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Habitat specialisation and resource availability determine dispersal behaviour in four afro-tropical butterflies

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Abstract

1. Ecological demands, such as sex and environmental conditions, determine species' behaviour, such as dispersal, and shape local population structures. However, only marginal knowledge of these factors exists for afro-tropical insects so far.

2. Therefore, we performed a mark–release–recapture study in the coastal region of Kenya over a period of 2 months, covering the dry and the rainy seasons. As study species, we used four co-occurring but ecologically diverging butterfly species, the forest species *Bicyclus safitza* and *Junonia natalica* and the savannah species *Junonia oenone* and *Byblia ilithyia*. The study area represents an ecosystem mosaic consisting of anthropogenic habitats as well as natural forest and savannah, assessed by detailed landscape mapping.

3. We obtained 1701 capture events, comprising 1224 individuals with an overall recapture rate of 24% (ranging from 15% to 48%). The analyses based on these results allowed an assessment of the population ecology, dispersal behaviour and habitat preferences of these species.

4. Demographic models inferred different patterns of population dynamics among species. All species preferred the habitats they were known for. The observed dispersal distances were rather low ranging from a mean of 25 to 72 m, referring to taxa and sexes. The dispersal extrapolations were unreliably low for the negative exponential function, while the values for inverse power function were credible. The latter predicted a considerably higher long-distance dispersal capacity in males than in females of the forest species *B. safitza* and *J. natalica*, while females dispersed more than males in the savannah species *J. oenone* and *B. ilithyia*.

5. Our results obtained from these four ecologically diverging afro-tropical butterfly species underline that species' behaviour, such as dispersal, is strongly determined by habitat preferences, sex and the availability of resources.

KEYWORDS
dispersal behaviour, habitat mosaic, habitat preference, mark–release–recapture, population structure, resource availability, sex

INTRODUCTION

Ecological needs of species determine their behaviour and subsequently their population structure. Species representing a broad ecological amplitude are mostly widely distributed and can be found in various habitat types (Mangels et al., 2017). In consequence, such species cover large areas across the landscape and may build up strong and intermixing local populations (Engler et al., 2014). Such taxa are mostly more dispersive than more specialised species and thus migrate throughout landscapes. This enables high levels of individual exchanges among populations, including long-distance dispersal. In contrast, species with specific habitat requirements, such as taxa relying on defined habitat structures and resources, mostly occur locally restricted (Curtis et al., 2015). In consequence, such taxa do not cover large fractions of landscapes and rarely disperse to adjoining populations (Curtis et al., 2015).

Demographic structures of populations may also shape population structures and species' behaviour. Butterflies, for example, show sex-specific movement behaviours. Females frequently fly less than males (Junker et al., 2010). In particular, they have been observed to be little dispersive in the phase of laying the majority of their eggs. In contrast, males frequently fly around and patrol in search of potential mating partners, but mostly not dispersing larger distances while doing so (Ebert & Rennwald, 1991). Dispersal behaviour may also vary over lifetime. Thus, dispersal over longer distances has been mainly observed towards the end of the lifetime of non-migratory species, while at the beginning, individuals are mainly focusing on reproducing and egg-laying close to their place of larval development (Ebert & Rennwald, 1991).

In addition, the relationship between habitat preference, the degree of ecological specialisation and behaviour of species is frequently complemented by environmental factors. Thus, high resource availability can change their behaviour and thus may cause that they become comparatively less mobile, whereas in times of scarce resource availability, individuals may travel larger distances and thus disperse across a landscape (Dover & Settele, 2009; Habel et al., 2018). This phenomenon was observed in a previous study for butterflies in the dry coastal forest of East Africa where individuals showed high site fidelity and largely remained inside of their specific natural forest ecosystem during the rainy season, a period characterised by high resource availability. In contrast, the same taxa dispersed across the landscape and even visited anthropogenic habitats such as tree plantations during the dry season, a period characterised by limited resource availability in this natural forest ecosystem (Habel et al., 2018).

In this publication, we analyse the effects from intrinsic and extrinsic factors on species' population dynamics (i.e., densities including their demography) and behaviour, in particular dispersal. We synchronously studied four co-occurring butterfly species across a habitat mosaic in southern Kenya in a mark–release–recapture (MRR) study. The four butterfly species differ in their ecological preferences: *Bicyclus safitza* and *Junonia natalica* mainly rely on forest-like habitats, while *Junonia oenone* and *Byblia ilithyia* mainly occur in savannah-like open habitats, including disturbed anthropogenic landscapes (Kyerematen, Acquah-Lamptey, et al., 2014; Kyerematen, Owusu,

et al., 2014; Larsen, 1991, 2005; Rogo & Odulaja, 2001). Based on the data and the results obtained for these species, we test the following two hypotheses:

1. Ecological specialisation and habitat preference determine population structure and dispersal of a butterfly.
2. General behaviour and dispersal strongly vary between sexes and depend on the availability of resources.

MATERIALS AND METHODS

Study area

The study area is located in southern Kenya, north of Mombasa (3.861° S; 39.648° E–3.866° S; 39.655° E). Most of the once widely distributed coastal forest has been converted into settlements and agricultural land, such as fields for subsistence agriculture and tree plantations (Azeria et al., 2007; Lovett, 1998; Myers et al., 2000; Wass, 1995). This situation has become even worse within the past few years due to increasing demographic pressure. In consequence, the study area (in total about 69.89 ha, 8.71 ha without the forest block; Figure 1) represents a mosaic of various habitat types such as natural forest (here the sacred Mijikenda forest Kaya Kambe), shrubs, orchards with mango or coconut trees, fields with cassava, banana and bell pepper plants as well as settlements. The region is characterised by two rainy seasons. Normally, the long rains are from end of March to July (600 mm precipitation), and the short rains in October and November (300 mm precipitation; Jaetzold et al., 2010). We conducted the MRR campaign from the end of February until mid–April 2022, covering the dry season and the transition between the dry and the rainy season.

Study species

We studied four species of Nymphalidae, three Nymphalinae (i.e., *B. ilithyia*, *J. oenone*, *J. natalica*) and one Satyrinae (*B. safitza*). Of these, the joker *Byblia ilithyia* (Drury, 1773) is distributed in most parts of the African savannah regions (east, south, west) but also in geographically restricted parts of India and Sri Lanka (Larsen, 1991; Larsen, 2005). It is found in most of Kenya and in a large variety of more open habitats but is more a dry-zone specialist than the closely related *B. anvatara* and is not exceeding much above 1500 m asl in the highlands. The larvae always feed on Euphorbiaceae (*Dalechampia*, *Tragia* and *Ricinus*). Furthermore, the butterflies are attracted by exuding plant sap (Larsen, 1991). In few cases (e.g., in Benin), migrations of *B. ilithyia* were observed (Larsen, 1978).

The dark blue pansy *Junonia oenone* (Linneus, 1958) is widespread all over tropical Africa, Madagascar and south-western Arabia (Larsen, 1991, 2005). It is found in a wide variety of habitats, mostly in open areas but not in closed forests and even is seen as ecosystem disturbance indicator (Kyerematen, Acquah-Lamptey, et al., 2014; Kyerematen, Owusu, et al., 2014). The species is less a dry-zone species as the closely related *J. hierta* and *J. orythia*. Its larvae feed on
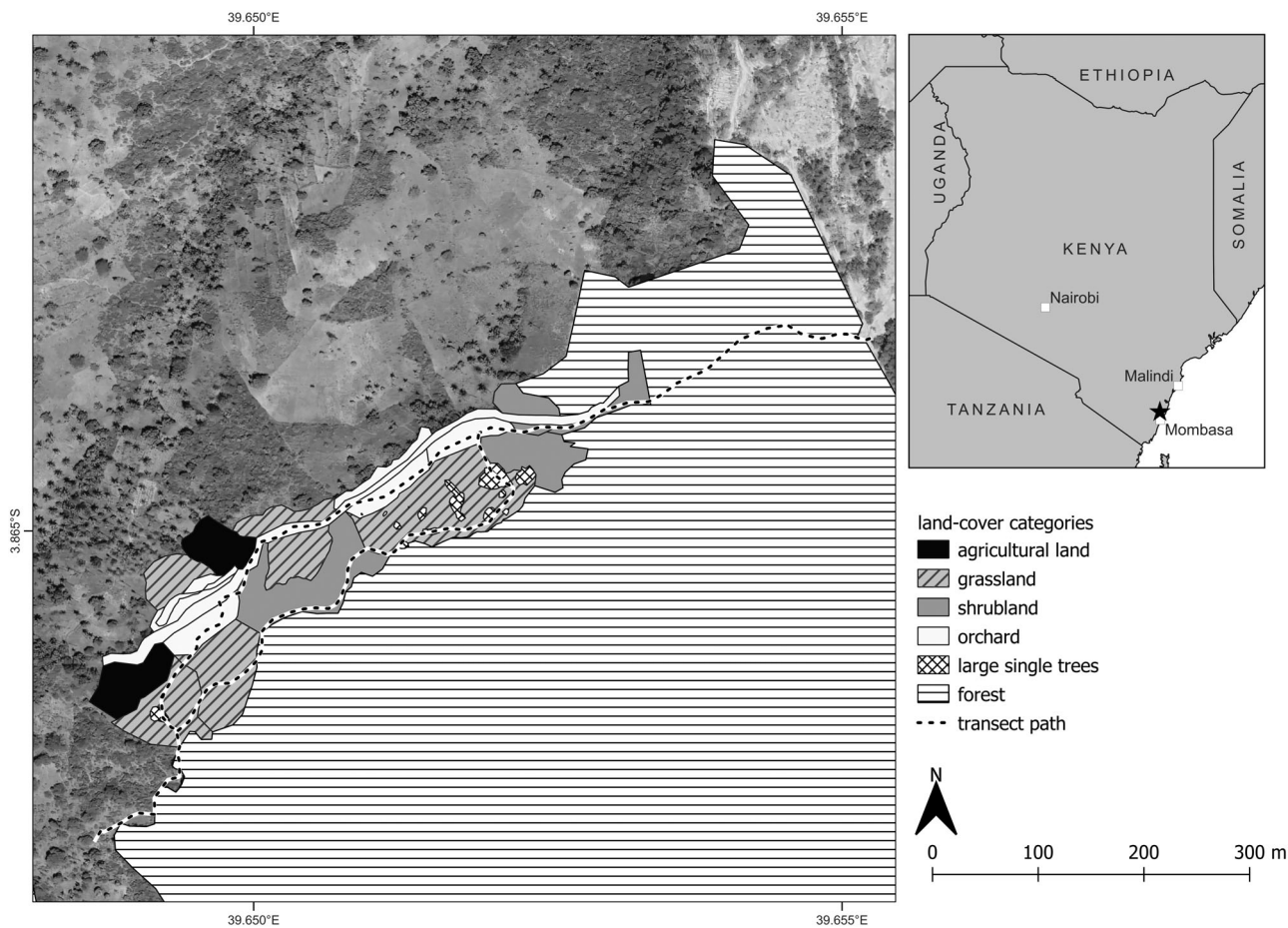
FIGURE 1 Study site in southern Kenya (star in small map on the right) and the study area displaying the path (dotted line) transgressing the different habitat types located at the forest border of Kaya Kambe forest.

Acanthaceae (*Asystasia*, *Isoglossa*, *Justicia*, *Paulowilhelmia* and *Ruellia*; Larsen, 1991).

The Natal pansy *Junonia natalica* (Felder, 1860) is widespread in eastern and southern Africa in forested habitats but can also be found in the Kenyan coastal area in somewhat more open areas; in the Kenyan highlands, the species is rarely found in altitudes above 2000 m asl. Its larvae feed on a variety of different Acanthaceae (*Asystasia*, *Barleria*, *Hygrophila*, *Justicia*, *Paulowilhelmia*, *Phaulopsis* and *Ruellia*). Imagoes are frequently attracted to horse manure (Larsen, 1991).

The common bush brown *Bicyclus safitza* (Hewitson 1851) is widely distributed in the savannah biome all over sub-Sahara Africa (Larsen, 1991; Larsen, 2005) where it is mostly found in woodlands, forests and thickets (Kyerematen, Acquah-Lamptey, et al., 2014, Kyerematen, Owusu, et al., 2014). In Kenya, it is less well represented in the wetter western parts of the country (Larsen, 1991). Like for all Satyrinae, the larvae feed on Poaceae such as *Erharta erecta* (Larson, 1991).

Collection of data

For the collection of MRR data, we synchronously marked individuals of these four species with a water-proof pen over a period of

2 months. We walked a predefined path, which semi-randomly covered the entire study area and all habitat types (Figure 1). We classified the habitats according to the land-cover into agricultural land, grassland, shrubland, orchard and forest. Habitat geometries were acquired as polygon data using a HUAWEI MediaTab 5 with GPS support and the android application ArcGIS Field Maps from ESRI. Data acquisition was supported by a predefined input form and offline available satellite image as background data to ease orientation in the field. For each of these habitat types, the following habitat characteristics were collected: Canopy cover, litter coverage, presence of shrubs, presence of herbs (each categorised into the following classes, 0%, >5%, >15%, >30%, >45%, >60%, >75%, >90%). Furthermore, we assessed the availability of water, fruits (both categorised into yes or no) and the availability of blossoms (none/0, little/5–10, medium/10–50, many/>50 blossoms). All parameters were assessed by one person (MAM).

The marking of individuals of the four study species was done along the predefined path between 25 February and 13 April 2022 (in total 38 field days). The path was walked in slow pace, and all individuals of the four taxa were caught with a butterfly net. This was conducted between 7:30 AM and 3:30 PM under sunny to cloudy (but not rainy) weather conditions and at temperatures >25°C. To avoid passing the same paths or areas on the same time of day every

day, we defined various starting points and alternated them among days. The number of people conducting field work varied from one to five (mean = 2.23). This might affect the results as the efficiency of work might have varied. We accounted for this aspect when calculating MRR models (see below). Before netting individuals, we observed each individual and noted its behaviour. Hereby, we differentiated among the following categories: feeding, flying, resting, interaction and copula. For each individual caught, we measured detailed locational information using a Garmin GPSMap 64S, and the individuals were then marked with a waterproof pen (with a running number). Sex (male/female) was determined by assessing the genitalia, and the age was estimated based on wing condition, considering the following categories: 1 (completely undamaged wings including all marginal cilia), 2 (undamaged wings but without cilia), 3 (wings slightly to moderately damaged) and 4 (all wings heavily damaged; see Wendt et al., 2021, Zimmermann et al., 2005). Recaptures were not counted if performed at the day of marking to avoid potential capture–release–trauma and thus artefacts with respect to behaviour and dispersal (Gall, 1984; Watt et al., 1977).

Statistics

The demographic structure was analysed under an open population formulation of the Jolly–Seber model, allowing entries and exits of individuals to and from the population (POPAN model; Schwarz & Arnason, 1996). The model estimates the following parameters: probability of an individual to enter the population (p_{ent}), survival probability (φ), capture probability (p) and gross population size (N). The specimen's sex and wing condition on first capture were treated as individual covariates. The parameters φ, p_{ent} and N were tested for their dependence on sex by fitting multiple models with all combinations of sex-dependent and -independent parameters. φ and p_{ent} were additionally tested for factorial, linear and quadratic time dependence. All tested models estimated the dependence of φ on wing condition, which served as a proxy for the age of individuals. Likewise, we estimated individual capture probability (p) in dependence of the number of people catching butterflies in the field because more people are likely to be more effective in catching and processing butterflies. A full list of models is given in Appendix 2. In total, we ran 98 models for each of the four species (7 φ × 7 p_{ent} × 1 p × 2 N). We then calculated a final ensemble model per species that was based on all models that obtained a corrected AIC score with a difference smaller than two from the AICc score of the top model. All analyses were conducted in RMark v.2.2.7 (Laake, 2013), which served as a frontend to the software Mark (Linux v. 9.0, White & Burnham, 1999).

A dependence of dispersal activity on habitat was assessed by plotting distances between first and second capture against principal habitat characteristics. The latter resulted from a principal component analysis (PCA) on the correlation matrix of the recorded canopy cover, presence of shrubs, presence of herbs, presence of flowers, litter cover, availability of fruits and distance from the stream bed. Midpoints of the recorded habitat parameter ranges (see above) were

used; however, zeros were treated as such. Respective habitat parameter values were assigned to each individual by querying the values from the polygons containing the records of the specimen in QGIS (www.qgis.org). Since one individual can potentially be found in multiple polygons, the median of all values of each habitat parameter was used as input to the PCA. The distance to the riverbed was summarised as its mean.

We tested for differences in mean dispersal distances between females and males per species with two-sided t-tests in R (v. 4.2.0; R Core Team, 2022). Distance measures between the first and second capture locality of the same specimen were therefore log-transformed. Furthermore, the travelled distances were divided into distance classes (20, 30 and 50 m intervals, respectively), separately for each species and sex. To check for any potential artefacts caused by the chosen interval sizes, we analysed and compared these three interval size classes. The inverse cumulative percentage of these classes was determined, which corresponds to the probability density function, that is, the dispersal kernel.

Based on these classes, the probabilities of dispersal flights were assessed by distance extrapolation. We used two frequently applied regression analyses, the negative exponential function (NEF) and the inverse power function (IPF). NEF tends to underestimate rare long-distance movements, whereas the IPF may encounter problems with 'zero' movements (Kuras et al., 2003). For calculations, only realised classes were included; none realised classes remained empty and did not enter the model. The data were linearly transformed with a semi-ln plot for the NEF analyses or with a double-ln plot for the IPF analyses. In both equations, 'P' stands for the proportional probability that an individual will travel at least as far as the distance D and 'a' for the intercept of the regression. NEF operates with the dispersal constant K as slope, whereas IPF uses the variable n as slope, which represents the effect of distance on dispersal (Ehl et al., 2018).

$$P_{NEF} = ae^{-kD} \text{ or } \ln P = \ln a - kD.$$

$$P_{IPF} = aD^{-n} \text{ or } \ln P = \ln a - n(\ln D).$$

We selected the best model and the most suitable interval size, based on calculated stability indices (i.e., R^2) of the calculated curves, which corresponds to the proportion of explained variance of the dependent variable by the independent variable. This allowed extrapolations of the population's proportion that should travel distances exceeding the extent of the study area. The calculations were performed separately for males and females.

RESULTS

We performed a total of 1701 capture events, comprising 1224 individuals (Table 1, Supplementary File S1). Recapture rates ranges from 15.0% (males *J. oenone*) to 48.1% (males *B. safitza*); the overall rate was 24.0% (Table 1). The number of captures over time differed among the four species, being roughly constant in *B. safitza* and

TABLE 1 Captured individuals, recaptured individuals, number of recaptures and recapture rate (recaptured/captured individuals).

| Species	Captured individuals	Recaptured individuals	Recaptures	Recapture rate (%)
Bicyclus safitza	122 (52/70)	56 (25/31)	105 (47/58)	45.9 (48.1/44.3)
Byblia ilithyia	247 (112/135)	81 (38/43)	149 (81/68)	32.8 (33.9/31.9)
Junonia natalica	155 (62/93)	40 (14/26)	62 (21/41)	25.8 (22.6/28)
Junonia oenone	700 (234/466)	117 (35/82)	161 (53/108)	16.7 (15.0/17.6)

Note: Numbers of males (first value) and females (second value) are given in parentheses.
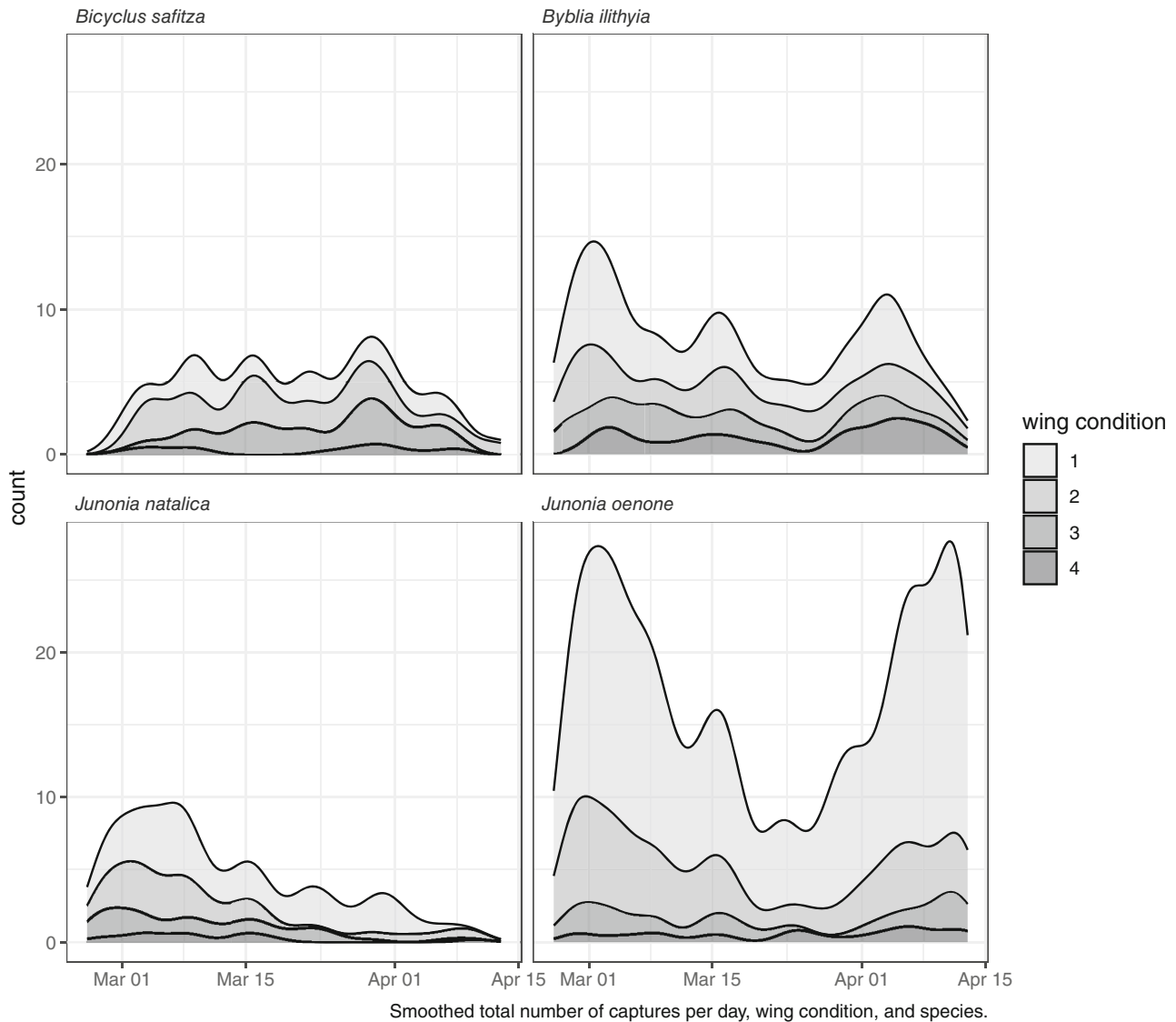
FIGURE 2 Smoothed total number of captures per day, wing condition and species.

B. ilithyia, decreasing in *J. natalica* and strongly reduced around 20 March in *J. oenone* (Figure 2). Hence, the number of recaptures over time strongly differed among the four species (Supplementary File S2). *Bicyclus safitza* individuals were increasingly recaptured until the beginning of April, when the number of recaptures strongly decreased. Recaptures of *J. natalica* were less abundant and also decreased with the beginning of April. Recaptures of

B. ilithyia and *J. oenone* both decreased until about 20 March and then, in contrast to the before mentioned species, increased again with the first rains in the beginning of April. Most individuals were captured resting or flying. In *B. safitza*, *J. natalica* and *J. oenone*, more individuals were found resting than flying. The difference was most pronounced in *B. safitza*. Contrasting, distinctly more individuals of *B. ilithyia* were found flying (Figure 3).
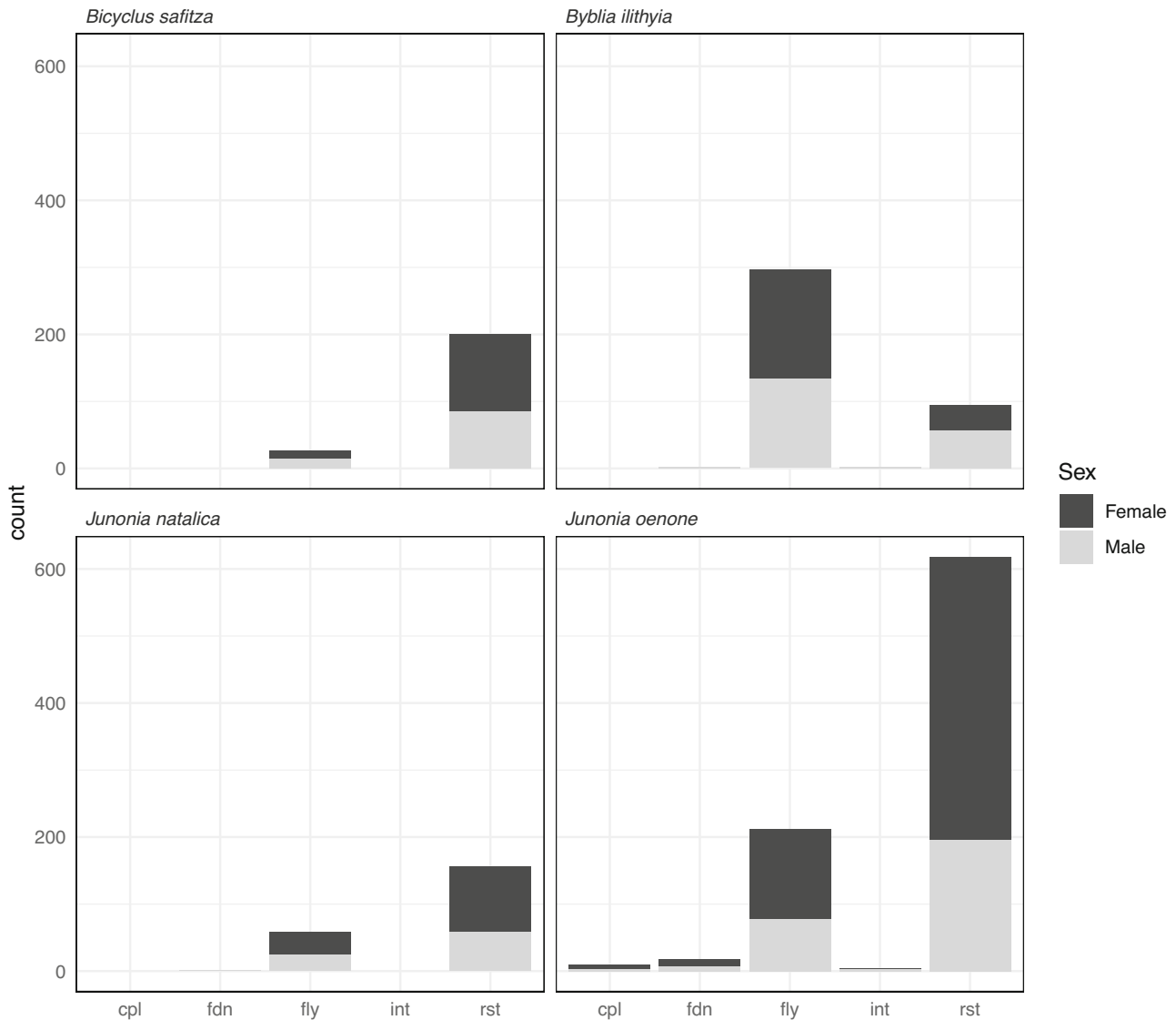
FIGURE 3 Comparison of observed behaviour among the four studied species. cpl, copula; fdn, feeding (nectaring); fly, flying; int, interacting; and rst, resting.

Demography

Demographic models inferred different patterns of population dynamics among species (Figure 4). In *B. safitza* and *J. natalica*, an estimated rise of population size was followed by a decrease towards the end of the study period. Contrastingly, *B. ilithyia* and *J. oenone* showed increasing population sizes with the exception of male *B. ilithyia*. The contrary development of male and female population size in *B. ilithyia* was unique among the investigated species, which otherwise showed concerted fluctuations of sexes. A comprehensive list of model evaluations is given in Supplementary File S3.

According to the models, the common pattern between *B. safitza* and *J. natalica* was caused by constant to decreasing entry rates in combination with constant to decreasing survival rates (Supplementary Files S4 and S5). On the contrary, entry rates of the two other species were estimated to increase over time with constant

(*B. ilithyia*, Supplementary File S6) or inverse bell-shaped (*J. oenone*, Supplementary File S7) survival rates. Common patterns across all species were generally lower abundances of males (exception: *B. ilithyia*) and of individuals with lower wing quality, which indicates a higher age, and an impact of sex on at least one model parameter (φ, p_{ent} or N). Few exceptions without influence of sex occurred in single subordinate models.

Use of habitats

Analysis of habitat use revealed two patterns exhibited by the four species. PCA assembled parameter values associated with forest habitats (high values for canopy cover, litter cover and the availability of fruits) at low values of the first principal component so that forest and open habitats could solely be distinguished by this component
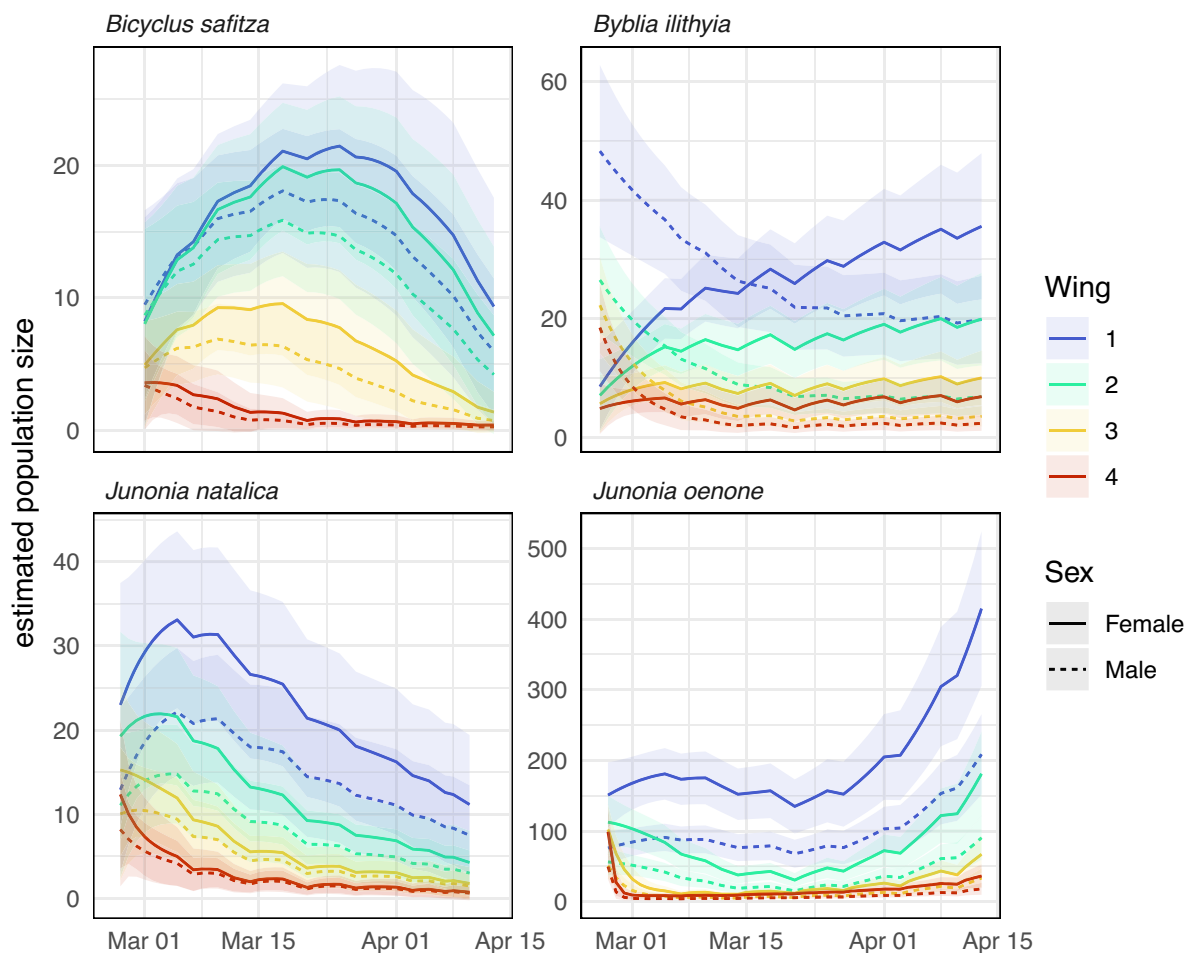
FIGURE 4 Population size dynamics of the four investigated species over the study period. Estimates were based on weighted average models of single best fit models. 4, red line, the bottom line; 2, green line, the second highest.

(Supplement Files S8 and S9). *Junonia natalica* and in particular *B. safitza* clearly preferred forest associated habitats (Figure 5). *Byblia ilithyia* and *J. oenone* were generally found in more open habitats, but *B. ilithyia* also occurred frequently in transition areas with characteristics of forest and open habitats. Hence, this ecological link was more pronounced in *J. oenone*, of which most occurrences were clearly recorded in open habitat (Figure 5).

Dispersal

A total of 294 individuals of the marked individuals were recaptured at least once so that dispersal distances could be calculated. Dispersal distances were generally found to be higher in *B. ilithyia* and *J. oenone* (Figure 6). Separated by sex, the four species had mean dispersal distances ranging from 25 m (females *B. safitza*) to 72 m (females *B. ilithyia*); median values ranged from 15 m (male *B. safitza*; female *J. natalica*) to 55 m (females *B. ilithyia*). Means differed significantly among sexes for the open land species *J. oenone* and *B. ilithyia*, with higher means in females (*U* tests: both *p* < 0.005). In *B. safitza* and *J. natalica*, mean values of males were more than twice as high as in

females, but the differences were not significant (Table 2). After log transformation resulting in a normal distribution of residuals, comparisons of mean dispersal distances of males and females resulted significant only in *J. natalica* (*t* test: adjusted *p* = 0.005). The male *J. natalica* mean dispersal was estimated to be $e^{1.0053} = 2.73$ times of mean female dispersal (Figure 5). Maximum dispersal distances observed ranged from 112 m (females *B. safitza*) to 348 m (males *B. safitza*). Maximum dispersal was higher in males in *B. safitza* and *J. natalica* but in females in *J. oenone* and *B. ilithyia* (Table 2).

Extrapolations to assess the long-distance dispersal potential yielded high R^2 values for both functions applied (Appendix 9–1); only NEF extrapolations for females of *B. safitza* and *J. natalica* had values below 0.8 for all three interval sizes used for calculations. Applying NEF (Appendix 9–2 to 9–4), the estimated dispersal potential was extremely low for all species and sexes with a maximum of 0.13% reaching at least 1 km in males of *B. safitza* based on 50 m intervals (Appendix 9–4); for females, no values higher 0.001% were reached. IPF resulted in much higher dispersal probabilities, which even though were relatively low. Exemplarily, the results for 30 m intervals are shown in Table 3, the ones for 20 and 50 m intervals in Appendix 9–5 and 9–6; however, results were quite similar in all cases. Again, sexual
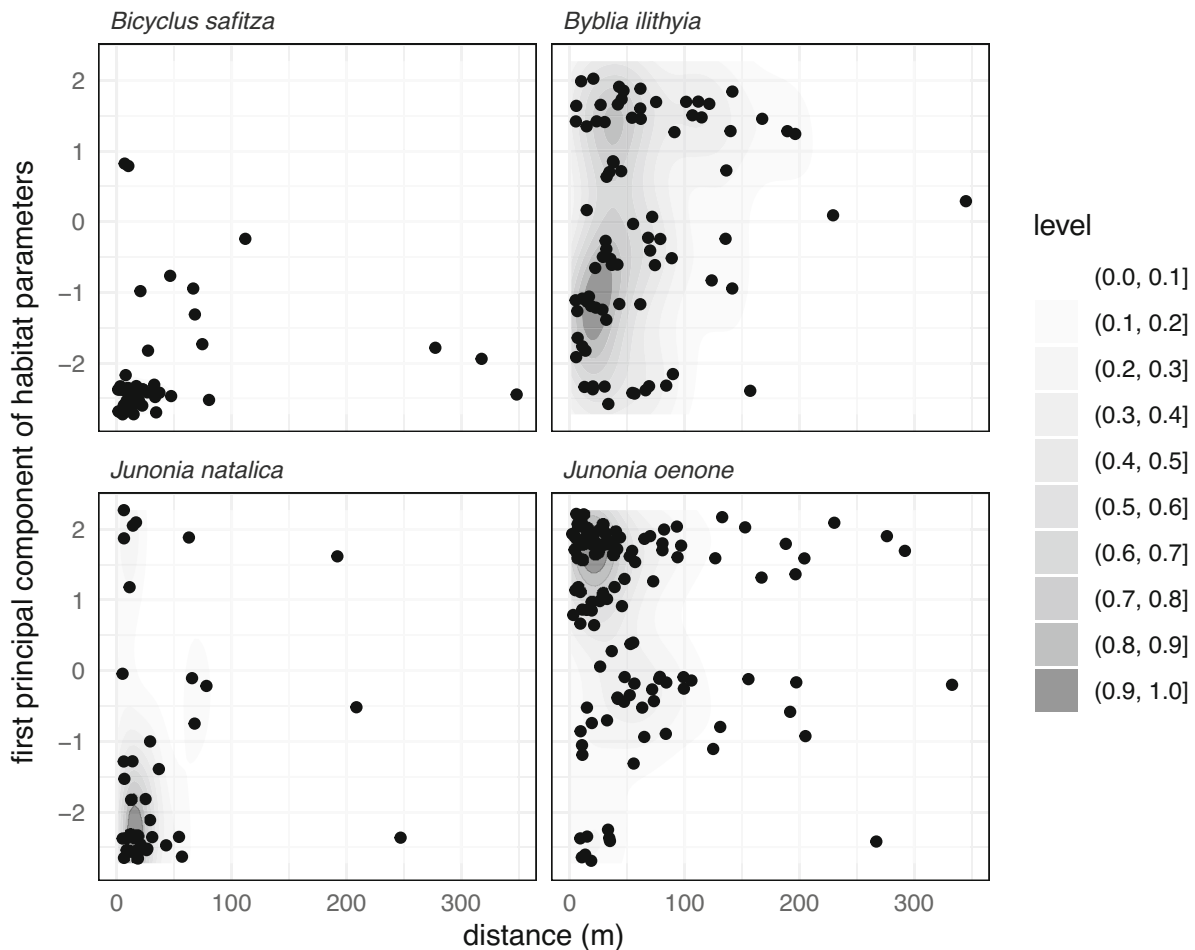
FIGURE 5 Dependence of dispersal activity on habitat configuration. The first principal component is displayed on the y-axis and expresses canopy cover, litter cover and the availability of fruits at lower values, which correspond to features of forest dominated habitats. The presence of flowers, shrubs and herbs was largely represented on the second principal component and is therefore not represented in the plot. The x-axis illustrates the linear distance between the first and the second capture of an individual. Background shading illustrates the density of points.

differences between *B. safitza* and *J. natalica* on the one hand and *J. oenone* and *B. ilithyia* on the other were obtained. Thus, males of the first two species are assumed to reach dispersal distances of 1 km in more than 2% of the individuals, while the probability was 0.04 and 0.21%, respectively, for females. Males of these species even had a realistic chance to reach distances up to 5 km. In turn, females were assumed more likely to disperse larger distances in *J. oenone* and *B. ilithyia*, but the difference between sexes was much less in these species and the general likelihood to perform long-distance flights considerably less, i.e. less than 0.6% for 1 km in all cases.

DISCUSSION

We found clear differences in habitat preference, niche width, behaviour and population structures among the four studied afro-tropical butterfly species, and a significant linkage existed between ecological specialisation and behaviour. Thus, individuals of *B. safitza* and *J. natalica* occurred most often in shaded areas and their movements

were mainly restricted to forested sites. On average, they showed higher site fidelity but higher differences in dispersal among sexes than individuals of *B. ilithya* and *J. oenone*, which in contrast showed a preference for open land, but were associated with a large range of other habitat types, with the widest ecological niche found for *B. ilithya*.

These findings correspond with previous data on forests and open land butterfly species (Namu et al., 2008). Thus, other afro-tropical forest butterflies are also strongly restricted to and mostly remain within their habitats (Borghesio & Wagura, 2014; Habel et al., 2023; Nyafwono et al., 2014), which are characterised by specific abiotic and biotic conditions, such as humid and cool microclimates as well as specific habitat structures (Habel et al., 2013). Consequently, they only rarely leave forests and bridge open landscapes (but see Konvicka et al., 2008 for an exception from temperate regions). Nevertheless, the dispersal potential of forest species is often intermediate to high, for tropical and temperate species likewise—but restricted to inside forests (Cassel-Lundhagen & Sjögren-Gulve, 2007; Fric & Konvicka, 2007; Habel et al., 2023; Konvicka et al., 2008; Vlasanek
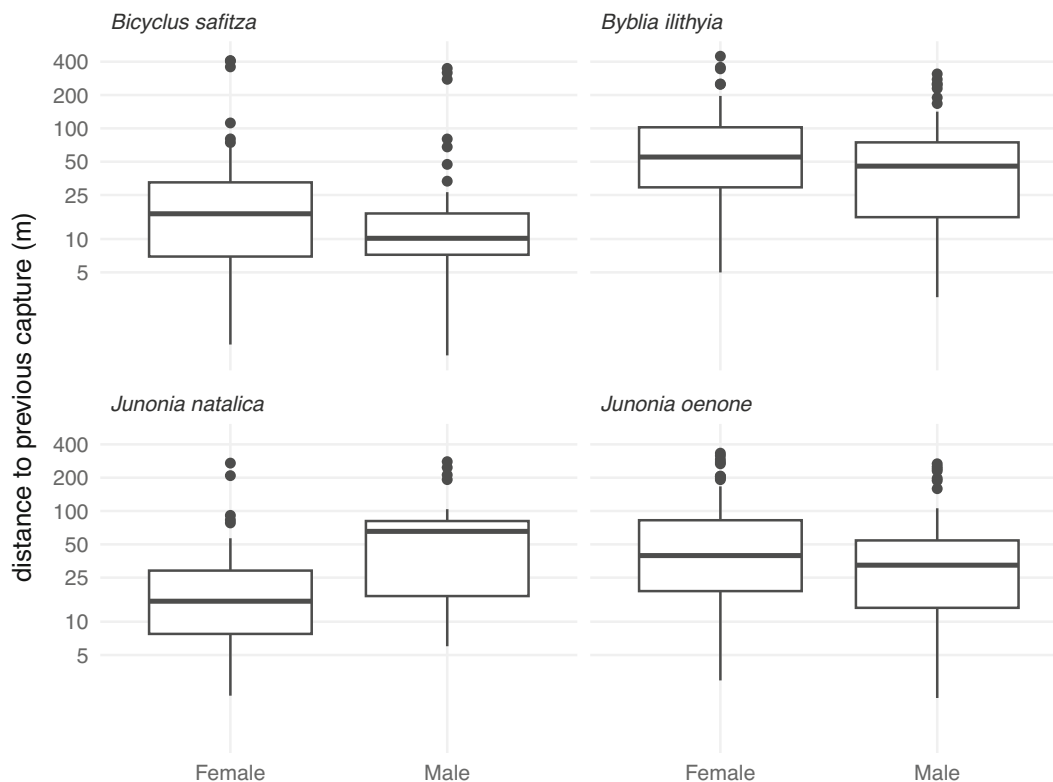
FIGURE 6 Comparison of distances between first and second captures of males and females of the four studied species. The only significant comparison was found between males and females of *J. natalica*.

TABLE 2 Mean with standard deviations, median and maximum dispersal distance of four afro-tropical butterfly species, distinguished by sex, in the Kaya Kambe forest region, southern Kenya.

	Mean ± sd (m)	Median (m)	Max. Distance (m)	N
B. safitza M	53.0 ± 100.1	14.6	348	25
B. safitza F	25.0 ± 26.9	17.1	112	30
J. natalica M	58.0 ± 72.9	28.7	247	14
J. natalica F	28.2 ± 40.5	15.4	209	26
J. oenone M	49.0 ± 54.9	32.4	230	35
J. oenone F	66.4 ± 72.8	39.6	333	82
B. ilithyia M	53.7 ± 53.7	37.9	229	38
B. ilithyia F	72.2 ± 62.9	55.1	345	43

Note: Applying Mann–Whitney *U* test, mean distances differed among sexes for *Junonia oenone* ($p = 0.004$) and *Byblia ilithyia* ($p < 0.0001$), but not for *Bicyclus safitza* and *Junonia natalica* (both $p > 0.1$). N stands for the number of individuals.

et al., 2013). In contrast, numerous afro-tropical savannah species are much more opportunistic in the choice of their habitats (Habel et al., 2018; Larsen, 1991; Schmitt et al., 2020; Scriven et al., 2017) and their assumed dispersal ranges from highly sedentary to migratory (Larsen, 1991). Thus, these savannah species seem to be as variable in their dispersal behaviour as temperate non-forest species are (Bink, 1992) with many case studies performed with MRR so far (e.g. Ehl et al., 2019; Fric et al., 2010; Junker et al., 2021; Konvickova et al., 2023; Pennekamp et al., 2014; Zimmermann et al., 2005).

In general, habitat specialists respond highly sensitive to environmental changes such as shifts in habitat structures and the reduction of habitat quality through anthropogenic activities, as also shown for afro-tropical forest butterflies in Taita Hills, southern Kenya (Schmitt et al., 2020). In addition, due to their high site fidelity, such species can only reach a new potential habitat with difficulty and are thus often subject to stochastic extinction processes, which occur more frequently in small and isolated populations than in large and interconnected ones (Melbourne & Hastings, 2008).

TABLE 3 Extrapolations performed with the inverse power function (IPF) of the dispersal probability (in %) over four distances based on dispersal distances collected for four afro-tropical butterfly species, distinguished by sex, in the Kaya Kambe forest region, southern Kenya.

	1 km	2 km	3 km	5 km
B. safitza M	2.25	1.15	0.777	0.474
B. safitza F	0.0364	0.0074	0.0029	0.0009
J. natalica M	2.02	0.916	0.577	0.323
J. natalica F	0.208	0.0651	0.0330	0.0140
J. oenone M	0.456	0.151	0.0791	0.0350
J. oenone F	0.570	0.184	0.0947	0.0411
B. ilithyia M	0.383	0.117	0.0586	0.0245
B. ilithyia F	0.539	0.170	0.0866	0.0370

Note: Extrapolations are based on 30 m intervals.

Looking at the larger distance estimates for our four study species, their dispersal power was low if compared with butterfly species from Kenyan mountain forests (Habel et al., 2023), but also in comparison with temperate Central Europe (Ehl et al., 2019, Fric et al., 2010, Junker et al., 2021, Konvickova et al., 2023, Pennekamp et al., 2014, Zimmermann et al., 2005). In general, the extrapolated dispersal probabilities over larger distances based on NEFs were implausibly low in all four species and for all three distance classes used (i.e., 20, 30, 50 m), a more general fact as pointed out already by Baguette (2003). In contrast, calculations based on IPFs were much more realistic (cf. Baguette, 2003) and consistent for all distance classes applied. Therefore, we built up our discussion on the results based on the latter function. Importantly, extrapolations of the probability of longer dispersal events for the two forest species using IPF obtained an about 10 times higher likelihood of reaching distances larger 1 km in males than females, while they were higher in females than males in the two savannah species, but only moderately.

Habitat restriction and movement behaviour may strongly vary between sexes and may frequently depend on the age of an individual and on environmental conditions such as resource availability. Thus, males of typical forest species travel significantly larger distances than females do, as males are often on the search for mating partners and/or patrolling along their territorial boundaries to drive away potential intruders (Brakefield, 1982; Kingsolver, 1983). In line with this, our two forest species showed a more narrow ecological amplitude but a higher dispersal power of males than the two savannah species. This is a typical phenomenon also found in temperate forest butterflies (Bennett et al., 2013; Cassel-Lundhagen & Sjögren-Gulve, 2007). The males of forest butterflies are often on the wing, patrolling and looking for mating with females, and thus may travel large distances.

In contrast, in our two savannah species, the movement behaviour is much more uniform, with higher mean values but smaller maxima, in particular in males. The modelled dispersal distances even showed that females moved more than males. This trend has also been frequently demonstrated for open land butterfly species of

temperate regions, especially as females sometimes bridge longer distances to successfully colonise new habitats and to establish new local populations (see also Cannone & Pignatti, 2014, Fric & Konvicka, 2007, Fric et al., 2010). Note that these behavioural differences in our study cannot be due to marking campaign related phenology as the recruitment curves of our forest versus savanna species were not synchronised within the two species pairs (Figures 2 and 3).

Furthermore, population dynamics frequently rely on changing environmental conditions. Thus, population densities of afro-tropical butterfly species decrease and distances travelled increase significantly in times of scarce resource availability (e.g., flowers, fruits, water) but they show high population densities and high site fidelity during rainy seasons (Habel et al., 2018; Schmitt et al., 2020). During this time, flowers, water ponds and ripe fruits are available throughout the landscape and thus there is no need to disperse over larger distances (Habel et al., 2022). In our study, however, we observed only slight changes in population dynamics of the two savannah species (but not of the two forest species) over time as possible reaction to seasonality.

Furthermore, the remaining fragments of the former continuous East African coastal forest belt are important as reservoirs for the regional supply with water. Consequently, due to more equal water accessibility within these forests, the availability of resources is more constant there than in the dryland savannah ecosystems of East Africa, where significant fluctuations with sometimes extreme amplitudes were observed for butterflies (Schmitt et al., 2021). These dry savannah regions are particularly known for sudden mass appearances of arthropods with the beginning of the rainy season and the appearance of food resources (Chang'a et al., 2010; Pareek & Trivedi, 2011). Furthermore, already Dixey (1929) showed the occurrence of two distinct generations for *B. ilithya* (one of our two savannah butterfly model species) with different phenotypes during rainy and dry season. However, according to our data, we found largely consistent capture and re-capture rates during our data recording for this species. Significant responses to seasonality might also exist for forest species but were not observed during our study.

In addition, changes in the demographic structures, such as sex ratio, often occur. For example, numerous temperate butterfly species show pronounced protandry (i.e., eclosion of males prior to females), obviously a fitness advantage to guarantee successful mating of females (see Iwasa et al., 1983; Junker et al., 2010; Petersen, 1947). However, this phenomenon was not observed in any of our four species. Proterandry also should be mostly restricted to species from seasonal environments that have non-overlapping generations. To our knowledge, it therefore has not yet been demonstrated for afro-tropical butterflies in the wild, although captive breeding of *Bicyclus anynana* revealed a few days shorter developmental time of males under such standardised conditions (Zijlstra et al., 2002). However, this quicker development in males should not translate into proterandry in continuously flying species like in our here analysed examples.

Furthermore, the only marginal expression of population dynamics (including changes in demography, density and dispersal behaviour) observed over the transition from dry to rainy season might also be

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related to the high degree of anthropogenic over-shaping of the landscape. Thus, an earlier study on butterflies in a largely undisturbed dry savannah region with adjoining agricultural landscapes in eastern Kenya showed highly significant population fluctuations in the undisturbed ecosystem but much less in the anthropogenic landscape (Schmitt et al., 2020). This may be due to the permanent availability of resources in gardens and fields, which buffers the natural fluctuations in population numbers.

In contrast to the temperate regions where many MRR studies have already been performed and were we have a relatively good picture of the dispersal power of butterflies representing a large array of ecologically different species, our knowledge on East African butterflies in this respect is still very limited. The very low dispersal capacity of all butterfly species analysed in this study and the high dispersal observed in two large forest butterfly species in the humid mountain forests of Taita hills in southern Kenya (Habel et al., 2023) show the high need for further MRR studies in East Africa at different localities and in different habitat types and throughout the years, also including the plain rainy season, to really get a comprehensive understanding of butterfly mobility as already archived for temperate regions.

AUTHOR CONTRIBUTIONS

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CONFLICT OF INTEREST STATEMENT

All authors declare that there exist no conflict of interest.

DATA AVAILABILITY STATEMENT

All data are available as electronic appendices.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Supplementary File S1. [Excel sheet] Raw data of captured and recaptured specimens, including species, specimen ID, capture coordinates, sex, behaviour, wing condition, capture time, recapture indication and number of people involved in the capture event.

Supplementary File S2. [pdf figure] Smoothed total number of recaptures per day, wing condition and species.

Supplementary File S3. [Excel sheet] Comprehensive list of models that were inferred per species. Models are ranked by corrected AIC (AICc). The dependencies of the model parameters Phi, p, pent and N on covariates (sex, time, wing and no. persons) are given. Constant parameters are represented by a 1. npar = number of parameters in the model, AICc = corrected Akaike information criterion, DeltaAICc = difference in the AICc in comparison to the best-ranked model.

Supplementary File S4. [pdf with several plots] Illustrations of inferred parameter values for *Bicyclus safitza* over time. The figure on page one illustrates the averaged model. Figures on subsequent pages illustrate all single models with DeltaAICc that were averaged.

Supplementary File S5. [pdf with several plots] Illustrations of inferred parameter values for *Junonia natalica* over time. The figure on page one illustrates the averaged model. Figures on subsequent pages illustrate all single models with DeltaAICc that were averaged.

Supplementary File S6. [pdf with several plots] Illustrations of inferred parameter values for *Byblia ilithyia* over time. The figure on page one illustrates the averaged model. Figures on subsequent pages illustrate all single models with DeltaAICc that were averaged.

Supplementary File S7. [pdf with several plots] Illustrations of inferred parameter values for *Junonia oenone* over time. The figure on page one illustrates the averaged model. Figures on subsequent pages illustrate all single models with DeltaAICc that were averaged.

Supplementary File S8. Plot of the loadings of the original habitat parameters as calculated in the PCA for PC1 and PC2.

Supplementary File S9. Importance of principal components and PCA loadings.