Living on the Forest Edge: Flexible Habitat Use in Sedentary Pied Flycatchers Ficedula Hypoleuca during the Non-Breeding Season

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Living on the forest edge: flexible habitat use in sedentary Pied Flycatchers *Ficedula hypoleuca* during the non-breeding season

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Seasonality affects the availability of resources within the African non-breeding environment of migratory songbirds. We are generally unaware of how songbirds respond to such seasonal dynamics, especially at small spatial scales that are relevant for individual birds. In this study we focus on the question of how migratory songbirds use small scale variation in seasonality in their non-breeding environment. Therefore, we measured individual movements of European Pied Flycatchers *Ficedula hypoleuca* in relation to habitat differences in foliation in a non-breeding site in Comoé National Park, Ivory Coast. Through a combination of remote sensing and radio tracking we show that flycatchers change their habitat use during the second half of the non-breeding season, where at the start of this period flycatchers occupy both savannah and forest, whereas with progressing foliation, after savannah burning and with the onset of the first rainfall, they narrow their site use in favour of savannah. Further measurements of arthropod abundance show that this behaviour is related to increasing numbers of particular arthropod groups during foliation, which indicates that flycatchers might track seasonal changes in food availability by moving between habitats on a small spatial scale. We hypothesize that individuals reduce their susceptibility to seasonality by establishing territories on the forest edge, where they can access both savannah and forest habitat, and thereby explore a wider variety of resources under different circumstances. In conclusion, these findings indicate that small-scale heterogeneity likely plays a key role in the ability of flycatchers to cope with seasonal dynamics on a local scale.

Key words: Pied Flycatcher, non-breeding season, seasonality, arthropods, habitat use, radio-tracking, remote sensing, NDVI

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Non-breeding environments of Afro-Palearctic migratory passerines are characterized by pronounced seasonal changes. These are mainly driven by fluctuations in rainfall, which follow the cyclic movements of the Intertropical Convergence Zone, resulting in spatio-temporal variation in vegetation dynamics across the African continent (Beresford *et al.* 2019). As a result of this variation the specific seasonal dynamics that birds encounter during the non-breeding season depend on the timing and location of residency. Most Afro-Palearctic migrants spend the non-breeding period in the dry or humid regions north of the equator. Their subsequent residency coincides with the dry season which is generally characterized by wilting of the

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vegetation (Moreau 1972, Zwarts *et al.* 2023). Within the Sahel this dry season typically extends beyond the onset of spring migration, whereas a few hundred kilometres towards the south (in the Sudanian and Guinean regions) most migrants depart after the first rainfall, and consequently experience regrowth and foliation of the vegetation at the end of the non-breeding season (Zwarts *et al.* 2023).

Seasonal changes in vegetation conditions affect the availability of environmental resources that are important for the survival of migratory passerines. Most notably, food availability of insectivorous migrants is widely believed to be positively linked with vegetation greenness, as their prey species either directly (e.g. herbivores, detritivores) or indirectly (carnivores) rely on the consumption of plant material (Schaub *et al.* 2011. Kristensen *et al.* 2013, Thorup *et al.* 2017). Additionally, seasonal change in leaf cover might affect the risk of predation. Arboreal species in particular often rely on leaf cover to protect themselves against avian predators (Walther & Gosler 2001, Carrascal & Alonso 2006). Similarly, changes in foliage density also affect the availability of shade which plays a vital role in thermoregulation of songbirds in tropical environments (Wolf & Walsberg 1996, Cunningham *et al.* 2015, Martin *et al.* 2015). Given the variation in the resources that are affected, seasonal vegetation dynamics can differentially affect species, depending on their respective ecological traits.

One possible response of migratory songbirds to seasonality is tracking environmental shifts in resources. For example, various migrant species move along with shifts in plant growth within the African continent, and thereby visit multiple sites throughout the non-breeding period (e.g. Thorup *et al.* 2017, Koleček *et al.* 2018, Norevik *et al.* 2019). Although most studies on migrant species in Africa lack direct observations of environmental conditions, and the associated behavioural ecology during the non-breeding season (but see Schlaich *et al.* (2016) for an example in Montagu's Harriers *Circus pygargus*), these large-scale movements are widely interpreted as an adaptive behaviour by which birds track seasonally available resources. Despite the seeming advantage of avoiding local declines in resources, through large-scale movements, other species are known to remain (largely) sedentary throughout the non-breeding period (e.g. Salewski 1999, Kristensen *et al.* 2013). This reflects an ability of these birds to cope with seasonality within their local environment.

In order to determine how songbirds are able to cope with seasonality on a local scale, we need fine-

Photo 1. Savannah right after burning of the undergrowth during the dry season. Trees and shrubs are largely defoliated, and the soil is covered by ash litter (30 December 2018).

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scale observations. However, most of our knowledge about the spatial behaviour of songbirds during the non-breeding season is based on imprecise tracking data from light-level geolocators (Rakhimberdiev *et al.* 2016). We are generally unaware of individual movements at fine levels, as would be described by radio-tracking studies (e.g. Stünzner-Karbe 1996, Willemoes *et al.* 2018). Additionally, many studies use remote-sensed indices such as the Normalised Difference Vegetation Index (NDVI) to measure environmental conditions on large spatial scales (e.g. Balbontín *et al.* 2009, Schaub *et al.* 2011, Kristensen *et al.* 2013) This is unsuitable for detecting variation on smaller scales, such as different seasonal patterns between tree species (Mahamane *et al.* 2007, Park *et al.* 2019, Fawcett *et al.* 2021). We also often lack detailed insight into the non-breeding ecology of species to interpret patterns in remote sensed datasets, such as relationships between NDVI and specific resources (Piersma 2020). Altogether, we are generally unaware of how songbirds respond to seasonal resource dynamics in the non-breeding area, especially at small spatial scales that are relevant for individual birds.

In this study we focus on the question of how migratory songbirds use small-scale heterogeneity in vegetation within the non-breeding environment. Therefore, we measured individual habitat use in relation to seasonal dynamics in foliation within a non-breeding site of the European Pied Flycatcher *Ficedula hypoleuca*, hereafter called flycatcher. Flycatchers are Afro-Palearctic migrants with a non-breeding range within the Guinean and Sudanian ecoregion of West Africa (Ouwehand *et al.* 2016). Previous observations from non-breeding sites suggested that flycatchers are territorial and occupy non-overlapping home-ranges (Stünzner-Karbe 1996, Salewski *et al.* 2002, Willemoes *et al.* 2018); also that individuals can use the same sites from arrival after mid-September until the onset of spring migration around April (Stünzner-Karbe 1996, Salewski *et al.* 2002). However, individuals have also been observed to shift between locations in forest and savannah habitats that were sometimes hundreds of meters apart (Stünzner-Karbe 1996). Based on this background we hypothesize that flycatchers respond to seasonality by tracking heterogeneity in the distribution of resources on small spatial scales.

To establish the relationship between site selection of flycatchers and small-scale variation in seasonality, we use a combined approach of remote sensing and radio tracking. Therefore we (1) investigate the possibility of using small-scale NDVI to quantify vegetation greenness in the environment, (2) describe how the site use of flycatchers is related to habitat and foliation and (3) describe the association between the observed patterns in site use and arthropod abundance.

METHODS

Study area

The study was conducted in Comoé National Park, Ivory Coast (8°45.875'N, 3°47.189'W) within a plot covering c. 69 ha in the immediate vicinity of the Comoé field station (for a description of the area see Ouwehand *et al.* 2023). Study site selection was based on high densities of flycatchers found in the national park during previous research (Salewski 1999). The vegetation within this plot mainly consists of savannah woodland, characterized by an open canopy of mostly deciduous trees and shrubs, with species such as *Terminalia macroptera*, *Daniellia olivieri* and *Combretum nigricans*, and a well-developed grass layer which is annually burned during the midst of the dry season (late December–January; Rüth 2008). During the year of this study the burning occurred around January 7 (determined by satellite imagery, Landsat-8, U.S. Geological Survey). The savannah is interspersed with forest patches, which are different from savannah woodland due to the absence of burning, and a denser shrub and canopy layer. Further heterogeneity also exists within these patches, where the edges are dominated by *Anogeissus leiocarpus*, a deciduous tree with a relatively open canopy, whereas the centre is characterized by a relatively dense canopy layer with a mixture of both deciduous and evergreen species (e.g. *Diospyros abyssinica*, *Cola cordifolia*). Another type of forest, hereafter called gallery forest, can be found along the border of the Comoé River, which somewhat resembles the vegetation in the forest patches, but with a more homogenous species composition and a higher dominance of evergreen shrubs and trees (e.g. *Diospyros abyssinica*).

General fieldwork

The data in this study was collected between 12 February and 15 April 2020. As part of ongoing research since 2017 we conducted regular surveys to collect observations of flycatchers in the study area (Ouwehand *et al.* 2023). We recorded the coordinates of each observation by means of a handheld GPS and tried to identify the individual if it had been colour-ringed. Based on these observations we selected specific individuals which we subsequently tried to catch by means of a mist net, or, occasionally, a baited

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spring-trap. We focused our catching efforts on individuals that had not been previously caught, and individuals that were carrying a geolocator from the previous season. Newly caught individuals were equipped with an aluminium colour ring for individual recognition. We established the age of individuals (1st winter/2nd calendar year or >2nd calendar year) by means of presence or absence of juvenile greater coverts and tertials, and wear and shape of tail feathers (Svensson 1992, Jenni & Winkler 1994). The sex was initially determined by the presence or absence of distinct male plumage characteristics, such as dark tail feathers and coverts, and after the onset of pre-breeding moult also by white forehead patches and dark coverts. In case birds lacked any of these distinctive male characteristics we collected a blood sample for molecular sexing (following Kahn *et al.* 1998), allowing us to distinguish between females and males with female-type plumage.

Remote sensing

In order to measure spatiotemporal changes in vegetation conditions we used UAV-derived aerial imagery, which allows for a high spatiotemporal sampling resolution (Park *et al.* 2019, Fawcett *et al.* 2021). We used a consumer-grade quadcopter (DJI Phantom 4 multispectral) with the software DJI GS Pro (DJI Technology, Shenzhen) to create an automated image acquisition plan for the study area and its immediate surroundings. The image angle was set at 90° with a frontal overlap of 70% and a side overlap of 60% between adjacent pictures, and pictures were taken at an altitude of 113 m yielding a resolution of 6.0 cm^2/pixel. Images were taken once every eight days during the period 12 February to 14 April. We used the program Pix4D v. 4.6.4 (Pix4D, Lausanne) to aggregate all images from the same date and bandwidth into a comprehensive raster file. The red and NIR rasters were subsequently used to calculate the NDVI of individual pixels and these values were finally stored in a new NDVI raster for each observation date.

NDVI and fresh foliage cover

In parallel with remote-sensing, we conducted a ground-truthing study to verify the biological basis of observed spatiotemporal differences in NDVI. Therefore, we specifically monitored fresh foliage cover within individual tree crowns and grass layer transects. For the tree monitoring we selected 14 of the most common species within the area, for each of which we located four trees on regular spaced locations throughout the study plot. We only selected trees in the upper canopy to ensure visibility on the aerial imagery. These trees were subsequently visited every eight days to

Photo 2. Savannah during foliation, with trees and shrubs including *Burkea africana*, *Piliostigma thonningii*, *Terminalia macroptera* and *Daniellia oliveri*. The soil is partly covered by fresh grown forbs and perennial grasses (6 March 2020).

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Photo 3. The savannah after complete foliation of trees and shrubs, including *Crossopteryx febrifuga*, *Burkea africana* and *Terminalia macroptera*. The grass layer almost completely covers the soil (and thereby is further developed than during the study period) and will further develop during the rainy season (27 April 2018).

visually estimate the proportion of the crown circumference covered by fresh (i.e. green) leaves on a 10-point scale, which was done from a distance of c. 10–20 m from the trunk. These observations were initially collected by different observers in the field, but we also took pictures to compare estimations of different observers. After we detected a significant difference in estimates between observers, we used these pictures to get new estimates from a single observer (WB) which were used for the final analysis.

Additionally, we measured the amount of fresh plant material within grass layer transects by means of line-point interception. These sampling locations were selected within the vicinity of the arthropod sampling sites (see next paragraph) and consist of two 10-m line transects placed in perpendicular directions from a shared starting point. Following Herrick *et al.* (2005) we established the relative cover of fresh plant material (i.e. green leaves) within these transects by dropping a metal pin at each 20-cm interval along a reference rope that marked the transect. If this pin touched any green plant material it was scored as a 1, and in any other case (and also when the pin touched senescent plant material) it was scored as a 0. The relative cover of each 10-m transect was then calculated as the sum of scores divided by the total number of trials ($n = 50$). In total we sampled each transect three times during the period 26 February to 13 March. To analyse the relationship between grass coverage and remote sensed NDVI we then made a post-hoc selection of those transects which were directly visible on the aerial imagery, and not completely masked by trees. This resulted in a final sample of transects which were exclusively placed on the open savannah ($n = 8$). We also used the same interception to describe differences in habitat characteristics between sites that we classified as either forest or savannah. Therefore, we scored the relative cover of specific types of vegetation (sum of senescent and green plants) and litter on the first observation date. We specifically distinguished the categories shrubs (perennial woody plants), forbs (herbaceous plants), herbaceous litter (fallen non-woody plant material), woody litter (fallen branches and wood) and ash litter (burned plant material).

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We used ArcGIS v. 10.8.1 (ESRI, Redlands, CA) to extract values of individual trees and transects from the remote sensed NDVI rasters. For this purpose, we initially plotted the coordinates of individual trees and transects on a true colour map. Next, we used reference pictures from the field to visually correct for any inaccuracies in the GPS location of these objects. Then we created a new shapefile that was used to draw polygons for the surface area of the individual canopies and transect. For trees we used the green rasters to outline the maximum expanse of the canopy (including leaves and branches) during the study period. For the transects we created a 0.5-m buffer polygon around the central axis of the transect, representing the ground-sampling area and its immediate surroundings. To confine these polygons to the vegetation of interest, we excluded all parts that were covered by overhanging branches on any date. The adjusted polygons for trees and transects were then used to derive the mean NDVI from the underlying raster cells for different dates. Next, these values were linked to the most recent ground-based observations of foliage cover for the same canopies or grass transects. On average the observation dates differed by 2.33 ± 0.48 days for transects and 0.78 ± 0.54 days for trees.

Radio tracking

We used radio tracking to quantify individual site-use of flycatchers and its relationship with vegetation conditions. Therefore, we randomly selected individuals (i.e. independent of age, sex and capture history) among our captured birds, which we subsequently equipped with a 0.53-g solar-powered radio transmitter (type CTT LifeTag, Cellular Tracking Technologies, Rio Grande, NJ) attached by means of an elastic leg-loop harness. The rechargeable nature of LifeTags enabled us to track individuals over longer periods than with conventional transmitters, although these tags only transmit signals when directly exposed to sunlight, resulting in zero pulses in dark or shaded habitats or if feathers cover the tag. For this reason, we modified the tags by adding a transparent plastic cap on top, which prevented feathers from covering the solar cell. Furthermore, to lessen the risk of entanglement we clipped the antenna down to 86.5 mm. In total we equipped 13 flycatchers with a radio transmitter (Table 1), for which we excluded four individuals with insufficient data from the analysis. In three cases this was likely due to a technical failure, including one instance where we could confirm that the plastic cap had disjoined from the tag, which was therefore covered by feathers (individual 61526652). The other excluded individual (61335200) was overall well detected, but with too few detections within approximately 50 m from receiver nodes (see next paragraph) to measure site selection over time.

To localize individuals, we made use of 21 solar-powered autonomous receivers (CTT Node, v. 1), hereafter called ‘nodes’, which we placed in an isometric grid at an individual distance of approximately 200 m. To maximize charging we placed the nodes in treetops, where the solar cells were exposed to full sunlight throughout the day. Nodes can receive LifeTags within a maximum range of c. 300 m, and each reception is stored in a data file with the tag-ID (an identification number based on the unique frequency of tags), date, time, and the strength (RSSI) of the signal. After initial storage the nodes retransmit this data to a central receiver (CTT SensorStation v. 2.0), which compiles the data including the node-ID (an unique identification number) into a single data file.

Location estimation

In our initial setup we aimed to estimate individual positions per time interval by triangulation of receptions from different nodes. Therefore, we created a habitat-specific calibration curve for RSSI as a function of distance, based on observations of tagged individuals with known locations in the field (6 individuals, 45 locations). Following the R-documentation ‘Localization.R’ (https://github.com/cellular-tracking-technologies/celltracktech) the curve was restricted to follow an asymptotic regression function, for which we calculated the parameter estimates by means of non-linear least squares. Next, we used this calibration curve to triangulate locations of tagged birds within the node-grid. However, based on unrealistic outcomes (which included unlikely shifts in subsequent locations, and cluttering of estimated locations at exact distances between nodes), which was likely due to the uncertainty of distance estimation at relatively low RSSI values (Figure S1), we concluded that this method would be unsuitable for our purpose. Instead, we opted for an alternative approach where we established spatial behaviour of tagged birds by determining presence within a radius of 50 m from each node (i.e. an area of 7854 m^2). Using this approach we avoided the uncertainty in position estimation at large distances (i.e. near the asymptote of the calibration curve), while the scale proved to be sufficiently small to detect within-individual shifts in site selection. For this approach we derived the predicted RSSI value at a distance of 50 m from the calibration model (Figure S1) and selected all detections for which the RSSI value

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was equal to or larger than the resulting value. Next, we grouped the observations per 5 minutes and selected only the cases where a bird was detected at least five times within the 50-m range of a node. This selection was made to reduce the influence of single detection errors, and thereby the probability of falsely considering a bird to be present. For each selected period we determined the site where a bird was most likely present, which in most cases was simply the only site in which a bird was detected ($n = 5641$). In alternative cases where birds were detected on multiple sites ($n = 527$), we assigned presence to the site with >50% of detections. Periods in which this condition was not met ($n = 75$) were removed from the analysis.

Arthropod sampling

In order to establish the relationship between vegetation conditions and food availability for flycatchers, we monitored the abundance of arthropods within the environment. Based on our own observations and a previous study of Salewski (1999) we knew that flycatchers in the study area were mainly insectivorous and foraged in a wide range of substrates using a range of foraging techniques. However, we lacked a priori insight into the relative importance of specific arthropod groups within the diet, as well as the relative intake from different strata of the vegetation. To capture a broad range of potential available arthropod food sources we used pitfalls and malaise traps, which capture ground-dwelling and aerial (but low flying) arthropods respectively. These trap types capture arthropods passively and therefore the number of captures depend on both the abundance and activity of arthropods, which are thus best described as measurements of 'activity-abundance' (McCravy 2018), although we will shortly refer to this as 'abundance'. In total we sampled at eight locations which were placed within the different vegetation types inhabited by flycatchers. These locations were placed near two separate woodland patches, along a vegetation gradient from closed canopy forest to open canopy savannah woodland. In addition, we selected a single trapping site within the gallery forest, which differs in its (spatial) characteristics from the forest patches.

Each location was sampled by means of three pitfall traps and one malaise trap (for dimensions of traps see Ouwehand *et al.* 2023: but note that sampling design differs from this study). The pitfalls were placed along a line at 5-m intervals, all within c. 10 m from the malaise trap. These traps were alternately opened and closed for four days, yielding an average sampling duration of 3.99 ± 0.16 days. Sampling was initiated on all sites on 23 February, but the total sampling period was unequal between sites, due to an unplanned reduction in personnel because of the Covid-19 pandemic. As a result, four sites were sampled until 10 March, and the other four until 8 April.

In each sampling round we collected two arthropod samples on each site: one sample from the malaise trap and a pooled sample from the three pitfall traps. The samples were conserved in ethanol and placed in a fridge for short-term storage. Captured arthropods were processed by measuring the body length excluding external body parts like antennae, legs and wings, and we removed arthropods with a body length <3 mm, which we expected not to be prominent food sources for flycatchers. We identified all other arthropods on taxonomic order level.

To analyse potential food abundance, we made a selection of items that we considered to be realistic prey

Table 1. Proportion of soil covered by specific types of vegetation and litter within forest ($n = 8/4$ distinct locations) and savannah ($n = 8/4$ distinct locations). Numbers show the proportion of times that a pin that was dropped along a 10-m line transect ($n = 50$, interval = 20 cm) touched the specified type of vegetation or litter (multiple categories possible), based on the estimated marginal means from a GLMM. Confidence intervals and significance of the difference between habitats are only given in case the variance is > 0 in both habitats.

	Forest		Savannah			
Variable	Proportion ± SE	95% CI	Proportion ± SE	95% CI	χ^2	p
Shrubs	0.03 ± 0.00	0.03 - 0.03	0.21 ± 0.08	0.10 - 0.45	14.03	< 0.001
Forbs	0.11 ± 0.04		0.00 ± 0.00		-	-
Grass	0.03 ± 0.00	0.03 - 0.03	0.21 ± 0.08	0.10 - 0.45	23.39	< 0.001
Herbaceous litter	0.94 ± 0.05	0.85 - 1.04	0.22 ± 0.02	0.18 - 0.27	152.61	< 0.001
Woody litter	0.06 ± 0.03	0.02 - 0.14	0.01 ± 0.01	0.00 - 0.04	5.18	0.020
Ash litter	0.00 ± 0.00		0.77 ± 0.04		-	-

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for flycatchers. Since large arthropods are underrepresented in the flycatcher diet we used order-specific length criteria to remove unlikely prey items from the analysis (for details see Ouwehand *et al.* 2023). Our final measurement consists of the number of arthropods per order per sample, where we assume independence between the number of items from different orders. This assumption was violated in a few cases where we observed large numbers of driver ants *Dorylus* spp. in our traps, which saturated the collection bottle and presumably diminished the trapping rate of other arthropods. We tried to remove these events from our dataset by discarding samples with extremely high numbers of Hymenoptera, which were identified by having a probability of <0.01 given a Poisson distribution for all Hymenoptera samples from the same trap type (5.0% of malaise samples, $n = 2$; 15.8% of pitfall samples, $n = 6$).

Spatial and temporal NDVI

We use separate NDVI-based proxies for habitat and foliation to describe vegetation conditions in time and space. In general arthropods prefer to consume fresh leaves, whereas older leaves are better protected against herbivory (Aide 1993). In order to generate a proxy for the amount of fresh leaves, which is potentially linked to the abundance of arthropods that might serve as food for flycatchers, we calculated the difference in NDVI relative to the first observation date (12 February), hereafter called $\text{NDVI}_{\text{temp}}$. In addition, we used the (absolute) NDVI values from this first observation date (i.e. prior to most foliation of deciduous vegetation) to describe foliation characteristics that are also typical for habitats. These NDVI values, hereafter called $\text{NDVI}_{\text{habitat}}$, range between low values for vegetation that is completely defoliated during the dry season, and high values for vegetation that remains green. In describing the habitat use of flycatchers, we refer to the lower end of $\text{NDVI}_{\text{habitat}}$ values as savannah, and to higher end values as forest. This broad habitat classification captures an important part of the variation in $\text{NDVI}_{\text{habitat}}$ within the study area (ANOVA: $F_{1,14} = 487.35$, $P < 0.001$; forest: mean ± SE: 0.59 ± 0.01, savannah: 0.18 ± 0.01, data based on eight sites in both habitats with a radius of 20 m, of which we assigned the habitat in the field). However, by preserving the continuous variable $\text{NDVI}_{\text{habitat}}$ in our analysis, instead of classifying habitat into forest or savannah, we address the further heterogeneity of vegetation that exists as a continuum across these broad habitat classes (e.g. varying mixtures of evergreen and deciduous vegetation).

Analysis

All statistical analyses were done using R v. 4.1.2 (R Core Team 2022). We used linear mixed effect models (LMM) from the 'lme4' package (Bates *et al.* 2015) to analyse the relationship between NDVI and foliage cover. In the canopy models we fitted random intercepts for tree-ID (an identification number for individual trees) nested within species. Similarly, we fitted a random intercept for transect-ID (an identification number for individual transects) in the grass layer models. Additionally, we fitted a random intercept for Date (date of the drone footage as a categorical factor) in all models to account for the relatedness of data points from the same date (e.g. due to shared light conditions). We established the relationship between foliage cover and NDVI by adding foliage cover as a linear term to the model. We additionally explored the possibility for a quadratic relationship by adding a squared term of foliage cover, which we only retained if this model performed significantly better than the nested (linear) model, as established by means of a likelihood ratio test with a significance level of $P < 0.05$. We established model performance by calculating the marginal R^2 for the fixed effects, and the conditional R^2 for both fixed and random effects. Furthermore, we used a LMM to test for differences in foliation between habitats, where we modelled $\text{NDVI}_{\text{temp}}$ as response of the predictors date (numeric), $\text{NDVI}_{\text{habitat}}$ and their two-way interaction, where we fitted a random intercept for each level of location-ID to account for the relatedness of repeated measurements of the same locations. To compare site features between forest and savannah habitats, we used a generalized linear mixed model (GLMM) with a Poisson error distribution. In this model we also fitted a random intercept for each level of location-ID to account for the relatedness between the two transects that we considered per location. We used habitat (category) as a predictor and added an offset for the total number of trials per transect ($n = 50$), which thereby allowed us to extract the estimated marginal means of the response as a rate/ proportion of cover for the whole transect.

In order to establish the association between site selection and habitat, we follow a similar procedure as described by Holbrook *et al.* (2019). Therefore, we initially established the available habitat by calculating the arithmetic mean $\text{NDVI}_{\text{habitat}}$ of each individual home-range, subsequently called the 'available $\text{NDVI}_{\text{habitat}}$', which we define as all sites that were visited by an individual throughout the entire tracking period. Next, we established the used habitat within

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eight-day periods by calculating the mean $NDVI_{habitat}$ of used sites weighted for the proportion of visits, hereafter called the 'used $NDVI_{habitat}$' (see Figure 6 for a visual example of this procedure). We then used a LMM to establish the across-individual relationship between available and used habitats over time, where we modelled 'used $NDVI_{habitat}$' as a response variable, with the predictors 'available $NDVI_{habitat}$', Date (numeric) and their two-way interaction, and we added random intercepts for each level of 'individual' to account for the relatedness between repeated measurements of the same individuals. We additionally aimed to describe the relationship between the available habitat and the relative amount of foliation in sites that birds used over time, for which we used the same model terms with 'used $NDVI_{temp}$' as the response variable. This variable was also calculated as the mean $NDVI_{temp}$ of used sites weighted for the proportion of visits.

To allow for a further interpretation of patterns in habitat use in terms of spatial behaviour, we established the extent to which individuals revisited the same sites within their home-ranges over time. Therefore, we calculated the Shannon equitability index (E_h) for used sites, based on the occurrence of node-ID's across the different eight-day periods that individuals were tracked. This value ranges between 0 and 1, where a value of 1 would indicate that an individual visited the same sites every eight days during the entire tracking period, whereas low values represent a higher diversity in used sites over time. We then used a linear model to establish the between-individual relationship between habitat (within home-ranges) and home-range use, for which we treated the equitability of sites as a response variable, and available $NDVI_{habitat}$ as a linear predictor.

We performed two model selection analyses to explore the relationship between NDVI and the arthropod numbers within the pitfall and malaise traps. For this purpose, we used GLMM's with the number of arthropods (total count per order per catching event per site) as response variable with a negative binomial error distribution. In each model we included an offset for catching days, to account for differences in sampling duration, and random intercepts for round-ID and location-ID to account for the relatedness between samples from the same dates and locations. Additionally, we always included 'order' as a fixed factor in the model. We considered three potential relationships

Photo 4. Undergrowth of a forest patch during the dry season. The tree and shrub layers remain (partly) foliated (2 January 2019).

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between arthropod numbers and NDVI: (1) no relationship, represented by a 'null model' without NDVI terms, (2) an overall log-linear relationship, represented by a model with main $NDVI_{(x)}$ terms ($NDVI_{habitat}$ and $NDVI_{temp}$) and (3) a log-linear relationship that differs between orders, represented by a model with main $NDVI_{(x)}$ terms and their two-way interactions with taxonomic order. In order to analyse the relationship between NDVI and arthropod abundance we acquired NDVI values by following the same procedure as described for the vegetation ground-truthing. The dates of these drone observation differed by 3.00 ± 1.23 (mean ± SD) days from the mid-date of the (four-day) sampling period. Since we possess no prior knowledge about the spatial scale at which our arthropods measurements are related to NDVI in the environment, we included scale as a variable in our analysis. Therefore, we created ten circular buffers ranging from 10 m to 100 m around the trapping sites to calculate the mean NDVI at different scales. These buffers were used to specify ten different sub-models for relationships 2 and 3, which we parametrized with $NDVI_{(x)}$ values from each scale. We used AICc values to select a confidence set of best performing models, which included the minimum number of models with a cumulative AICc weight of >0.95. We used the model weight to calculate the weighted estimate and weighted standard error for the NDVI coefficients within this set of models (following Symonds & Moussalli 2011). To assess the model fit we also calculated the marginal R^2 and conditional R^2 of the best performing models. To compare the trends of different taxonomic orders within forest and savannah habitat we used the estimates of both the $NDVI_{temp}$ and arthropod models. Therefore, we first calculated the least-squared means for $NDVI_{temp}$ over time for the average $NDVI_{habitat}$ of forest (mean = 0.59) and savannah (mean = 0.18) sites, which we then supplied to the arthropod models to predict the number of arthropods in both habitats.

RESULTS

The study period in 2020 was relatively dry when compared to the foregoing years (Figure 1), where the timing of the first rainfall (21 March) was about a month later than the average for the period 2016–2019 (mean: 23 February, range: 5 February – 11 March). Also, the cumulative amount of rainfall for the study period was lower than in any of the previous four years, with a total of 32.0 mm by 15 April (2016–2019, mean: 103.4 mm, range: 93–114 mm).

NDVI ground-truthing

Despite the low amounts of rainfall, we observed considerable spatiotemporal change in NDVI during the study period, where overall patches of closed-canopy forest appeared to show high and stable NDVI values throughout the study period, whereas the NDVI in open savannah sites shifted from low to higher values later in the season (Figure 2).

When focusing on the (savannah) grass layer, the NDVI values were relatively low in the beginning of February, with minor temporal increase during the following period (Figure 3). Based on our ground-based measurements we find that only a minor part of the spatiotemporal variation in NDVI of grass layer transects could be attributed to grass cover (marginal

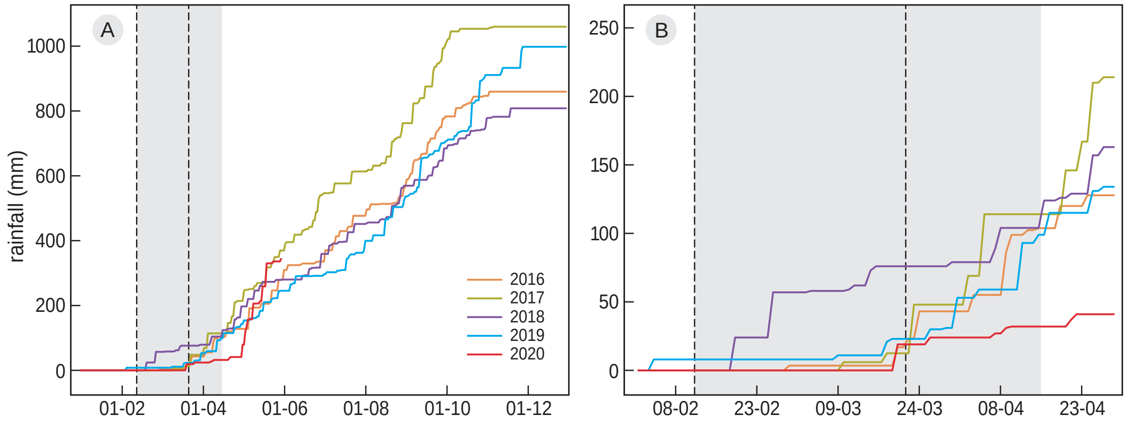

Figure 1. Cumulative amount of rainfall within the study area in Comoé National Park for the years 2016–2020. The grey area marks the period with NDVI and arthropod measurements, and dashed lines show the period in which Pied Flycatchers were tracked. Measurements were obtained on a daily basis by means of a rain gauge (data: Comoé Research Station, Ivory Coast).

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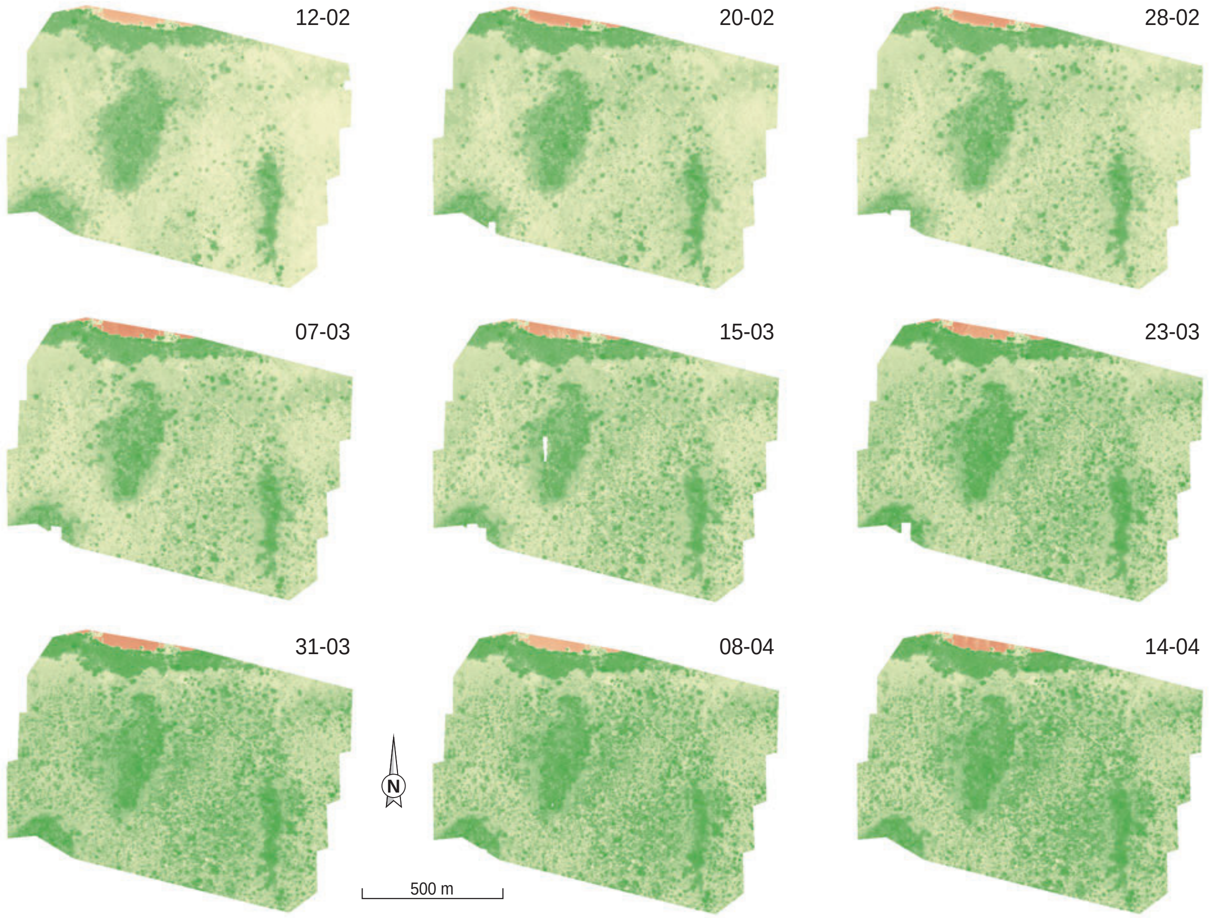

Figure 2. NDVI maps of the study area in Comoé National Park for the period 12 February to 14 April 2020. NDVI values are based on multispectral images that were collected every eight days by means of a drone.

$R^2 = 0.10$), which showed a positive linear effect on NDVI ($\chi^2_1 = 17.75$, $P < 0.001$, $\beta = 0.43 \pm 0.10$). Most of the remaining variance could be attributed to site and date specific influences that were captured by random effects within our model (conditional $R^2 = 0.94$; Table S1B).

For the canopy layer we observed large variation in temporal NDVI patterns between tree species. In some species NDVI increased steeply (e.g. *Burkea africana*) while for others it remained relatively constant over time, at either high (e.g. *Cola cardifolia*) or low (e.g. *Anogeissus leiocarpus*) values (Figure 3). Based on our ground-based measurements we found that these temporal patterns were largely attributable to changes in foliage cover (marginal $R^2 = 0.50$), for which we established a quadratic relationship with NDVI ($\chi^2_2 = 492.77$, $P < 0.001$; $\beta_{\text{linear}} = 0.53 \pm 0.05$, $\beta_{\text{quadratic}} = -0.18 \pm 0.06$). The remaining variance is largely explained by species, date and tree-specific characteristics that were captured by the random effects in the model (conditional $R^2 = 0.93$, Table S1A).

Although the relationship between foliage cover and NDVI for the canopy and grass layer was differently shaped, respectively quadratic and linear, the slopes of these relationships were similar within the range observed in both layers (Figure S3). The additional main difference in NDVI (canopy: estimate = 0.35 ± 0.03; grass layer: estimate = 0.22 ± 0.03) could be explained by the relative level of these layers in the vegetation. Aerial imagery of an open canopy might capture vegetation from underlying strata whereas an open grass layer will mostly reveal the soil surface, which might again differ in reflectance due to the presence or absence of (burned) litter (Table 1). Therefore, ground-truthing results supported the use of $\text{NDVI}_{\text{temp}}$ to describe changes in foliage cover (i.e. foliation) and $\text{NDVI}_{\text{habitat}}$ to express spatial differences that are mostly related to habitat.

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General movement behaviour

In total we tracked the spatial behaviour of nine flycatchers for an average duration of 28 days (range: 14–40; Table 2, Figure S3A). During this period individuals visited on average 5.22 sites (range: 3–9). The number of detections were unequally distributed across the daylight period. The number of receptions peaked between 8:00 and 9:00 am., and subsequently decreased throughout the day with a slight rise around 16:00 (Figure S3B). During the tracking period three of the nine individuals remained undetected within the node grid for periods of one to six days (Figure S4). Given that these birds were still detected by the directional antenna's, this pattern likely arose from periods of residence beyond the detection range of the nodes. We also observed individual movements within the node grid, as apparent from the use of new sites and changes in relative presence at previously visited sites (Figure 4).

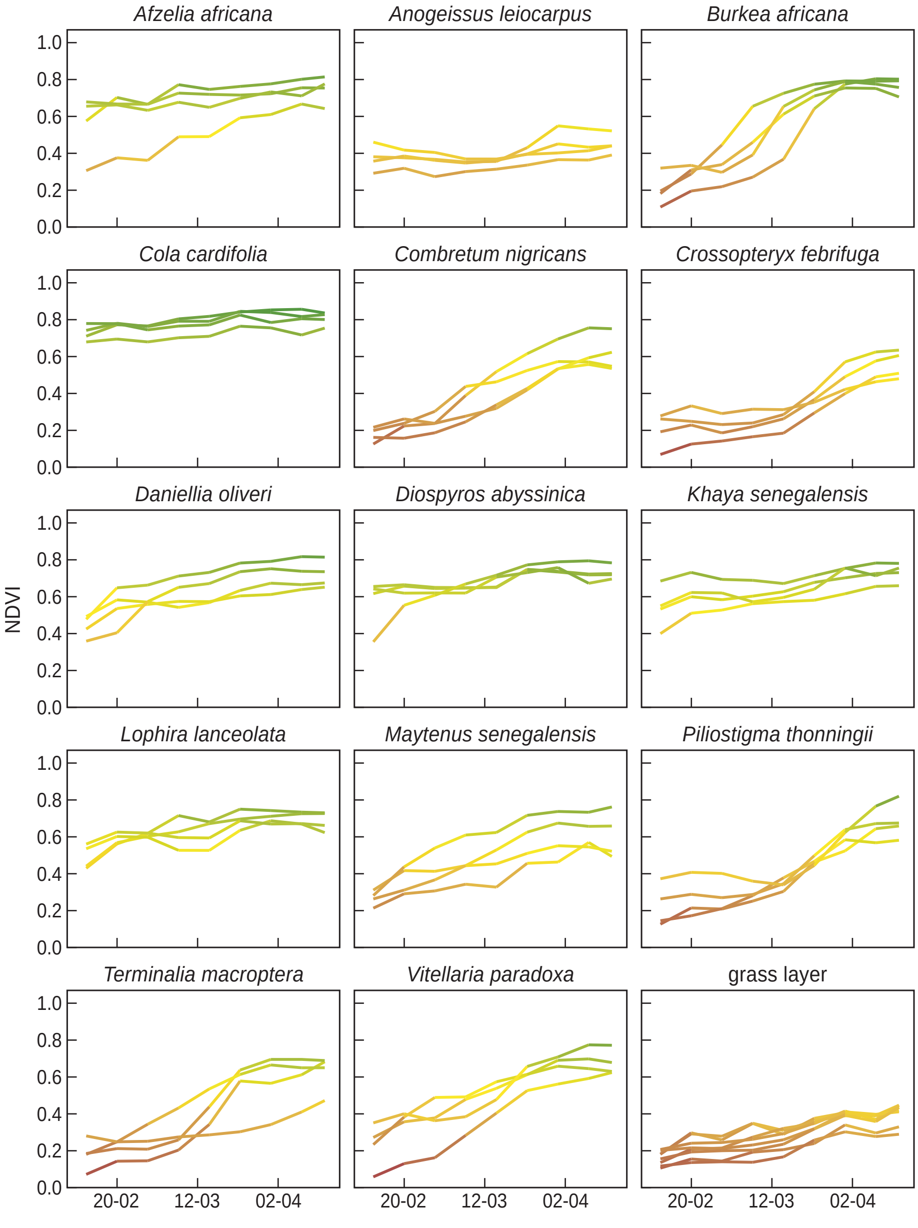

Figure 3. NDVI values for the canopy of individual trees and grass layer transects during the period 12 February to 14 April 2020. Lines show average NDVI values for individual tree crowns (n = 4 per species) and grass layer transects (n = 8) over time. Colour coding matches the y-axis.

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Table 2. Meta-data of radio-tagged Pied Flycatchers captured between 10 February and 15 March 2020 (n = 13). Detailed site use data is shown for individuals that were included in the site use analysis (n = 9). The total number of detections are given for nodes (local receivers used in the site use analysis) and directional Yagi antennas (used for detecting presence or absence within a larger range); Age: 2 = second calendar year/first winter, >2 = after second calendar year; # presence = total number of 5-minute periods that a bird was located within 50 m from a node; # periods = number of 8-day periods during which a bird was tracked.

Tag-ID	Sex	Age	Start tracking	# detections (Nodes)	# detections (Yaggi)	Last seen (Yaggi)	Included	Tracking days	# presence used	# periods $\text{NDVI}_{\text{habitat}}$	# periods $\text{NDVI}_{\text{temp}}$	# nodes visited	# nodes/period (range)
61332A2D	Female	> 2	7 Mar	92.057	7.925	3 May	Yes	14	689	3	3	3	2–3
6133522A	Female	2	25 Feb	107.194	11.008	21 Apr	Yes	25	304	4	4	9	2–7
6133522D	Female	2	22 Feb	196.887	292.285	30 Apr	Yes	28	748	5	5	3	2–3
61520019	Male	2	13 Feb	153.205	36.641	18 Apr	Yes	37	375	3	2	7	4–7
6152002A	Male	> 2	14 Feb	350.043	545.483	5 May	Yes	36	2039	6	5	7	1–5
61520766	Female	> 2	24 Feb	104.717	122.829	6 May	Yes	26	513	4	4	4	4–4
61521978	Male	2	20 Feb	35.847	576	4 May	Yes	30	194	5	5	4	2–4
61524B66	Female	> 2	6 Mar	96.229	40.693	17 Apr	Yes	15	242	3	3	4	2–4
61611E2A	Male	2	10 Feb	94.334	1.474	2 May	Yes	40	516	6	5	6	1–6
61335200	Female	2	28 Feb	13.189	30.495	30 Apr	No	–	–	–	–	–	–
61347F00	Female	> 2	4 Mar	3.982	4.223	7 May	No	–	–	–	–	–	–
61523319	Female	> 2	15 Mar	0	0		No	–	–	–	–	–	–
61526652	Male	> 2	13 Feb	44.842	1.546	3 May	No	–	–	–	–	–	–

Photo 5. Edge of a forest patch with view towards the savannah. The undergrowth mostly consists of evergreen shrubs, whereas the canopy layer is dominated by *Anogeissus leiocarpus*, a deciduous tree species that typically occurs in forest edges (19 December 2018).

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However, all flycatchers showed a high degree of within-individual overlap in site use over time (E_h used sites: mean: 0.95 ± 0.03, range: 0.90–1.00).

NDVI change

All sites showed an increase in NDVI during the tracking period (Figure 5A). However, the amount of foliation ($\text{NDVI}_{\text{temp}}$) differed between habitats (interaction $\text{NDVI}_{\text{habitat}} \times$ date: $\chi^2_1 = 117.83$, $P < 0.001$). The savannah showed higher foliation rates than forest habitats (Figure 5B). The used $\text{NDVI}_{\text{temp}}$ of tracked flycatchers will thus increase during the tracking period, whereas the specific amount of increase can be influenced through habitat selection.

Habitat selection

On average, the tracked flycatchers increased their use of savannah towards the end of the tracking period, as demonstrated by a linear decrease in used $\text{NDVI}_{\text{habitat}}$ over time ($\chi^2_1 = 13.85$, $P < 0.001$, $\beta_{(10\text{ days})} = -0.02 \pm 0.01$; Figure 7A). During the same period the average amount of foliation across used sites increased at an accelerating rate (Figure 7B), as shown by a quadratic increase of $\text{NDVI}_{\text{temp}}$ over time ($\chi^2_2 = 512.59$, $P < 0.001$, $\beta_{\text{linear}} = 0.31 \pm 0.02$, $\beta_{\text{quadratic}} = 0.11 \pm 0.01$).

When considering site-use behaviour, there appeared to be a negative relationship between the available $\text{NDVI}_{\text{habitat}}$ within home-ranges and the degree to which

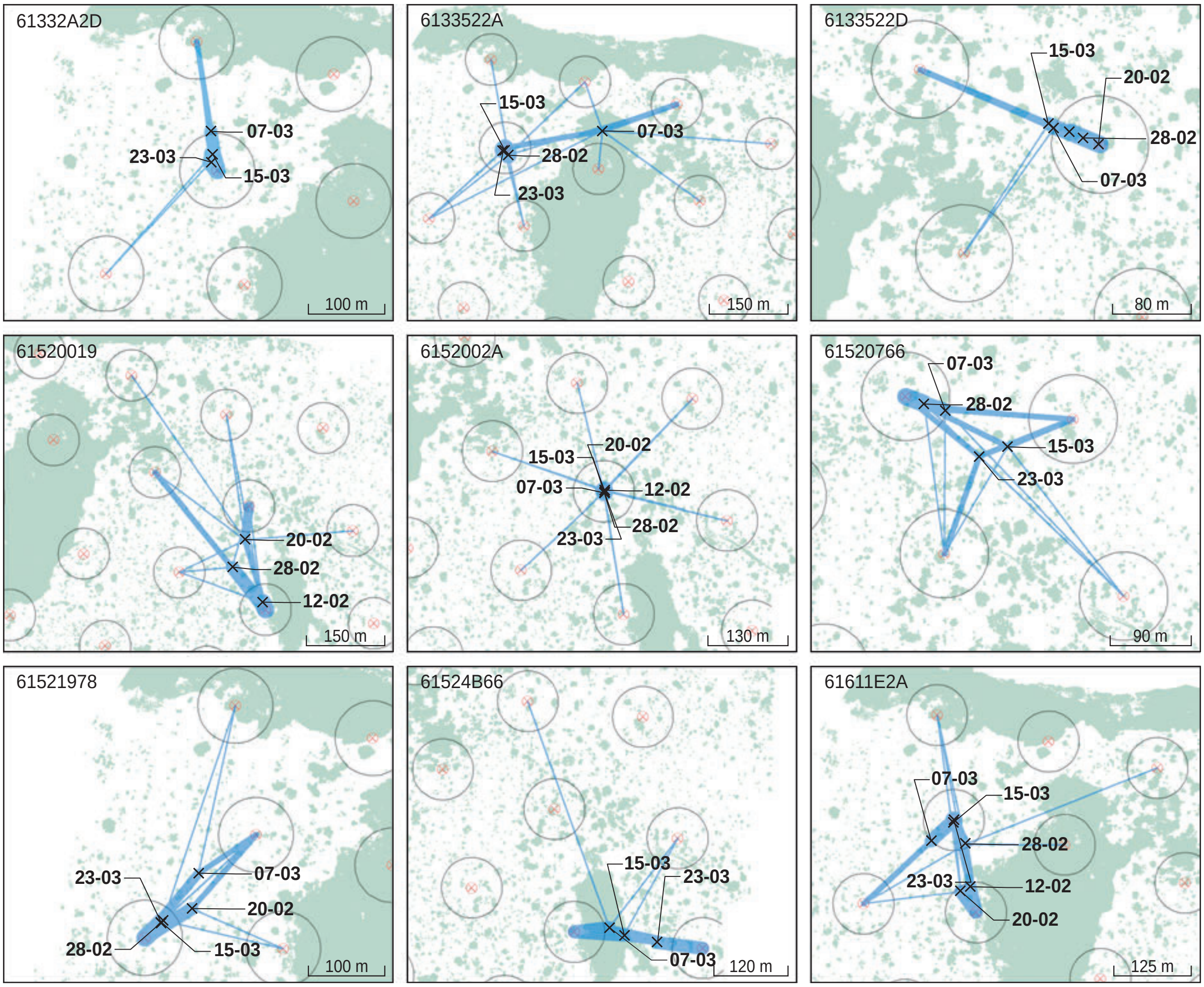

Figure 4. Individual movements of radio-tracked Pied Flycatchers based on presence near nodes. Red markers depict node locations, for which the circles mark the range (radius: 50 m) around nodes in which the presence of individuals was measured. For illustrative purposes the centre location is plotted per 8-day period (black cross), calculated as the mean location of all visited nodes weighted for the proportion of visits. Blue lines connect the centre locations to the associated nodes, where line width represents the proportion of visits (range: <0.01–1.00). The green areas in the background show the distribution of forest patches (large filled areas), and individual canopies in the savannah.

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individuals visited the same sites over time ($\beta = -0.28 \pm 0.15$, $F_{1,7} = 3.67$, $P = 0.10$). This suggested a tendency of individuals with more forested home-ranges to visit fewer of the same sites over time. In accordance, individuals with more forested home-ranges showed a larger temporal decrease in used $\mathrm{NDVI}_{\mathrm{habitat}}$ (available $\mathrm{NDVI}_{\mathrm{habitat}}$ × date: $\chi^2_1 = 7.46$, $P < 0.01$). Consequently, the variation in used $\mathrm{NDVI}_{\mathrm{habitat}}$ between individuals decreased during the tracking period. All individuals used a narrower range of $\mathrm{NDVI}_{\mathrm{habitat}}$ values at the end of the tracking period, values that more closely resembled savannah (Figure 8B). Given the differences in foliation between the habitats we expected changes in habitat-use to result in a higher increase of $\mathrm{NDVI}_{\mathrm{temp}}$ over time for birds with more forested home-ranges. However, we did not find a significant interaction between $\mathrm{NDVI}_{\mathrm{habitat}}$ and date ($\chi^2_1 = 0.27$, $P = 0.60$). Instead, the outcomes showed a consistent difference over time, insofar that the used $\mathrm{NDVI}_{\mathrm{temp}}$ of birds within more forested home-ranges was relatively lower compared to birds with more savannah in their home-range ($\chi^2_1 = 11.61$, $P < 0.001$). At the same time the absolute values of used $\mathrm{NDVI}_{\mathrm{temp}}$ increased for all individuals as a result of overall foliation in the environment ($\chi^2_1 = 130.00$, $P < 0.001$, Figure 8B).

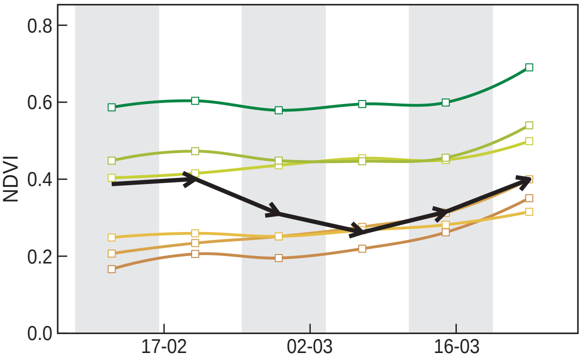

Figure 6. Example of individual site use for tag-ID '61611E2A'. To establish site selection we compared the weighted mean NDVI of visited sites (arrowed line) to the mean NDVI of the total home-range (coloured lines). These comparisons were done at the level of 8-day periods (marked by alternating grey and white areas), yielding repeated measurements of the same individuals over time.

NDVI and arthropod abundance

To further assess the potential role of food availability in the relationship between NDVI and site use of flycatchers, we explored the connection between NDVI and arthropod abundance, using the data of 3218 captured arthropods (malaise: $n = 1567$, pitfalls: $n = 1651$), belonging to eight taxonomic orders (malaise: $n = 7$, excluding Blattodea, pitfalls: $n = 7$, excluding Lepidoptera). The temporal variation in the numbers of captures between taxonomic orders and trap types was large (Figure 9).

A set of six models best explained the observed variance in the numbers of captured terrestrial arthropods (Table S2A). All these models include an interaction between $\mathrm{NDVI}_{(x)}$ and order, with $\mathrm{NDVI}_{(x)}$ measurements taken within a range between 10 m and 60 m from trap sites. The model-averaged estimates for $\mathrm{NDVI}_{\mathrm{habitat}}$ from these models reflect habitat-related

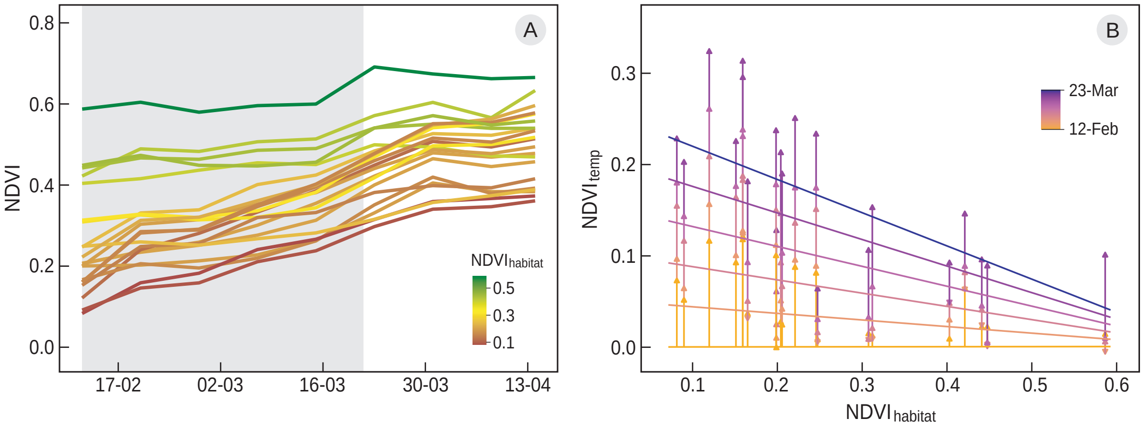

Figure 5. (A) Average NDVI for areas around nodes (radius: 50 m, $n = 21$) per 8-day period. Line colours are based on the NDVI on 12 February, which is used as a proxy for habitat ($\mathrm{NDVI}_{\mathrm{habitat}}$). (B) Interaction between $\mathrm{NDVI}_{\mathrm{habitat}}$ and the amount of foliation ($\mathrm{NDVI}_{\mathrm{temp}}$) for the same sites, measured as the difference in NDVI relative to 12 February. Arrows show the trajectories of the same sites over time. Lines represent the estimates marginal means for $\mathrm{NDVI}_{\mathrm{temp}}$, based on the interaction between the linear effects of Date and $\mathrm{NDVI}_{\mathrm{habitat}}$, which indicate a larger amount of foliation in savannah, i.e. low $\mathrm{NDVI}_{\mathrm{habitat}}$, compared to forest.

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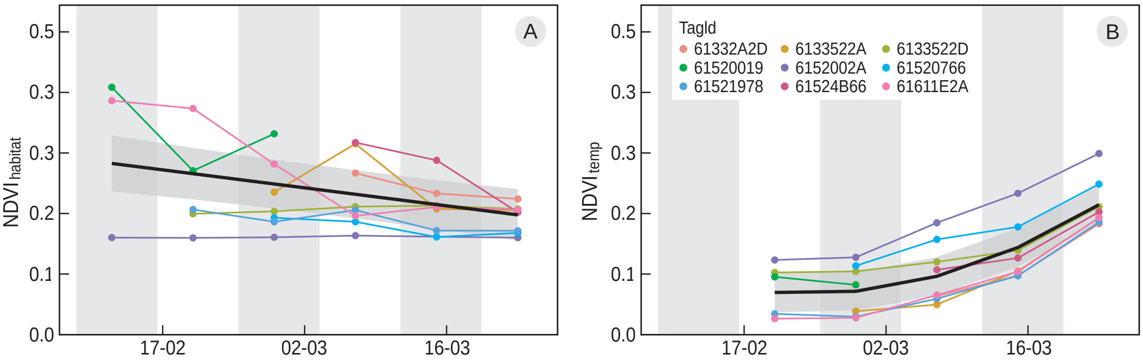

Figure 7. (A) Average $\mathrm{NDVI}_{\mathrm{habitat}}$ values of sites used by radio-tracked flycatchers (n = 9) over time. The black line gives the linear effect of date (± 95% CI) based on an LMM, which shows an average decrease in the use of forest over time. (B) Average $\mathrm{NDVI}_{\mathrm{temp}}$ based on the same used locations. The model prediction shows a quadratic increase in the amount of foliation within used sites over time. The alternating grey and white areas mark the 8-day periods that are used in the analysis.

differences in captures per order (Table 3). In the orders Hemiptera and Orthoptera the amount of forest habitat was positively associated with the number of captures, whereas this association was negative in Hymenoptera. For $\mathrm{NDVI}_{\mathrm{temp}}$ the confidence interval of the estimate only excludes zero in Hemiptera, where the number of captures were positively associated with the amount of foliation. For the malaise traps the number of captures were best explained by seven models that incorporate $\mathrm{NDVI}_{(x)}$ measurements from a radius of 30 m to 70 m (Table S2B). Similar to the pitfalls, all of these models included an interaction between $\mathrm{NDVI}_{(x)}$ and taxonomic order. The model-averaged estimate for $\mathrm{NDVI}_{\mathrm{habitat}}$ did not exclude zero in any of the orders, reflecting no effect of habitat on the captured numbers of flying arthropods, although for some orders there appeared to be a directional tendency (Table 3). For $\mathrm{NDVI}_{\mathrm{temp}}$ the model-averaged estimates did not include zero for Diptera and Lepidoptera, demonstrating a positive association between foliation and the number of captured Lepidoptera while the numbers of captured Diptera showed an opposite trend.

Based on these model outcomes we expected different dynamics in arthropod abundance between habitats (Figure 10). During the study period some

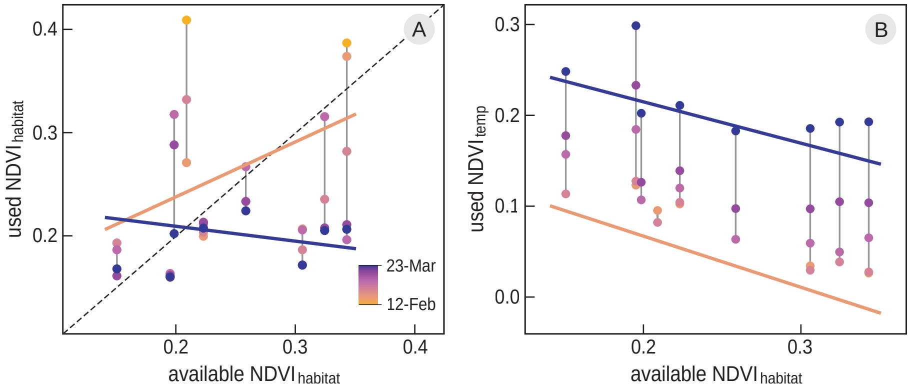

Figure 8. (A) Relationship between the average $\mathrm{NDVI}_{\mathrm{habitat}}$ within individual home ranges (available $\mathrm{NDVI}_{\mathrm{habitat}}$) and sites that were used by individuals (used $\mathrm{NDVI}_{\mathrm{habitat}}$) over time. Lines connect observations of the same individuals. The dashed line illustrates when birds use sites in proportion to their availability. The model predictions show that birds increased their use of savannah during the study period, where birds with more forested home-ranges show the change in habitat use over time. (B) Relationship between the average $\mathrm{NDVI}_{\mathrm{habitat}}$ within individual home-ranges (available $\mathrm{NDVI}_{\mathrm{habitat}}$) and the change in NDVI relative to 12 February ($\mathrm{NDVI}_{\mathrm{temp}}$), for sites that were used by individuals over time. The predictions show that, at any time during the study, birds with forested home-ranges used sites with lesser amounts of foliation compared to birds with savannah home-ranges. The predictions in both graphs are based on an LMM with an interaction between the linear predictors date and available $\mathrm{NDVI}_{\mathrm{habitat}}$, and given for 20 February (when $\mathrm{NDVI}_{\mathrm{temp}} > 0$) and 23 March.

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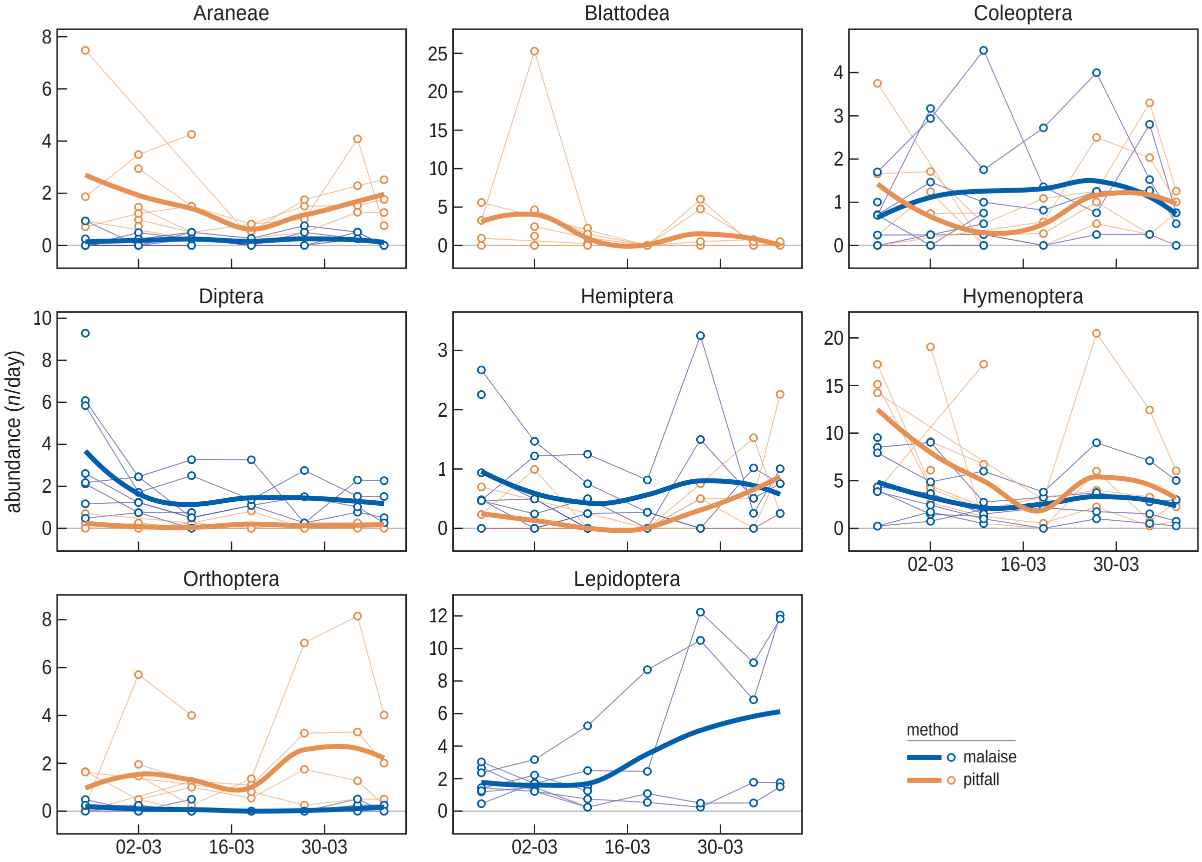

Figure 9. Average daily captures per 4-day trapping period for different orders. Lines connect datapoints from the same trapping locations and fattened lines show the overall smoothed means per trapping method. Note that the y-axis differs between taxonomic orders.

orders should become more abundant on the savannah (e.g. flying Lepidoptera and ground dwelling Hemiptera) whereas other orders should remain stable (e.g. ground-dwelling Orthoptera) or decrease (e.g. groundwelling and flying Hymenoptera). The predictions for forest habitat showed little variability over time, where in general arthropod abundance is predicted to remain stable throughout the study period.

DISCUSSION

Movement behaviour

By tracking small-scale movement behaviour, we show that flycatchers are flexible in their habitat use. In particular we show that flycatchers occupy both savannah and forest habitat and narrow their site use to savannah during the second half of the non-breeding season, where individuals with more forested home-ranges show the largest change over time. These changes involve adjustments in site use intensity of sites that were revisited over time, and the abandonment or use of new sites within home-ranges. Flexibility in site use of flycatchers is in accordance with previous findings of Stünzner-Karbe (1996) who also observed individual movements from forest to savannah during the second half of the non-breeding season, with more birds present in forest at the start of the non-breeding period. Our observations from previous seasons (based on colour-ringed individuals) confirm this pattern. These movements are likely typical for non-breeding flycatchers, and, for example, not a result of aberrant rainfall conditions during our study. Similar behaviour has been described in other species, for example by Brunner *et al.* (2022), who observed individual home-range adjustments between the wet and dry season in non-breeding Swainson's Warblers *Limnothlypis swainsonii* in the Neotropics. Brunner *et al.* (2022) found, as we did, that during the dry season some individuals already occupied home-ranges within the habitat that was later (during the wet season) also used by birds from other habitats, with the

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consequence that individuals differed in the degree to which they adjusted their site use over time.

Arthropods

Flycatchers influence their access to specific arthropod groups by moving between habitats that seasonally vary in arthropod abundance. We first show that the variation in NDVI due to habitat and foliation can have a different association with arthropod numbers, which also depends on taxonomic orders. These findings are in line with previous findings of taxa-specific numerical trends of arthropods in relation to seasonality in African environments (Nummelin & Nshubemuki 1998, Wagner 2001) as well as in the distribution of taxa across small-scale habitats (Blaum *et al.* 2009). Furthermore, we show that the relationship between vegetation conditions and arthropod numbers differs between our sampling techniques. This might be due to variation in this relationship among lower taxonomic levels, where our trap types (targeting either ground-dwelling or flying arthropods) will likely capture different species and life-stages that belong to the same orders (McCravy 2018). Altogether, these results do not support a simple relationship between NDVI and arthropod abundance, and therefore we require specific insight into the diet and behaviour of flycatchers to understand the implications for food availability.

A diet analysis by means of DNA meta-barcoding revealed that flycatchers in our study populations have a rather limited diet. Most of the consumed prey belong to two groups, namely Hymenoptera, and specifically the ant genus *Camponotus* (c. 40% of consumed biomass) and Lepidoptera (c. 20% of consumed biomass; Ouwehand, Verkuil & Both unpubl. data, based on two seasons in 2018–2019; see Verkuil *et al.* (2022) for methods). Our estimated trends for Hymenoptera from pitfall samples (which in contrast to flying Hymenoptera from malaise traps mostly concern ants, including the genus *Camponotus* as confirmed by DNA meta-barcoding of captured ants; Ouwehand, Verkuil & Both unpubl. data) show that ants are overall more abundant in the savannah than in forest, whereas their numbers are predicted to decrease during the time that flycatchers increase their use of this habitat (Figure 10). These opposing patterns contradict the notion that flycatchers track the availability of their most prominent prey group, *Camponotus* ants. The results do however show such a pattern for the second most prominent prey group, Lepidoptera, for which the predicted increase within savannah is in line with the increased use of this habitat by flycatchers. However, it is important to note that our estimated trend for Lepidoptera is solely based on adults caught in malaise traps, whereas our field observations indicate that the

Table 3. Model-averaged estimates and 95% confidence interval for the log-linear regression coefficients $\text{NDVI}_{\text{habitat}}$ and $\text{NDVI}_{\text{temp}}$, based on the best performing models for arthropod captures within pitfall and malaise traps (Table S2). Weighted estimates for which the confidence interval does not include zero are shown in bold.

Parameter	Taxonomic order	Pitfall		Malaise	
		Estimate ± SE	95% CI	Estimate ± SE	95% CI
(1) $\text{NDVI}_{\text{habitat}}$	Aranea	0.87 ± 1.36	–1.82 – 3.56	2.96 ± 2.03	–1.04 – 6.96
	Blattodea	2.37 ± 1.50	–0.58 – 5.32	– –	– –
	Coleoptera	–2.89 ± 1.60	–6.03 – 0.26	1.52 ± 1.66	–1.75 – 4.79
	Diptera	–0.56 ± 2.12	–4.75 – 3.62	1.86 ± 1.62	–1.32 – 5.05
	Hemiptera	**4.77 ± 2.09**	**0.65 – 8.89**	**2.39 ± 1.73**	**1.02 – 5.79**
	Hymenoptera	**–3.05 ± 1.36**	**–0.57 – –0.36**	–0.73 ± 1.59	–3.87 – 2.41
	Lepidoptera	– –	– –	–0.50 ± 1.63	–3.71 – 2.70
	Orthoptera	**4.03 ± 1.42**	**1.22 – 6.83**	4.54 ± 2.40	–0.19 – 9.26
(2) $\text{NDVI}_{\text{temp}}$	Aranea	–0.12 ± 2.69	–5.42 – 5.19	2.35 ± 3.21	–3.98 – 8.68
	Blattodea	–2.56 ± 3.07	–8.61 – 3.48	– –	– –
	Coleoptera	3.07 ± 3.10	–3.04 – 9.18	–0.26 ± 1.97	–4.15 – 3.62
	Diptera	–0.05 ± 4.22	–8.36 – 8.27	**–4.12 ± 1.93**	**–7.92 – –0.32**
	Hemiptera	**12.09 ± 4.03**	**4.15 – 20.03**	2.14 ± 2.24	–2.26 – 6.55
	Hymenoptera	–1.95 ± 2.97	–7.81 – 3.91	–1.75 ± 1.71	–5.11 – 1.62
	Lepidoptera	– –	– –	**5.78 ± 1.77**	**2.29 – 9.27**
	Orthoptera	0.73 ± 3.09	–5.37 – 6.82	1.96 ± 4.38	–6.66 – 10.59

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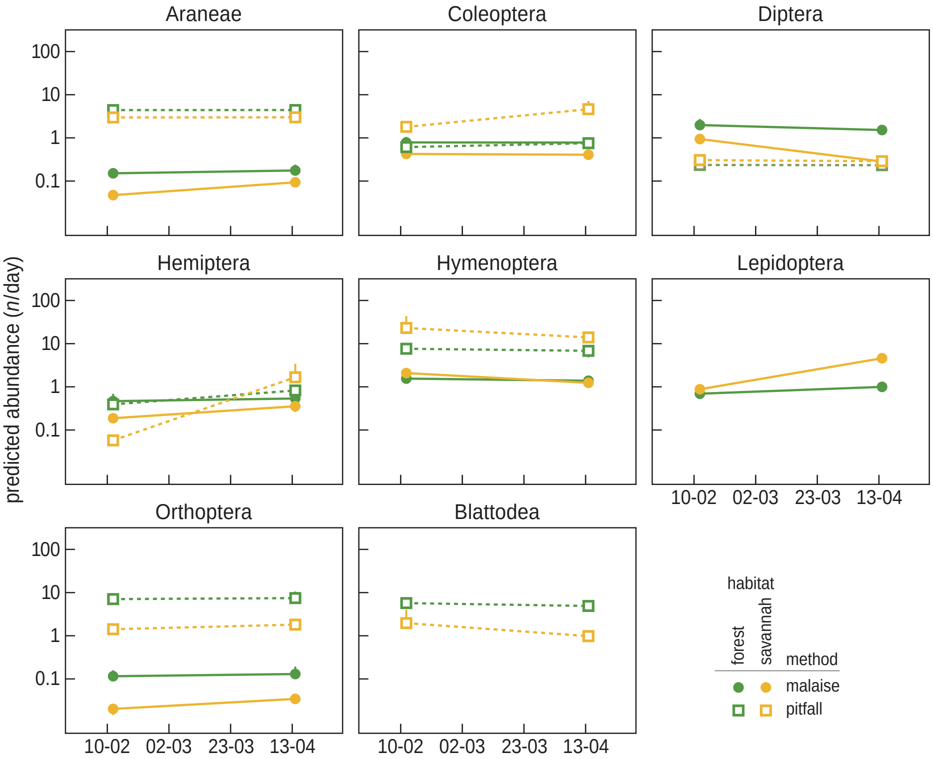

Figure 10. Estimated abundance for different arthropod orders within savannah and forest habitats over time. Predictions are based on the average $NDVI_{habitat}$ and $NDVI_{temp}$ of each habitat and their effects on arthropod abundance based on the model selection for malaise traps and pitfalls. Estimates are given for 12 February and 14 April, where error bars give the range of predictions from all selected models (Table S2).

Lepidoptera consumed by flycatchers also includes caterpillars. The absence of this prey group from our samples is likely due to the fact that caterpillars occur within canopies, whereas pitfall and malaise traps are designed to capture arthropods that move on or near the ground (McCravy 2018). Similarly, other arthropods groups that occur higher in the vegetation are likely underrepresented in our sampling, whereas foraging observations during our study show that the majority of foraging attempts of flycatchers were directed at leaves or branches within trees (85.7% on a total of 77 foraging attempts from 6 individuals), which is similar to that found by other studies (Stünzner-Karbe 1996, Salewski *et al.* 2002). Therefore, our findings might only have partially disclosed the dynamics of those arthropods that are relevant for foraging flycatchers. Despite these caveats, our results support the possibility that flycatchers use small-scale habitat heterogeneity to track seasonal changes in food availability.

We acknowledge that by only considering (log-) linear relationships with vegetation greenness, our models are unable to account for the short-term fluctuations in arthropod abundance that we observed (Figure 9, also see Ouwehand *et al.* 2023). Our field observations also confirm that flycatchers often exploit ephemeral food sources. This includes the previously described cases where we observed flycatchers foraging on temporal outbursts of caterpillars in canopies of *Daniellia olliveri* with fresh-grown leaves (February 2020) and in one occasion on berries in fruiting *Gymnosporia senegalensis* bushes (February 2018). Furthermore, we observed individuals that specifically foraged in flowering trees, for example in *Khaya senegalensis*, *Crossopteryx febrifuga* and *Terminalia macroptera*, where they might profit from concentrations of flower-visiting arthropods. In these examples the occurrence of food sources is associated with particular leafing and flowering stages of specific tree species. We recognize that such fine-scale dynamics are not addressed in our analysis, although they are relevant for explaining short-term behaviour. This is also indicated by Ouwehand *et al.* (2023) who found that individuals attained a higher body mass on days with higher numbers of arthropods. Despite the existence of such short-term dynamics, we are confident that the

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average trends in arthropod abundance are still useful for understanding the changes in flycatcher behaviour over a longer timescale (i.e. the duration of our study period).

Our findings are a demonstration of the need for restraints in using NDVI as a general proxy for food conditions of insectivorous migrants. By showing that the relationship between arthropod abundance and vegetation greenness depends on the specific taxa and sampling methods we challenge the validity of the common use of NDVI as a proxy for food availability, especially within studies that have no insight into the diet and foraging behaviour of species during the non-breeding season (e.g. Schaub *et al.* 2011, Kristensen *et al.* 2013, Thorup *et al.* 2017, Knight *et al.* 2019). We acknowledge that the small-scale dynamics in our study might differ from the dynamics that occur on the large scales that are considered in most tracking studies, however the applicability of large-scale simplified measurements will equally depend on the specific (small-scale) ecology of species. In addition, the applicability of large-scale NDVI as a resource proxy might be further hampered since such measurements discount small-scale heterogeneity in vegetation conditions, which we show plays a key role in the availability of resources during various parts of the season. In conclusion, we consider insight into the food sources of species and their relationship with vegetation conditions is a precondition for using remote sensing-derived proxies of food availability in studies on insectivorous songbirds. For most migratory species this will require investment in ecological fieldwork in situ.

Potential resources

Next to changes in the abundance of food resources, the observed changes in habitat use might also be influenced by an increase in food requirements over time. Our study period coincides with the period that flycatchers replace their tertials and a proportion of the body feathers, which on average starts around halfway through February and continues until the end of March (Salewski *et al.* 2004). During this period individuals experience rising energetic costs due to feather growth (Lindström *et al.* 1993). Furthermore, the end of our study period overlaps with pre-migratory fuelling, starting around 5 March within our population (Ouwehand *et al.* 2023). This period is characterized by hyperphagia and a steep increase in body weight (Ouwehand *et al.* 2023). Given the importance of successful fuelling for the timing of migration and survival and the role of plumage quality on sexual selection (Sirkiä & Laaksonen 2009), the fitness benefits of access to food resources will increase during these phases. As a result, individuals might favour access to food over other factors that might negatively affect (short-term) fitness, such as predation risk, during these stages. Such a shifting trade-off might already by itself (i.e. regardless of any change in food availability between habitats) initiate a change in habitat use over time, for example if predation risk is higher on the savannah. Although we lack insight into the role of predation, our observations suggest that movements towards the savannah coincide with increasing food sources, and are therefore unlikely to be solely driven by changes in risk-taking behaviour.

Photo 6. Flycatcher with radio-transmitter (7 March 2020).

The habitat shift that we observed near the end of the non-breeding period is an important part of individual movement strategies that unfold throughout the whole non-breeding season. As described by Stünzner-Karbe (1996), flycatchers are generally absent on the savannah during the first half of the non-breeding season, but start to settle in this habitat after (human-induced) burning in December-January. Colour-ring observations show that these settlers come from nearby forest patches where they occupy territories during the first part of the non-breeding season (Stünzner-Karbe 1996, Ouwehand & Bil unpubl. data). Based on these

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findings it is likely that those individuals that were already present within (homogenous) savannah sites at the start of our study (February) may have moved in from other places during the preceding months. These individuals probably express different movement behaviour to those birds that occupy home ranges on the boundary between forest and savannah habitat (i.e. the individuals with more heterogeneous territories in this study), for which (colour ring) observations indicate that they are more likely to stay within the same home-range throughout the non-breeding period (Ouwehand & Bil unpubl. data, Stünzner-Karbe 1996). The tendency of birds in savannah habitats showing a more consistent use of their home-range during the period of our study, might therefore differ from the site-use consistency of these birds during the entire non-breeding season.

We hypothesize that flycatchers can influence their susceptibility to seasonality through settlement decisions. Flycatchers are territorial during the non-breeding season (Stünzner-Karbe 1996, Salewski 1999, Willemoes *et al.* 2018), and individuals are therefore limited in their ability to access sites that are already occupied by conspecifics (Krebs 1982). Given this competition individuals might occupy sites that are temporarily unexploited, in order to ensure access to future (ephemeral) resources. This is in line with our finding that individuals did not often abandon sites, despite the changes in site use intensity. In this scenario, individuals with territories that include both forest and savannah habitat might explore a wider variety of resources under different circumstances, i.e. a more stable food supply in forest habitats during the dry season, and additional food in the more dynamic savannah during moult and fuelling. Alternatively, birds that do not occupy edge territories can relocate their territories from forest to the savannah when conditions improve in the latter. However, these individuals are thereby more reliant on resources in either habitat. Such benefits of heterogeneous territories are in accordance with the distribution of flycatchers in our study area, with highest densities of territories along the edges between forest and savannah habitat (see also Stünzner-Karbe 1996).

In conclusion, our findings indicate that small-scale heterogeneity likely plays a key role in the ability of flycatchers to cope with seasonal dynamics on a local scale. We do need further insight into the fitness benefits and existence of alternative movement strategies to determine the degree to which flycatcher populations rely on sedentary behaviour and small-scale habitat heterogeneity.

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SAMENVATTING

Het is vaak onduidelijk hoe trekkende zangvogels omgaan met seizoensveranderingen in Afrika, met name bij soorten die gedurende de winterperiode gebruikmaken van dezelfde verblijfplaats. In dit onderzoek richten we ons specifiek op de vraag of zangvogels zich aan seizoensveranderingen kunnen aanpassen door gebruik te maken van kleinschalige variatie in hun omgeving. Hiervoor hebben we naar overwinterende Bonte Vliegenvangers *Ficedula hypoleuca* in het nationaal park Comoé, Ivoorkust, gekeken. Met behulp van radiozenders laten we zien dat er halverwege de verblijfperiode van de vliegenvangers, in begin februari, relatief veel variatie bestaat in de mate waarin verschillende individuen het bos en de savanne gebruiken. In de daaropvolgende periode gaan individuen uit het bos meer gebruikmaken van plekken op de savanne, waarbij uiteindelijk alle individuen hoofdzakelijk dit habitat gebruiken. Deze verandering vindt plaats gedurende een periode van vergroening van de savanne, die gepaard gaat met een toename in het aanbod van specifieke insectengroepen. De verschuiving in het habitatgebruik van de vliegenvangers is daarmee mogelijk een reactie op een verbeterde voedselbeschikbaarheid in de savanne vergeleken met het eerste deel van de verblijfsperiode, waarin het bos waarschijnlijk betere voedselcondities biedt. Op basis van deze uitkomsten vermoeden we dat de vliegenvangers bij voorkeur territoria in bosranden vestigen, waardoor ze zowel toegang tot het bos als de savanne hebben, en zo beter in staat zijn om onder verschillende omstandigheden (voedsel)bronnen te vinden. Deze bevindingen bevestigen het belang van kleinschalige heterogeniteit voor de mate waarin de vliegenvangers gedurende de winterperiode op dezelfde plek kunnen verblijven.

RÉSUMÉ

Il est difficile de savoir comment les passereaux migrateurs font face aux changements saisonniers en Afrique, notamment les espèces qui sont fidèles à leurs territoires hivernaux. Nous avons donc spécifiquement cherché à savoir si ces espèces peuvent s'adapter en exploitant la diversité des habitats présents au sein de leur territoire. Pour cela, nous avons étudié des Gobemouches noirs *Ficedula hypoleuca* hivernant dans le Parc National de la Comoé, en Côte d'Ivoire. En utilisant des émetteurs radio, nous avons montré que début février, à la moitié de la période d'hivernage, il existe une importante variation individuelle dans les taux d'utilisation des habitats forestiers et de savane. Par la suite, les individus qui privilégiaient la forêt commencent à exploiter davantage la savane, jusqu'à ce qu'en fin d'hiver tous utilisent principalement cet habitat. Cette modification se produit pendant la période de verdissement de la savane, qui s'accompagne d'une augmentation de l'abondance de certaines espèces d'insectes. Ce changement dans l'utilisation des habitats est donc probablement une réponse à une augmentation de la disponibilité alimentaire dans la savane par rapport à la première partie de l'hiver, pendant laquelle la forêt est probablement plus nourricière. Sur la base de ces résultats, nous soupçonnons que les Gobemouches noirs établissent de préférence des territoires en lisière de forêt, ce qui leur donne accès à la fois à la forêt et à la savane. Ils sont donc plus à même de trouver suffisamment de nourriture tout au long de leur séjour. Ces résultats confirment l'importance de l'hétérogénéité des habitats à petite échelle, qui permet aux gobemouches d'occuper un même territoire pendant toute la période hivernale.

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SUPPLEMENTARY MATERIAL

Table S1. Regression coefficients and random effects of the linear mixed models for foliage cover and NDVI within the canopy layer and grass layer. The significance of the fixed effects is based on a type II Wald Chi-square test.

Model	**Fixed effect**	**Estimate**	**SE**	χ^2	***P***
(1) Canopy layer	Intercept	0.35	0.03		
	Foliage cover	0.53	0.05	113.34	<0.001
	Foliage cover (squared)	–0.18	0.06	10.46	0.001
	Random effect	**Variance**			
	Tree-ID	0.003			
	Species	0.003			
	Date (factor)	0.004			
	Residual	0.002			

Model	**Fixed effect**	**Estimate**	**SE**	χ^2	***P***
(2) Grass layer	Intercept	0.22	0.03		
	Foliage cover	0.43	0.10	17.75	<0.001
	Random effect	**Variance**			
	Transect ID	0.003			
	Date (factor)	0.001			
	Residual	0.000			

Table S2. Model selection results for the number of arthropods as function of NVDI for both malaise and pitfall trap samples. Only the best performing models with a cumulative AICc weight of >0.95, are shown. Models are ranked from lowest to highest AICc. OR = taxonomic order.

Model	NDVI Radius (m)	K	AICc	ΔAICc	AICc Weight	Cumulative Weight	Marginal R^2	Conditional R^2
(1) Pitfall traps								
OR × $\text{NDVI}_{\text{habitat}}$ + OR × $\text{NDVI}_{\text{temp}}$	30	24	1147.6	0.00	0.31	0.31	0.53	0.61
OR × $\text{NDVI}_{\text{habitat}}$ + OR × $\text{NDVI}_{\text{temp}}$	50	24	1148.5	0.85	0.20	0.51	0.53	0.61
OR × $\text{NDVI}_{\text{habitat}}$ + OR × $\text{NDVI}_{\text{temp}}$	40	24	1149.0	1.33	0.16	0.66	0.52	0.61
OR × $\text{NDVI}_{\text{habitat}}$ + OR × $\text{NDVI}_{\text{temp}}$	20	24	1149.0	1.34	0.16	0.82	0.52	0.60
OR × $\text{NDVI}_{\text{habitat}}$ + OR × $\text{NDVI}_{\text{temp}}$	60	24	1150.5	2.87	0.07	0.89	0.52	0.61
OR × $\text{NDVI}_{\text{habitat}}$ + OR × $\text{NDVI}_{\text{temp}}$	70	24	1152.0	4.38	0.03	0.93	0.52	0.61
OR × $\text{NDVI}_{\text{habitat}}$ + OR × $\text{NDVI}_{\text{temp}}$	80	24	1152.5	4.93	0.03	0.95	0.51	0.61
(2) Malaise traps								
OR × $\text{NDVI}_{\text{habitat}}$ + OR × $\text{NDVI}_{\text{temp}}$	50	24	1204.6	0.00	0.22	0.22	0.63	0.83
OR × $\text{NDVI}_{\text{habitat}}$ + OR × $\text{NDVI}_{\text{temp}}$	30	24	1205.1	0.49	0.17	0.39	0.63	0.83
OR × $\text{NDVI}_{\text{habitat}}$ + OR × $\text{NDVI}_{\text{temp}}$	60	24	1205.4	0.73	0.15	0.55	0.63	0.83
OR × $\text{NDVI}_{\text{habitat}}$ + OR × $\text{NDVI}_{\text{temp}}$	40	24	1205.5	0.82	0.15	0.69	0.62	0.83
OR × $\text{NDVI}_{\text{habitat}}$ + OR × $\text{NDVI}_{\text{temp}}$	80	24	1205.7	1.06	0.13	0.82	0.63	0.83
OR × $\text{NDVI}_{\text{habitat}}$ + OR × $\text{NDVI}_{\text{temp}}$	70	24	1206.0	1.36	0.11	0.93	0.63	0.82
OR × $\text{NDVI}_{\text{habitat}}$ + OR × $\text{NDVI}_{\text{temp}}$	90	24	1207.7	3.05	0.05	0.98	0.63	0.82

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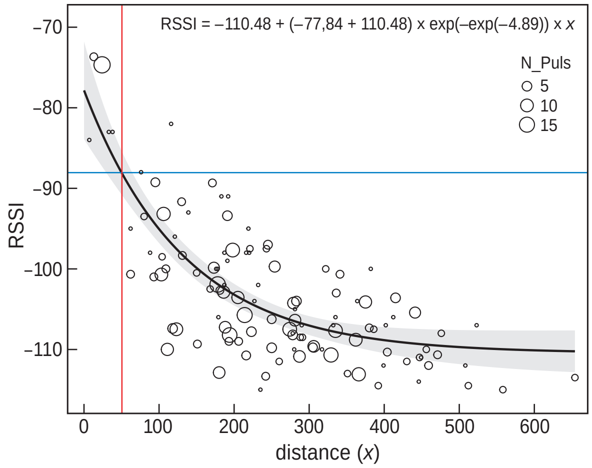

Figure S1. Relationship between received signal strength indicator (RSSI) and distance, based on node-receptions of tagged individuals that were simultaneously located in the field (n = 115/5 individuals, data collected between 26 February and 12 March). Each point represents at least one received signal from a known distance. In case a node received multiple pulses from a stationary bird, we considered it as one observation for which we calculated the mean RSSI. Dot size represents the pooled number of receptions per observation (average n/data point = 3.97, range 1–18). The plotted curve represents the best model fit based on an asymptotic regression function (±95% CI), for which the equation is given. The blue line shows the value of RSSI = –88.05, which was used as a cut-off to select observations within a threshold of 50 m (red line) from the nodes.

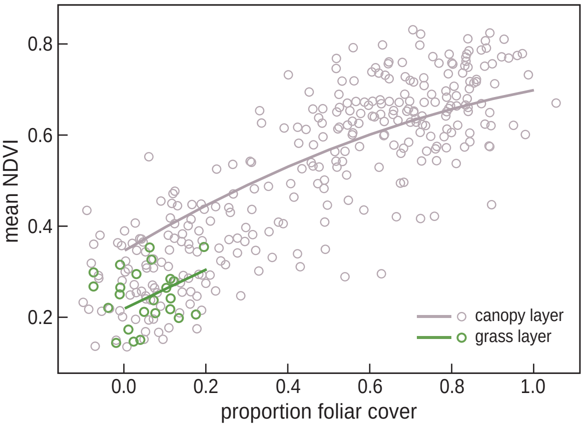

Figure S2. Relationship between NDVI and foliage cover for the canopy and grass layer. Points represent (repeated) observations of 48 individual trees within the canopy layer (total n = 276), and eight transects within the grass layer (total n = 24). Lines show the predictions from the linear mixed models for foliage cover and NDVI (Table S1).

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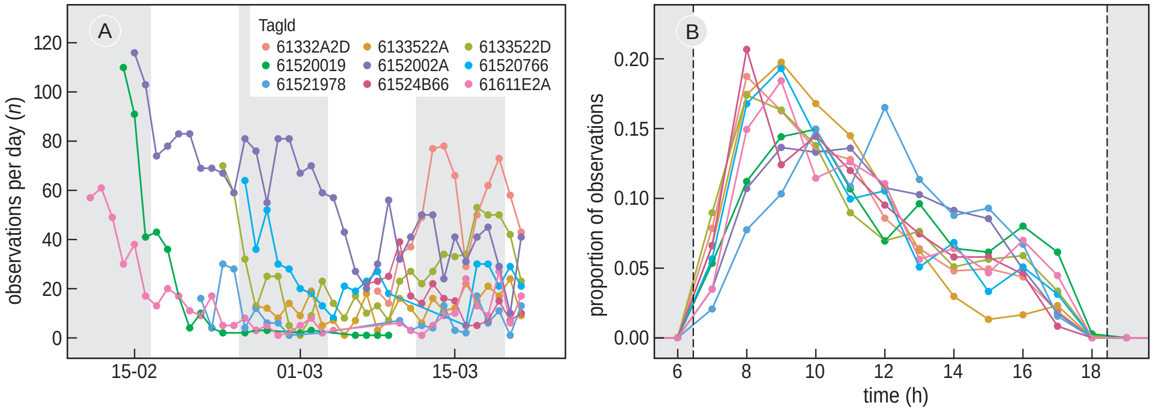

Figure S3. (A) Number of daily site-use observations for individuals included in the analysis (n = 9). The alternating grey and white areas mark the 8-day periods that are used in the analysis. (B) Distribution of observations throughout the day for the same site-use observations, calculated as the proportion of observations per hour. Dashed lines show the time of sunrise and sunset within the study area on 3 March 2020.

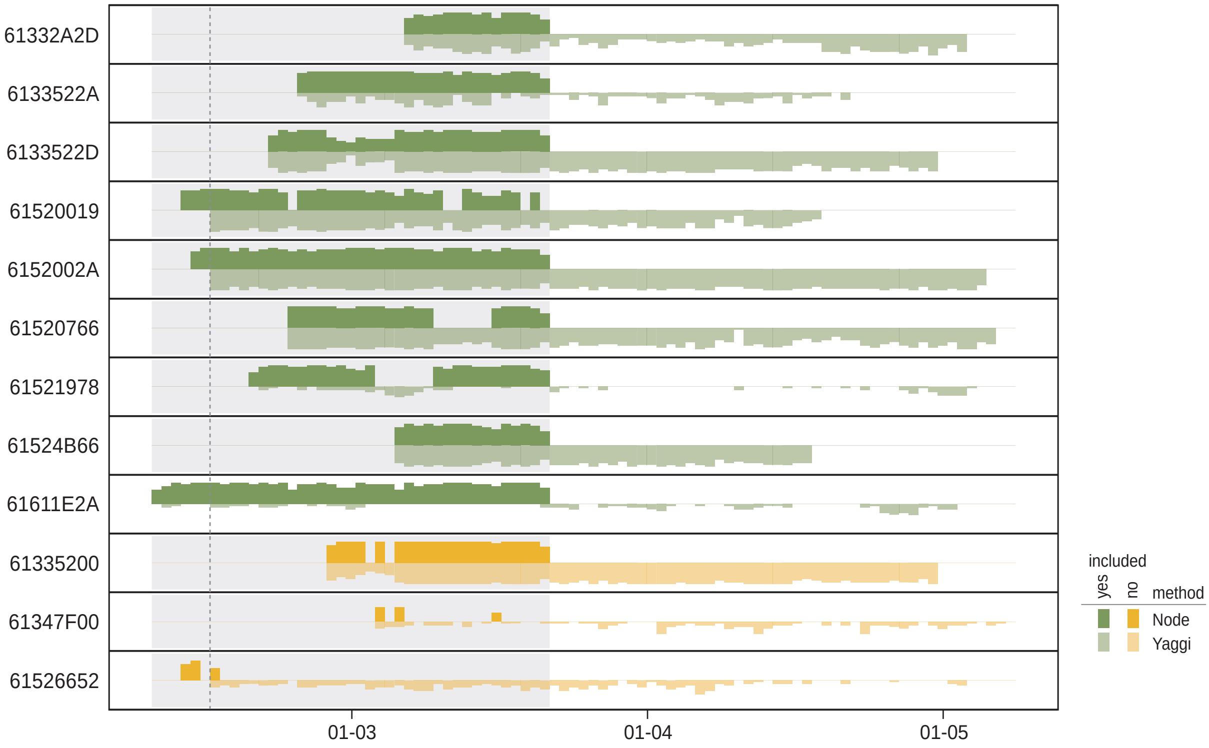

Figure S4. Daily presence of tagged individuals based on detections by nodes (dark coloured/upper bars) and directional Yaggi antenna's (light coloured/lower bars). The height of the bar shows the number of hours per day during which an individual was observed at least once (max = 12 h). The dashed line shows the start of the period during which Yaggi antennas were activated. Note that this figure is based on unfiltered data, including detections estimated at >50 m from nodes that are not included in the site selection analysis.

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