is the per-minute rate of oxygen consumption (mL O2 kg^{-1} min^{-1}) and v is velocity-while-moving (in m s^{-1}). The per-second measures of oxygen consumption were then transformed into units of energetic consumption (Joules kg^{-1} s^{-1}) using a conversion factor of 20.1 J mL^{-1} O2 (Ellerby et al., 2003; Marsh et al., 2006). To calculate the cost of transport (i.e., per-unit-distance energy expenditure, in Joules kg^{-1} m^{-1}) for each observed step, the total per-second energetic costs within that step were summed and then divided by the net displacement distance of the step.

To investigate the effect of habitat type on the energetic cost of transport, we fit a linear mixed-effect model (LMM) with the cost of transport for each observed step as the response variable and habitat type as the predictor, with roads as the reference category. Categorical label (i.e., active transient, local transient, or resident), individual identity, and date were fit as crossed random effects. Subsequently, we generated confidence intervals for our model's estimates as the 95% quantiles of the outputs of one thousand bootstrapped and re-modelled iterations of our dataset.

Results

Dispersal Data

We recorded a total of 6,649,730 GPS fixes from 31 individuals, from which we used 2,034 segments of 50m net displacements (i.e., observed steps). The majority of the steps in our dataset came from transient birds making large, active dispersal movements (51.5%), followed by local transient movements (28.5%), and non-dispersing residents (20%). Generating 20 alternative steps for each observed step resulted in a total of 42,714 50m steps, of which we removed 547 (26 observed steps and 521 alternate) where no value could be assigned to one of the environmental covariates at the endpoint of the step (empty data), leaving 42,168 steps

(2,008 observes) used for the Step-Selection Model. On average, individuals made a 50m step in 2 minutes (range: 4.2 s to 10.4 min).

Habitat availability

Acacia scrub represents the largest component of cover within our study area (Fig. 1), occupying approximately 73 % of the area, followed by black cotton (19 %), bare soil (5.2 %), riverine (2.1 %) and glades (0.7%). For the different cover types, we recorded no steps on black cotton soil (0 %), with the majority of steps (86.3 %) in acacia scrub, followed by glades (8.6 %), bare soil (3.6 %), riverine (1.5 %). Of all the observed steps, 189 (9.3 %) were recorded on roads and 11 (0.55 %) at water bodies.

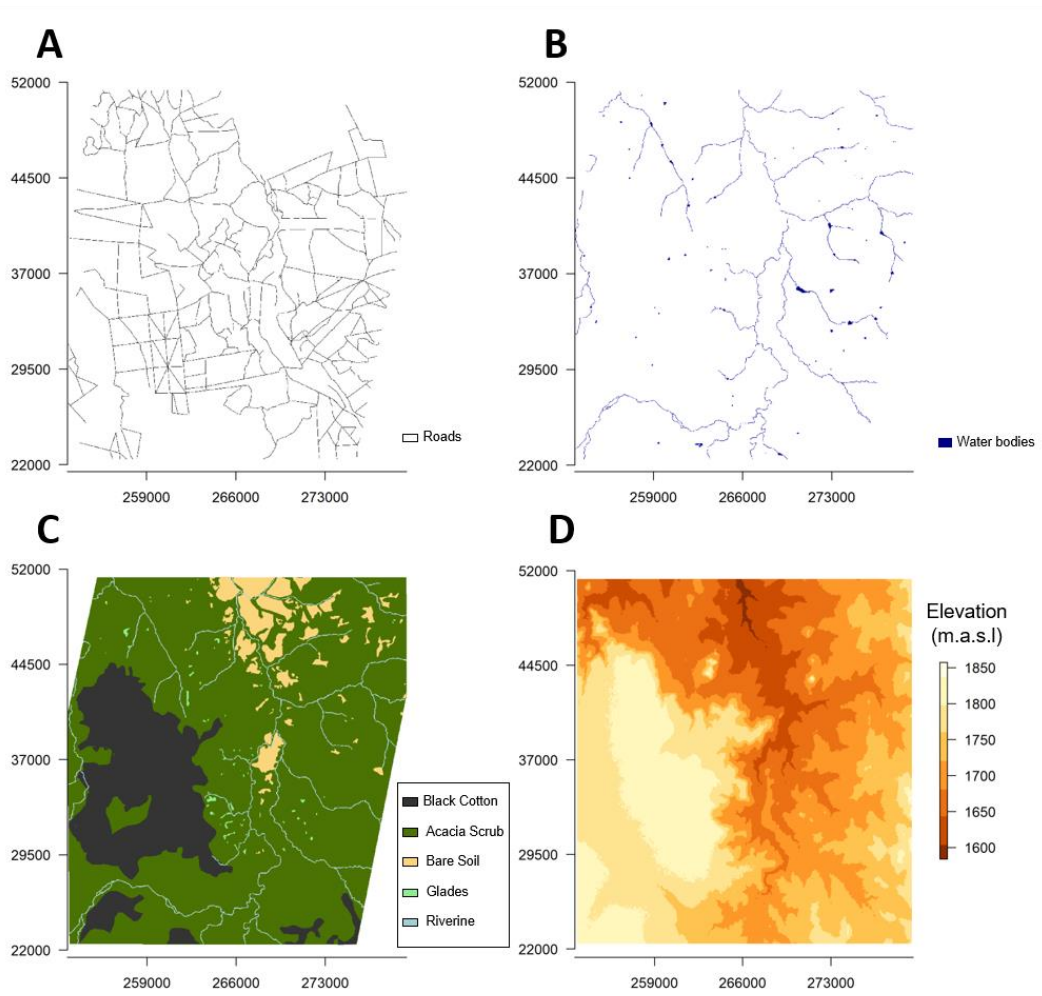


Figure 1: Raster layers of habitat covariates across our study area. Habitats were classified according to the presence of roads (A) and waterbodies (B), as well as by predominant cover type (C) and elevation (D) in meters above sea level. Axes show Universal Transverse Mercator (UTM) coordinates.

Habitat Selection

We found distinct differences in habitat selection by transient birds versus residents, and across different types of transience behaviours (Fig. 2; full model results available in Table S1). During days when transient birds made large displacements, they expressed significant positive selection for roads ($\beta = 1.29$, 95% CI = 0.87 to 1.72, $p < 0.001$), glades ($\beta = 1.97$, 95% CI = 0.37 to 3.57, $p < 0.05$), and acacia scrub ($\beta = 1.59$, 95% CI = 0.20 to 2.97, $p < 0.05$). Further, transient birds expressed a negative, but not significant, selection for areas surrounding water bodies ($\beta = -1.81$, 95% CI = -3.65 to 0.04, $p > 0.05$) and no significant preference for bare soil ($\beta = 1.35$, 95% CI =-0.35 to 3.06, $p > 0.05$), or based on terrain ruggedness ($\beta = 1.00$, 95% CI = -0.62 to 2.62, $p > 0.05$). When making smaller, local movements, transient birds expressed a similar preference for moving along roads ($\beta = 0.62$, 95% CI = 0.19 to 1.04, $p < 0.01$) but avoided areas of acacia scrub ($\beta = -1.8$, 95% CI = -3.00 to -0.70, $p < 0.01$). Transient birds showed no preference towards glades ($\beta = -1.01$, 95% CI = -2.38 to 0.36, $p > 0.05$) or water bodies ($\beta = -0.27$, 95% CI = -1.63 to 1.08, $p > 0.05$) during local movements, while rugged terrain ($\beta = 0.06$, 95% CI = -2.07 to 2.18, $p > 0.05$) was again not important in their movement decisions. Non-dispersing, resident individuals from the natal groups of dispersers, on the same days as the dispersers were transient, showed a strong preference for glades ($\beta = 3.07$, 95% CI = 1.02 to 5.17, $p < 0.01$), but no preferences for or against other habitat types (including roads and bare soil) or based on terrain ruggedness. The only steps made into bare soil habitats came from transient birds on days of large displacements, and no such data were available for local transience movements or from non-dispersing residents.

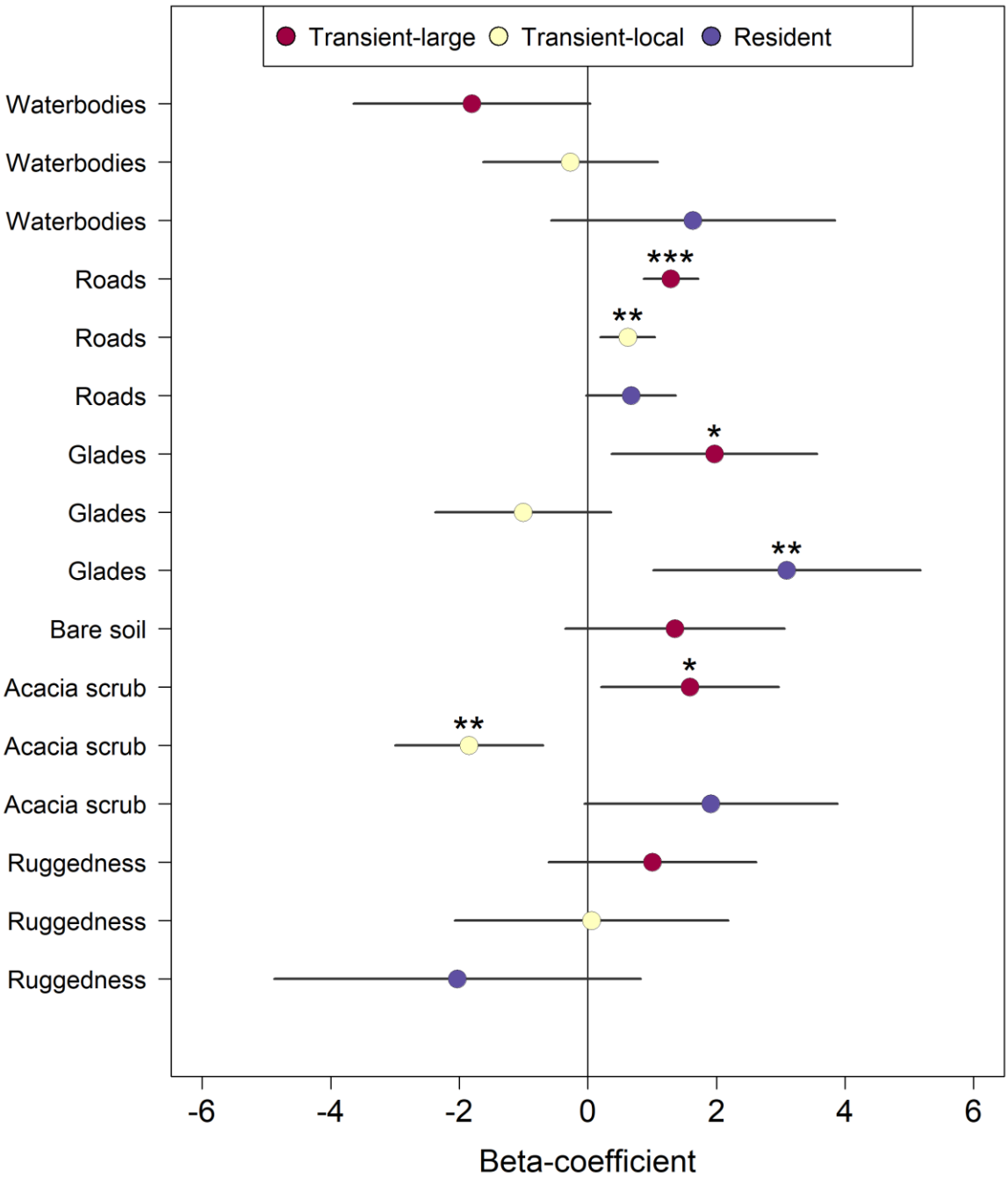
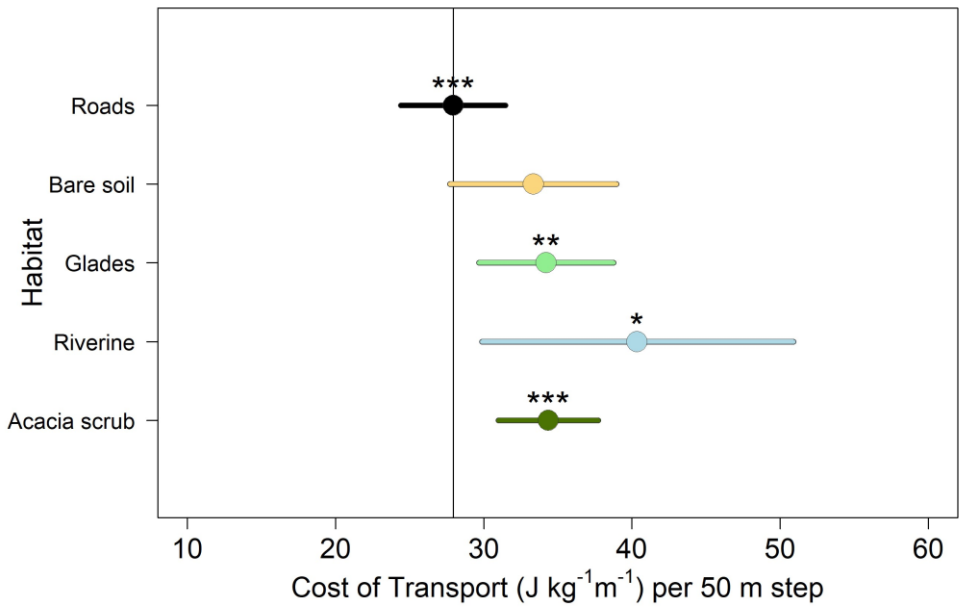


Figure 2: Estimated selection coefficients for each habitat covariate according to stage. Points represent estimated beta-coefficient values from our step-selection analysis. Horizontal lines represent 95% confidence intervals, indicating strength of habitat selection preferences for (where $\beta > 0$) or avoidance of (where $\beta < 0$) a given habitat type. Stages correspond to: transient dispersers when making large displacements (Transient-large, red), transient dispersers when moving locally (Transient-local, yellow), and non-dispersing residents (Residents, purple). Stars above a point indicate the statistical significance (*** *p<0.001*, ** *p<0.01*, **p<0.05)* of a given estimate.

418 Energetic efficiency in different habitats

419 When travelling on roads, individuals averaged a significantly lower energetic cost of transport
420 compared to other habitats (intercept term: $\beta = 27.95$ J $kg^{-1}m^{-1}$, 95% CI = 25.82 to 31.52). Bare
421 soil showed the second lowest cost of transport ($\beta = 33.36$, CI = 29.04 to 39.24, $p > 0.05$), but
422 was statistically comparable to roads. Relative to roads, acacia scrub ($\beta = 34.36$, CI = 32.11 to
423 36.69, $p < 0.001$) and glades ($\beta = 34.21$, CI = 29.77 to 38.65, $p < 0.01$) had significantly higher
424 costs of transport. Riverine habitat had the highest energetic costs of transport ($\beta = 40.35$, CI
425 = 29.03 to 50.39, $p < 0.05$), although it also had a much lower sample size than the other
426 covariates. These differences in cost of transport translate to substantial differences in the
427 efficiency of movement (Fig. 3; full model results available in Table S2). Compared to the most
428 efficient habitat type—roads— birds displacing on bare soil came with an average increase of
429 19 % higher energetic costs for the same net distance (50m), with slightly greater increases in
430 energy expenditure for glades (22%) and acacia scrub (23% more), and the highest in riverine
431 habitats (44% more).



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433 **Figure 3: Changes in the energetic efficiency of movement according to habitat type during dispersal.**
434 Circles show estimates from linear mixed-effect model (LMM) of the energetic cost of transport per 50
435 m net displacement across habitat type (coefficient ± 95% confidence intervals) with significance (stars
436 above points: *** *p<0.001*, ** *p<0.01*, **p<0.05*) using roads as the reference category.

437

Discussion

Our study revealed significant shifts in habitat preferences by terrestrial birds during dispersal, with actively dispersing individuals showing greater preferences for habitats that correspond with a decrease in the cost of transport. Specifically, when vulturine guineafowl were more likely to select open habitat types, namely roads and glades, relative to vegetated acacia scrub and riverine habitats when making large displacements. These preferences correspond to the habitat types with the lowest average cost of transport (i.e., where birds can exhibit the most energetically-efficient movements). Our results therefore provide support for the hypothesis that changes in habitat preference expressed by animals during dispersal could be the product of selective pressures acting on the need to achieve large displacements in an energetically efficient manner.

In many species, the factors governing habitat selection and movement are the result of trade-offs between energetic efficiency and risk (Fahrig, 2007; Vásquez et al., 2002). A number of studies in large mammals (Dickie et al., 2017, 2020; Dickson et al., 2005; Roever et al., 2010; Strandburg-Peshkin et al., 2017) have found that individuals express preferences for linear landscape features, such as roads, during periods when they make larger displacements. For example, groups of olive baboons (*Papio anubis*) preferentially move along roads in the morning and evenings, when moving away from, and back to, their sleeping site (Strandburg-Peshkin et al., 2017). However, roads can also represent areas of higher disturbance and mortality risk (i.e., due to vehicle strikes), leading to a number of studies reporting avoidance of roads (Prokopenko et al., 2017; Scrafford et al., 2018; Sunga et al., 2017). In our study, we found that transient, dispersing individuals expressed a strong preference for moving along roads, especially during days where they were actively displacing across the landscape, while non-dispersing residents neither preferred nor avoided roads. Some of the differences between studies could represent the relative risk that road present. At our study site (the same area as the baboon study by Strandburg-Peshkin et al., 2017), most roads consist of infrequently used dirt tracks with irregular and low-speed traffic, meaning that the mortality risks to guineafowl is quite low (in eight years of following a population of 600-1000 birds, we know of only two birds killed by vehicles). By contrast, the potential gains in efficiency are high, both because roads allow individuals to move faster but also because they efficiently traverse habitat in a very direct manner. This is evident in birds experiencing a lower energetic cost of transport when moving along roads than in any other habitat in our study.

Besides roads, actively dispersing guineafowl also preferentially selected other open habitats, such as glades, when making large displacements. Our results also show a positive selection coefficient for bare soils, although this was not significant. Of note, bare soils were never used by non-dispersing individuals (i.e., residents in the dispersers' natal groups), likely because they generally correspond to areas with little to no suitable foraging habitat. By contrast, residents also showed a strong preference for glades, which are commonly used by vulturine guineafowl for foraging (Papageorgiou et al., 2019; Papageorgiou & Farine, 2020). Our data suggest that it is quite likely that, even when actively dispersing, individuals used glades for a mixture of active movement and foraging. This is because glades showed a significant increase in the cost of transport (22 %) relative to roads. While this difference could be attributed to a reduction in the directedness of movement that they can achieve on glades (relative to roads), we also found that the cost of transport was slightly higher than on bare soil, which should afford the same benefits in term of speed and directedness (as the grass is always quite short due to heavy grazing pressure). However, when combined with the observed preferences for roads and at least some movements in bare soils, especially during the more active periods of dispersal, our findings confirm that the energetic benefits that these habitats confer are likely to play an important role in their selection.

In addition to changing the energetic profile, the openness of the habitat is also likely to shape predation risk. In group-living species, individuals can substantially benefit from collective detection of predators (i.e., the many eyes hypothesis, Lima, 1995), which is likely to play a major role in the evolutionary ecology of vulturine guineafowl. Vulturine guineafowl are large and colourful, and live in a predator-rich environment that includes a full range of terrestrial (e.g., leopard *Panthera pardus*) and aerial (e.g., martial eagle *Polemaetus bellicosus*) predators. Of these, aerial predators are likely to be particularly risky for vulturine guineafowl. In fact, the only predation event we recorded during the active phase of dispersal was by a martial eagle. The risk of aerial predators was also captured by a previous study (Klarevas-Irby & Farine, 2023) finding that dispersers avoid making large movements during the middle of the day when theses predators are most active. Thus, if using open habitats introduces even more risk for individuals during the active phases of dispersal, which almost always make large displacements alone, this strengthens the support for the energy efficiency hypothesis.

Our study provides largely complementary evidence on habitat preferences during dispersal, and substantially extends previous work by explicitly quantifying the energetic benefits. Our

502 methodology—specifically the comparisons made within dispersers and to time-matched
503 residents—also allows us to generate particularly robust conclusions. Previous work has
504 typically compared the dispersal period to the habitat preferences of the same individuals
505 prior to dispersing (e.g., Mabry & Stamps, 2008; Miller et al., 1997). However, in many systems,
506 such as buzzards (*Buteo buteo;* Walls et al., 2005) and wolves (*Canis lupus;* Kojola et al., 2006),
507 the timing of dispersal is also linked to changes in ecological conditions (Shaw, 2020; Studds et
508 al., 2008). For example, in the vulturine guineafowl, dispersal is linked to periods of greater
509 rainfall (Klarevas-Irby & Farine, 2023), which is also likely to alter habitat conditions. However,
510 because vulturine guineafowl remain in temporally stable groups when not dispersing (see
511 Ogino et al., 2023), we can directly contrast the habitat preferences that individuals express
512 during dispersal to the habitat preferences that they would express (as part of their group)
513 when not dispersing. Further, because dispersers express a bimodal distribution in terms of
514 displacement during dispersal, we can further confirm that their habitat preferences for open
515 habitats are specifically linked to periods when they are making larger displacements. Hence,
516 changes in habitat preferences are not the result of changing suitability of the habitat for all
517 individuals, but arise due to the different benefits that they bring to individuals when
518 dispersing.

519 Our work contributes to a growing body of evidence (e.g., Hofmann et al., 2023) that the
520 habitat requirements of a species also includes habitats that facilitate effective dispersal. Thus,
521 studying habitat selection during dispersal can allow us to identify the need to consider whole
522 categories of habitat that dispersers use to bridge populations, which might be missed if we
523 look at the behaviour of a species when it is settled. Specifically, actively dispersing birds seem
524 to select roads and open habitats when covering large distances, but avoid these if they are
525 too risky (Prokopenko et al., 2017; Scrafford et al., 2018; Sunga et al., 2017). By estimating the
526 energetic cost of movement through different habitats, we were able to confirm that these
527 more open habitat types are on average more efficient in terms of energy expenditure. Finally,
528 we note that making large displacements is not limited to natal dispersal. Many animals—
529 especially those living in harsh environments—have to temporarily relocate to find resources
530 (e.g., nomadism or irruptive nomadism, Teitelbaum & Mueller, 2019), and future work may
531 also investigate whether animals can exhibit plastic habitat preferences linked to movement
532 under different contexts. In vulturine guineafowl, many such movements are made by groups
533 (Papageorgiou et al., 2021)—a pattern that is likely to be mirrored in many species with similar

ecological profiles—providing another interesting contextual change. By complementing existing studies, using step selection analysis on moving social groups could allow a rich comparison of whether plasticity in habitat selection can be expressed in similar ways when moving alone versus moving as a group.

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References

Armansin, N. C., Stow, A. J., Cantor, M., Leu, S. T., Klarevas-Irby, J. A., Chariton, A. A., & Farine, D. R. (2020). Social Barriers in Ecological Landscapes: The Social Resistance Hypothesis. In *Trends in Ecology and Evolution* (Vol. 35, Issue 2, pp. 137–148). Elsevier Ltd. https://doi.org/10.1016/j.tree.2019.10.001

Avgar, T., Potts, J. R., Lewis, M. A., & Boyce, M. S. (2016). Integrated step selection analysis: Bridging the gap between resource selection and animal movement. *Methods in Ecology and Evolution*, *7*(5), 619–630. https://doi.org/10.1111/2041-210X.12528

Batschelet, E. (1981). *Circular statistics in biology*.

Bonte, D., Van Dyck, H., Bullock, J. M., Coulon, A., Delgado, M., Gibbs, M., Lehouck, V., Matthysen, E., Mustin, K., Saastamoinen, M., Schtickzelle, N., Stevens, V. M., Vandewoestijne, S., Baguette, M., Barton, K., Benton, T. G., Chaput-Bardy, A., Clobert, J., Dytham, C., … Travis, J. M. J. (2012). Costs of dispersal. *Biological Reviews*, *87*(2), 290–312. https://doi.org/10.1111/j.1469-185X.2011.00201.x

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. In *Ecology Letters* (Vol. 12, Issue 3, pp. 197–209).

https://doi.org/10.1111/j.1461-0248.2008.01267.x

Dickie, M., McNay, S. R., Sutherland, G. D., Cody, M., & Avgar, T. (2020). Corridors or risk? Movement along, and use of, linear features varies predictably among large mammal predator and prey species. *Journal of Animal Ecology*, *89*(2), 623–634. https://doi.org/10.1111/1365-2656.13130

Dickie, M., Serrouya, R., McNay, R. S., & Boutin, S. (2017). Faster and farther: wolf movement on linear features and implications for hunting behaviour. *Journal of Applied Ecology*, *54*(1), 253–263. https://doi.org/10.1111/1365-2664.12732

Dickson, B. G., Jenness, J. S., & Beier, P. (2005). Dickson_et_alCougarCompoAnal_JWM2005.pdf. *Journal of Wildlife DIseases*, *69*(1), 264–276.

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*(5), 695–703. https://doi.org/10.1086/376430

ESRI. (2011). *ArcGIS Desktop: Release 10*. Environmental Systems Research Institute.

Fahrig, L. (2007). Non-optimal animal movement in human-altered landscapes. *Functional Ecology*, *21*(6), 1003–1015. https://doi.org/10.1111/j.1365-2435.2007.01326.x

Fieberg, J., Signer, J., Smith, B., & Avgar, T. (2021). A 'How to' guide for interpreting parameters in habitat-selection analyses. *Journal of Animal Ecology*, *90*(5), 1027–1043. https://doi.org/10.1111/1365-2656.13441

Gallagher, A. J., Creel, S., Wilson, R. P., & Cooke, S. J. (2017). Energy Landscapes and the Landscape of Fear. *Trends in Ecology and Evolution*, *32*(2), 88–96. https://doi.org/10.1016/j.tree.2016.10.010

Hämäläinen, S., Fey, K., & Selonen, V. (2019). The effect of landscape structure on dispersal distances of the Eurasian red squirrel. *Ecology and Evolution*, *9*(3), 1173–1181. https://doi.org/10.1002/ece3.4806

He, P., Klarevas-Irby, J. A., Papageorgiou, D., Christensen, C., Strauss, E. D., & Farine, D. R. (2023). A guide to sampling design for <scp>GPS</scp> -based studies of animal

societies. *Methods in Ecology and Evolution*, *14*(8), 1887–1905. https://doi.org/10.1111/2041-210X.13999

Hijmans, R. J. (2022). *raster: Geographic Data Analysis and Modeling. R package version 3.5-15.*

Hofmann, D. D., Cozzi, G., McNutt, J. W., Ozgul, A., & Behr, D. M. (2023). A three-step approach for assessing landscape connectivity via simulated dispersal: African wild dog case study. *Landscape Ecology*, *38*(4), 981–998. https://doi.org/10.1007/s10980-023-01602-4

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. https://doi.org/10.1186/2051-3933-2-13

Klarevas-Irby, J. A., Wikelski, M., & Farine, D. R. (2021). Efficient movement strategies mitigate the energetic cost of dispersal. In *Ecology Letters* (Vol. 24, Issue 7, pp. 1432–1442). https://doi.org/10.1111/ele.13763

Klarevas-Irby, J. A., & Farine, D. R. (2023). Diel patterns of movement reveal temporal strategies during dispersal. *Animal Behaviour*. https://doi.org/https://doi.org/10.1016/j.anbehav.2023.10.010

Kojola, I., Aspi, J., Hakala, A., Heikkinen, S., Ilmoni, C., & Ronkainen, S. (2006). Dispersal in an expanding wolf population in Finland. *Journal of Mammalogy*, *87*(2), 281–286. https://doi.org/10.1644/05-MAMM-A-061R2.1

Kranstauber, B., Smolla, M., & Scharf, A. K. (2023). *move: Visualizing and Analyzing Animal Track Data* (4.1.12). https://cran.r-project.org/package=move

Lima, S. L. (1995). Back to the basics of anti-predatory vigilance: the group-size effect. *Animal Behaviour*, *49*(1), 11–20. https://doi.org/10.1016/0003-3472(95)80149-9

Long, R. A., Bowyer, R. T., Porter, W. P., Mathewson, P., Monteith, K. L., Findholt, S. L., Dick, B. L., & Kie, J. G. (2016). Linking habitat selection to fitness-related traits in herbivores: the role of the energy landscape. *Oecologia*, *181*(3), 709–720. https://doi.org/10.1007/s00442-016-3604-7

Mabry, K. E., & Stamps, J. A. (2008). Dispersing brush mice prefer habitat like home. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1634), 543–548. https://doi.org/10.1098/rspb.2007.1541

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*(11), 2050–2063. https://doi.org/10.1242/jeb.02226

Mercker, M., Schwemmer, P., Peschko, V., Enners, L., & Garthe, S. (2021). Analysis of local habitat selection and large-scale attraction/avoidance based on animal tracking data: is there a single best method? *Movement Ecology*, *9*(1), 20. https://doi.org/10.1186/s40462-021-00260-y

Miller, G. S., Small, R. J., & Meslow, E. C. (1997). Habitat Selection by Spotted Owls during Natal Dispersal in Western Oregon. *The Journal of Wildlife Management*, *61*(1), 140. https://doi.org/10.2307/3802423

Ogino, M., Strauss, E. D., & Farine, D. R. (2023). Challenges of mismatching timescales in longitudinal studies of collective behaviour. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *378*(1874). https://doi.org/10.1098/rstb.2022.0064

Papageorgiou, D., Christensen, C., Gall, G. E. C., Klarevas-Irby, J. A., Nyaguthii, B., Couzin, I. D., & Farine, D. R. (2019). The multilevel society of a small-brained bird. In *Current Biology* (Vol. 29, Issue 21, pp. R1120–R1121). https://doi.org/10.1016/j.cub.2019.09.072

Papageorgiou, D., & Farine, D. R. (2020). Group size and composition influence collective movement in a highly social terrestrial bird. *ELife*, *9*, 1–16. https://doi.org/10.7554/eLife.59902

Papageorgiou, D., Rozen-Rechels, D., Nyaguthii, B., & Farine, D. R. (2021). Seasonality impacts collective movements in a wild group-living bird. *Movement Ecology*, *9*(1). https://doi.org/10.1186/s40462-021-00271-9

Planet Team. (2017). *Planet application program interface: In space for life on Earth*. https://api.planet.com

Prokopenko, C. M., Boyce, M. S., & Avgar, T. (2017). Characterizing wildlife behavioural responses to roads using integrated step selection analysis. *Journal of Applied Ecology*, *54*(2), 470–479. https://doi.org/10.1111/1365-2664.12768

R Core Team. (2022). *R: A Language and Environment for Statistical Computing*. https://www.r-project.org/

Reed, J. M., Boulinier, T., Danchin, E., & Oring, L. W. (1999). Informed dispersal:Prospecting by birds for breeding sites. In *Current ornithology* (pp. 189–259). Springer.

Riley, S. J., DeGloria, S. D., & Elliot, R. (1999). A Terrain Ruggedness Index that Qauntifies Topographic Heterogeneity. *Intermountain Journal of Sciences*, *5*(1–4), 23–27.

Roever, C. L., Boyce, M. S., & Stenhouse, G. B. (2010). Grizzly bear movements relative to roads: Application of step selection functions. *Ecography*, *33*(6), 1113–1122. https://doi.org/10.1111/j.1600-0587.2010.06077.x

Scrafford, M. A., Avgar, T., Heeres, R., & Boyce, M. S. (2018). Roads elicit negative movement and habitat-selection responses by wolverines (Gulo gulo luscus). *Behavioral Ecology*, *29*(3), 534–542. https://doi.org/10.1093/beheco/arx182

Shaw, A. K. (2020). Causes and consequences of individual variation in animal movement. In *Movement Ecology* (Vol. 8, Issue 1, p. 12). https://doi.org/10.1186/s40462-020-0197-x

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. *American Naturalist*, *182*(3), 298–312. https://doi.org/10.1086/671257

Signer, J., Fieberg, J., & Avgar, T. (2019). Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. *Ecology and Evolution*, *9*(2), 880–890. https://doi.org/10.1002/ece3.4823

Stamps, J. A. (2001). Habitat selection by dispersers: integrating proximate and ultimate approaches. In *Dispersal* (pp. 230–242). https://www.researchgate.net/publication/264623013

Strandburg-Peshkin, A., Farine, D. R., Crofoot, M. C., & Couzin, I. D. (2017). Habitat and social factors shape individual decisions and emergent group structure during baboon collective movement. *ELife*, *6*. https://doi.org/10.7554/eLife.19505

Studds, C. E., Kurt Kyser, T., & Marra, P. P. (2008). Natal dispersal driven by environmental conditions interacting across the annual cycle of a migratory songbird. In *PNAS* (Vol. 105, Issue 8). www.pnas.orgcgidoi10.1073pnas.0710732105

Sunga, J., Sayers, J., Cottenie, K., Kyle, C. J., & Ethier, D. M. (2017). The effects of roads on habitat selection and movement patterns of the american badger subspecies taxidea taxus jacksoni in Ontario, Canada. *Canadian Journal of Zoology*, *95*(11), 821–828. https://doi.org/10.1139/cjz-2016-0286

Teitelbaum, C. S., & Mueller, T. (2019). Beyond Migration: Causes and Consequences of Nomadic Animal Movements. *Trends in Ecology and Evolution*, *34*(6), 569–581. https://doi.org/10.1016/j.tree.2019.02.005

Therneau, T. M. (2020). *A Package for Survival Analysis in R.*

Theuerkauf, J., & Rouys, S. (2008). Habitat selection by ungulates in relation to predation risk by wolves and humans in the Białowieża Forest, Poland. *Forest Ecology and Management*, *256*(6), 1325–1332. https://doi.org/10.1016/j.foreco.2008.06.030

Thurfjell, H., Ciuti, S., & Boyce, M. S. (2014). Applications of step-selection functions in ecology and conservation. In *Movement Ecology* (Vol. 2, Issue 1, pp. 1–12). https://doi.org/10.1186/2051-3933-2-4

Van Dyck, H., & Baguette, M. (2005). Dispersal behaviour in fragmented landscapes: Routine or special movements? *Basic and Applied Ecology*, *6*(6), 535–545. https://doi.org/10.1016/j.baae.2005.03.005

Vásquez, R. A., Ebensperger, L. A., & Bozinovic, F. (2002). The influence of habitat on travel speed, intermittent locomotion, and vigilance in a diurnal rodent. *Behavioral Ecology*, *13*(2), 182–187. https://doi.org/10.1093/beheco/13.2.182

Walls, S. S., Kenward, R. E., & Holloway, G. J. (2005). Weather to disperse? Evidence that climatic conditions influence vertebrate dispersal. *Journal of Animal Ecology*, *74*(1), 190–197. https://doi.org/10.1111/j.1365-2656.2005.00914.x

Ward, M. P. (2005). Habitat selection by dispersing yellow-headed blackbirds: Evidence of prospecting and the use of public information. *Oecologia*, *145*(4), 650–657. https://doi.org/10.1007/s00442-005-0179-0

Winowiecki, L. A., Vågen, T. G., Kinnaird, M. F., & O'Brien, T. G. (2018). Application of systematic monitoring and mapping techniques: Assessing land restoration potential in semi-arid lands of Kenya. *Geoderma*, *327*(April 2016), 107–118. https://doi.org/10.1016/j.geoderma.2018.04.017

Young, T. P., Okello, B., Kinyua, D., & Palmer, T. M. (1998). KLEE: a long-term multi-species herbivore exclusion experiment in Laikipia, Kenya. In *African Journal of Range and Forage Science* (Vol. 14, Issue 1).

Young, T. P., Patridge, N., & Macrae, A. (1995). Long-Term Glades in Acacia Bushland and Their Edge Effects in Laikipia, Kenya. *Ecological Applications*, *5*(1), 97–108. https://doi.org/10.2307/1942055

Zollner, P. A., & Lima, S. L. (1999). Search Strategies for Landscape-Level Interpatch Movements. *Ecology*, *80*(3), 1019. https://doi.org/10.2307/177035

SUPPLEMENTARY MATERIAL

Supplementary Table S1. Results of the Step Selection Analysis. Significant values given in bold. NA values indicate no steps assigned to a given stage were assigned to a given habitat covariate. n_{total} = 42,167 steps (observed + alternate), $n_{observed}$ = 2,008 steps.

Habitat selection coefficients by stage—Transient (large displacements), Transient (local), or Resident

Formula: *Step* [observed vs alternate] ~ *Waterbodies:stage +Roads:stage + Cover type:stage + Ruggedness:stage + step*

Stage: Covariate	Sel. Coef.	exp(Coef)	se(Coef)	z	Pr(>|z|)
TransDis:Waterbody	-1.806	0.163	0.941	-1.920	0.055
TransLoc:Waterbody	-0.274	0.760	0.693	-0.396	0.692
Res:Waterbody	1.633	65.124	1.128	1.449	0.147
TransDis:Roads	**1.291**	**3.635**	**0.217**	**5.957**	**<0.001**
TransLoc:Roads	**0.618**	**1.855**	**0.216**	**2.861**	**0.004**
Res:Roads	0.669	1.951	0.355	1.882	0.060
TransDis:Glades	**1.966**	**7.141**	**0.816**	**2.408**	**0.016**
TransLoc:Glades	-1.006	0.366	0.699	-1.440	0.149
Res:Glades	**3.093**	**22.049**	**1.060**	**2.918**	**0.004**
TransDis:Bare soil	1.355	3.876	0.871	1.556	0.120
TransLoc:Bare soil	NA	NA	NA	NA	NA
Res:Bare soil	NA	NA	NA	NA	NA
TransDis:Acacia	**1.586**	**4.887**	**0.706**	**2.247**	**0.024**
TransLoc:Acacia	**-1.851**	**0.157**	**0.587**	**-3.152**	**0.002**
Res:Acacia	1.911	6.758	1.004	1.903	0.057
TransDis:Riverine	NA	NA	NA	NA	NA
TransLoc:Riverine	NA	NA	NA	NA	NA
Res:Riverine	NA	NA	NA	NA	NA
TransDis:Ruggedness	1.002	2.723	0.825	1.214	0.224
TransLoc:Ruggedness	0.055	1.057	1.084	0.051	0.959
Res:Ruggedness	-2.032	0.131	1.454	-1.397	0.162

Concordance = 0.533, se = 0.006

Likelihood ratio test = 99.11 on 16 df, p = 5 e -14

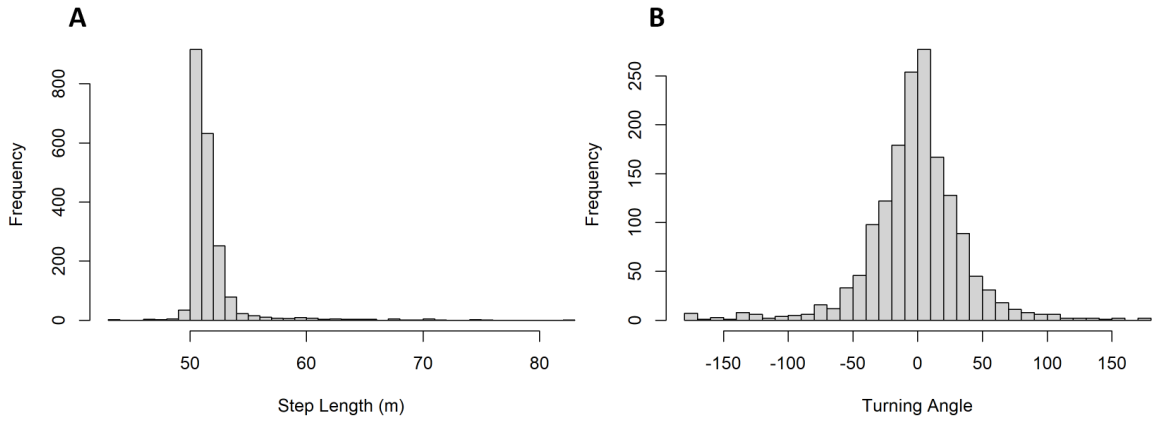
Wald test = 91.19 on 16 df, p = 2 e-12

Score (logrank) test = 98.25 on 16 df, p = 7 e -14

Stages: *TransDis* = transient dispersers on days with large displacements, *TransLoc* = transient dispersers during days of local movement, *Res* = non-dipsersing residents.

Supplementary Table S2. Results of the LMM of the total energetic cost of transport, in Joules kg^{-1} m^{-1}, over a 50 meter net displacement and its response to habitat type. Reference level of habitat is roads.

Energetic Cost of Transport per 50m step					
Equation: *Cost of transport ~ Habitat + (1|Stage) + (1|Individual) + (1|Date)*					
	Estimate	**Std. Error**	**df**	**t value**	**Pr(>|t|)**
Intercept	27.951	1.799	532.166	15.536	**<0.001**
Habitat: Bare soil	5.411	2.873	909.912	1.883	0.059
Habitat: Glades	6.258	2.313	1594.144	2.706	**0.007**
Habitat: Riverine	12.398	5.356	1759.968	2.315	**0.021**
Habitat: Acacia scrub	6.405	1.720	1747.342	3.724	**<0.001**
Random effects					
Groups	**Name**	**Mean Variance**	**Std.dev**		
Date	**Intercept**	7.19	2.667		
Individual ID	**Intercept**	3.730	1.931		
Stage	**Intercept**	0.000	0.000		
Residual		272.108	16.496		



Supplementary Figure S1. Distributions of step lengths (A) and turning angles (B) from 2,034 observed steps.