

Movements and occurrence in two closely related fritillary species

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Abstract. 1. Mobility may affect species' distribution patterns in heterogeneous landscapes, and it might impact fitness by influencing mating success, predation avoidance, and foraging success. Here, we studied causes and consequences of mobility patterns in butterflies: *Argynnis adippe*, a specialist constrained to warm microhabitats within woodland landscapes, and *A. aglaja*, a relative generalist that also inhabits grasslands, and tolerates lower temperatures. We explored associations of movement and occurrence patterns, population size and density, niche breadth, wing size, and different types of behaviour prior to capture by conducting a mark-release-recapture study on the Swedish island Öland.

2. We marked 1 935 *A. aglaja* and 123 *A. adippe* and achieved recapture rates of 9.5% (*A. aglaja*), and 8.9% (*A. adippe*). Estimated population densities were 5 066 and 814 individuals per km², for *A. aglaja* and *A. adippe*, respectively. *Argynnis aglaja* was less likely to perform long-distance flights according to estimated dispersal kernels, hinting at negative density-dependent dispersal in these species.

3. Although we detected the longest flight distances ever in these species in MRR studies (11.9 km for *A. aglaja* and 3.7 km for *A. adippe*), most butterflies were recaptured within 200 meters (60–80%). Low recapture rates along with low estimated residence times and the potential for long movement might indicate that many individuals left the study area, and that the species form open populations, stretching over large areas.

4. Despite significant differences in wing size and behaviour types, mean observed flight distances were similar in these species.

Key words. *Argynnis*, butterfly, mark-release-recapture, mobility, population density, wing size.

Introduction

A species' dispersal ability is a fundamental ecological characteristic, and differences in mobility may contribute to variation in population dynamics, distribution patterns, niche breadth, recolonization processes, habitat expansion, as well as genetic diversity and structure within and among populations (Cowley *et al.*, 2001b; Berry *et al.*, 2005; Hanski *et al.*, 2006; Liu *et al.*, 2011; Thomas *et al.*, 2011; Vlasanek & Novotny, 2015; Yildirim *et al.*, 2018). Understanding species' mobility patterns is therefore crucial, as variation in the capacity to move can

differently influence species' responses to habitat loss and fragmentation (Hanski, 2001; Öckinger *et al.*, 2010; Yildirim *et al.*, 2018). Knowledge about differences in movement patterns and population structure between species with diverging habitat requirements can help inform about the relationships between mobility, population density, and species traits, such as ecological niche breadth.

Mobility patterns can influence population densities and vice versa. While highly mobile species tend to have larger distributions, they usually form less dense populations as opposed to more sedentary species (Cowley *et al.*, 2001a,b). Similarly, population density can affect movement patterns. For example, both positive and negative density-dependent dispersal have been hypothesised as regulatory processes in population dynamics

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(Roland *et al.*, 2000; Poethke & Hovestadt, 2002; Enfjäll & Leimar, 2005; Matthysen, 2005; Nowicki & Vrabec, 2011). The former is a strategy to avoid overcrowding and intraspecific competition, such that individuals might rather be prone to leave a very dense population compared to sparsely occupied habitats (Konvicka *et al.*, 2011). On the other hand, negative density-dependent dispersal might be a mechanism to increase the chances of finding a mating partner. Low population density on a patch may also be reflective of low habitat quality and thus, the presence of conspecifics may be used as a hint for a suitable habitat patch (Kuussaari *et al.*, 1996).

Differences in ecological niche breadth can influence, and be influenced by, differences in mobility patterns, and these in turn can affect population structure and density. For example, specialist butterfly species often represent less mobile species as opposed to generalist species, which tend to have higher dispersal capacities (Warren *et al.*, 2001). As highly mobile species tend to form less dense populations (Cowley *et al.*, 2001a,b), generalist species might have larger distributions, but lower population densities on suitable patches. On the other hand, larger distribution areas and niche breadth are also frequently reported to be positively associated with a species' local population density (Inkinen, 1994; Gutiérrez & Menéndez, 1995; Hughes, 2000). Studying mobility and population density of closely related species with different degrees of generalism could therefore help understand how movement patterns, population dynamics, and niche breadth are connected, which is crucial for understanding a species' ecology and for developing management plans.

One morphological trait assumed to affect movement capacity in insects is body size (sometimes measured indirectly through e.g. wing span or thorax width), which is often used as a proxy for mobility (Nieminen *et al.*, 1999; Greenleaf *et al.*, 2007; Öckinger *et al.*, 2010; Kuussaari *et al.*, 2014). Numerous studies suggest that larger individuals tend to be able to cover longer flight distances (Nieminen *et al.*, 1999; Berwaerts *et al.*, 2002; Kalarus *et al.*, 2013; Skórka *et al.*, 2013a), and body size could also influence population densities, and the other way around. High population densities during the larval stage could lead to reduced larval development time, thereby decreasing the risk of resource depletion before metamorphosis. Larval food stress could thus reduce larval growth rate, which in turn might affect adult body size (Bauerfeind & Fischer, 2005). Metabolic rates are higher in larger species, and thus, the demands for nectar and larval food plants increase, which could lead to less dense populations in larger species owing to intraspecific competition (Niven & Scharlemann, 2005). Therefore, body size might not only influence mobility patterns because of increased physiological abilities of larger species to cover longer flight distances, but also indirectly via competition for resources in densely populated areas, which could induce positive density-dependent dispersal.

Further, mobility and occurrence patterns might differ between sexes, as shown for many different taxa (Beirincx *et al.*, 2006; Öckinger & Smith, 2007; Gros *et al.*, 2009). Higher mobility might also be reflected by certain types of behaviour, e.g. predominantly observed active behaviour such as flying and patrolling might be indicative of a more mobile species as

opposed to mainly observed sedentary activities such as sitting, sun basking, and nectaring.

Although numerous studies on butterfly mobility do exist, this important trait deserves further research, as it still remains unclear to what extent the above-mentioned factors may influence or be influenced by movement patterns. Moreover, many dispersal studies are constrained by the size of the study area, thus missing rare but critical long-distance movements. This study aims at broadening our knowledge about the connection of mobility, occurrence patterns, and species traits, such as specialization, body size, and behaviour in butterflies by comparing two closely related species with partially overlapping habitat requirements in a large study area.

The Dark Green Fritillary (*Argynnis aglaja*, Linnaeus 1758) and the High Brown Fritillary (*Argynnis adippe*, Denis & Schiffermüller, 1775) are well suited for investigating how mobility patterns correlate with population sizes and densities in a common and abundant, and a closely related, but rather rare species. *Argynnis aglaja* has a fairly stable distribution in Europe, while *A. adippe* is strongly declining in some parts of Europe and is not as widespread and abundant (Eliasson *et al.*, 2005; van Swaay *et al.*, 2010; Fox *et al.*, 2011; Ellis *et al.*, 2019). While the habitat use of the two species partly overlap, they seem to differ in the width of their respective occupied niches. *Argynnis adippe* is considered a habitat specialist whose requirements to the microclimate and larval foodplants confine the species to a very narrow niche (Asher *et al.*, 2001; Ellis *et al.*, 2019). While *A. adippe* larvae are constrained to *Viola* species, mainly *V. riviniana* and *V. hirta*, *A. aglaja* larvae can, depending on the geographic location, also be found feeding on *Bistorta major* (Forster & Wohlfahrt, 1955; Fric *et al.*, 2005; Tolman & Lewington, 2012), and Higgins and Riley (1970) even report *Persicaria* spp. as food plants for *A. aglaja*. *Argynnis aglaja* can be found breeding in cooler vegetation than *A. adippe* (Ellis *et al.*, 2010), one possible reason for its distribution ranging further north. Moreover, *A. adippe* butterflies are restricted to bracken (*Pteridium aquilinum*) dominated forest habitats, grass and *P. aquilinum* mosaics, and glades, clear-cuttings, and meadows in woodland dominated landscapes (Warren, 1995; Eliasson *et al.*, 2005). Contrastingly, besides *P. aquilinum* dominated habitats, *A. aglaja* uses a variety of flower-rich grassland habitats, such as chalk and limestone grassland, dry pastures, damp grassland, wet bogs, coastal grassland, dunes, and scrub (Zimmermann *et al.*, 2009; Ellis *et al.*, 2010). Both species are considered as relatively mobile (Cowley *et al.*, 2001b), however, dispersal in *A. adippe* is assumed to be restricted to 2 km, while *A. aglaja* has been reported to be able to cover distances of up to 10 km (Zimmermann *et al.*, 2009; Tolman & Lewington, 2012). Other factors contributing to divergent abundance and distribution of the two *Argynnis* species may include differences in body size and behaviour. To our knowledge, only a handful of studies on these species exist (e.g. Simonsen *et al.*, 2006; Zimmermann *et al.*, 2009; Bonsall *et al.*, 2014; Ellis *et al.*, 2019), and none of these earlier studies compared occurrence and movements between species within the same study area.

Here, we conducted a Mark-Release-Recapture (MRR) study on *A. aglaja*, and *A. adippe* on the Baltic island Öland, Sweden in order to answer the following questions: (1) Are there

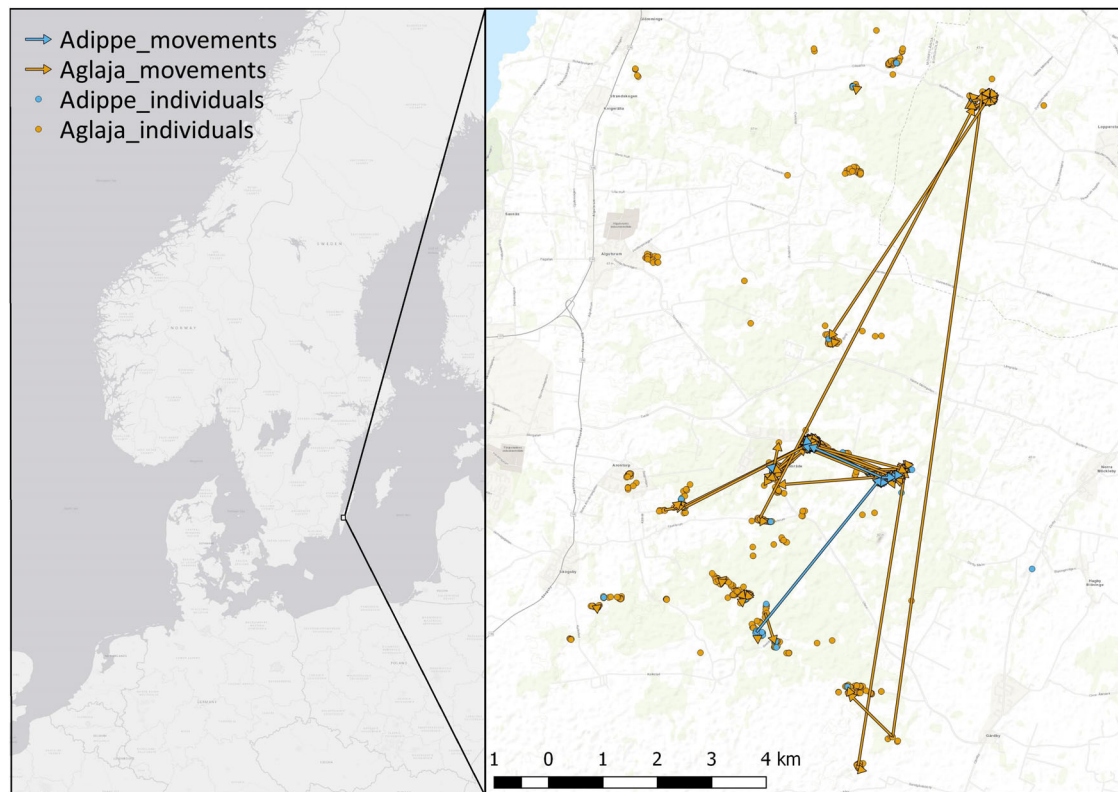


Fig. 1. Study area with spatial distribution and the movements of *A. aglaja* (orange) and *A. adippe* (blue) on central Öland, Sweden. Coordinates of center: 56.658531, 16.591771. Sources: Esri, DeLorme, HERE, TomTom, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Ordnance Survey, METI, swisstopo, and the GIS User Community. [Colour figure can be viewed at wileyonlinelibrary.com].

differences in movement patterns, population sizes, and densities between a specialist and a relative generalist species? (2) Can mobility patterns or niche breadth explain potential differences in adult population parameters, and are they associated with differences in body size? (3) Are observed behaviour types reflective of movement patterns? Following studies that positively linked species' distribution ranges with higher abundance on a local scale (Hughes, 2000; Cowley *et al.*, 2001a,b; Ranius *et al.*, 2011), we postulate that *A. adippe* forms less dense populations than the more common *A. aglaja*. We hypothesise that population densities influence mobility patterns and vice versa, such that high mobility might lead to less dense populations and that high population density might spur dispersal. These traits might be associated with body size insofar as larger individuals might be more dispersive. Finally, we explore whether and how the two species differ with respect to the type of behaviour displayed prior to capture, which could possibly reflect movement patterns and the other way around.

Material and methods

Study species

Both studied species occur in large parts of the Palearctic, however, *A. adippe* is not as widely distributed as *A. aglaja*

(Eliasson *et al.*, 2005; Tolman & Lewington, 2012). *Argynnis aglaja*'s distribution spreads from Northern Africa over Europe and Russia to Southeast Asia, and it is widely distributed throughout Scandinavia, ranging northwards until Southern Lappland. Similar to *A. aglaja*, *A. adippe* is distributed throughout most of the Palearctic region, ranging as far as temperate Asia, however, its Northern distribution only extends until central Sweden, and it has been reported to have become extinct in some parts of Northern Europe, due to intensified grazing and transformation of mixed open woodlands into dense coniferous forests (Warren, 1995; Franzén & Johannesson, 2007; Nilsson *et al.*, 2008; Fox *et al.*, 2011; Nilsson *et al.*, 2013). Both *A. aglaja* and *A. adippe* are univoltine species overwintering as eggs, that are often laid on or close to their larval food plants (Eliasson *et al.*, 2005).

Study area and data collection

A mark-release-recapture-study was conducted from June 25 to August 19, 2017, in the Midland Forest on the Baltic island Öland, Sweden (for a map including captured individuals and their movements, see Fig. 1). We studied a large area of 9 × 13 km on the central part of the island (coordinates of center: 56.658531, 16.591771; Fig. 1) which was chosen because it is diverse in habitats (forest, meadows, pastures,

clear cuts, wetlands etc.), both *A. adippe* and *A. aglaja* have previously been reported to occur here in good numbers, and their larval food plants, viz. *Viola* species are abundant and stable (Leidenberger *et al.*, 2016; Shah & Coulson, 2019). To assess all potentially suitable areas of habitat within the study area (viz. flower-rich open and semi-open areas within the Midland Forest, Supplementary Fig. S1), we examined satellite pictures provided by Esri® and landcover/vegetation maps provided by the Swedish Lantmäteriet (Lantmäteriet, 2009), visited these sites, and mapped them into polygons using Collector for ArcGIS 17.0.3. These potentially suitable areas were scanned for butterflies prior to the start of the MRR-study. Areas where butterflies occurred were visited daily, usually by two people, during fair weather conditions. Unoccupied, potentially suitable areas were visited at least twice. If previously unoccupied sites became occupied, we visited them daily, weather permitting. Sampling time on each site ranged from 20 minutes (when there were no or hardly any butterflies present) to 1 h (when there were many butterflies). The first and last *A. aglaja* individuals were marked between June 26 and August 17, and the first and last *A. adippe* between July 2 and August 17.

Butterflies were captured with a hand-held net, photographed (see below), and marked with a consecutive number on the underside of one hindwing using a fine-point Staedtler Lumo-color permanent marker. Handling time was less than 1 min for each butterfly. For every individual captured, species identity, sex, date, time of capture, and the coordinates were recorded using Collector for ArcGIS 17.0.3. For 19 individuals (1 *A. adippe*, 18 *A. aglaja*) the sex could not be determined in the field. Further, we noted the behaviour a butterfly was displaying prior to capture, i.e. active behaviour, where we discriminated between flying, territorial behaviour (defined as exposing a fast flight back and forward in the presence of another butterfly), and mating, and sedentary behaviour, where we discriminated between sitting, nectar feeding, and sun basking. In order to measure the wing size, a photograph of each butterfly was taken with a Samsung Galaxy J5 integrated phone camera with default settings (exposure time 1/213 s, ISO 64, f-stop f/1.9). Butterflies were photographed in front of millimetre paper, which was used as a reference for size measurements. Wing size was measured as the longest straight-line distance from the wing base to the apex on the underside of the forewing in the program ImageJ 1.52 h (Supplementary Fig. S2). Recaptured butterflies were not photographed again.

Data analysis

Abundance and population densities. We calculated the size of the mapped polygons (see above) of potentially suitable habitat, and estimated the number of occupied hectare grids within the study area for both species using QGIS 2.18.25. Population size, capture probability, and survival probability were estimated in the program MARK 9.0 (White & Burnham, 1999) using the Jolly-Seber method as implemented in POPAN, as it is suitable for repeatedly sampled open populations (Schwarz & Arnason, 1996). For K sampling occasions, the model estimates $K - 1$ parameters for survival probability (φ), K parameters for capture

probability (p), $K - 1$ parameters for probability of entry into the population ($pent$), and one parameter for the super-population size (N), consisting of all animals ever present in the population during the study period (Schwarz & Arnason, 1996). These parameter index matrices (PIMs) may be set to constant (\cdot), dependent on time (t), group (g , here: female/male), or group and time ($g*t$). In time-dependent models, not all parameters can be confidently estimated, as final survival and catchability, and initial entrance and catchability are confounded. For each parameter, we specified a parameter specific link function, namely the logit-function for p and φ -parameters, MLogit(1) for $pent$, (if $pent$ was group-dependent, MLogit(1) was used for the first group and MLogit(2) for the second), and Identity for N . We fitted all possible and sensible models to both *A. aglaja*, and *A. adippe*, verifying that all the parameters were properly estimated. We used the Akaike Information Criterion adjusted for small sample size, AICc (Hurvich & Tsai, 1989), to select the best-fitting model for our two respective datasets, *A. aglaja* and *A. adippe*. Models that generated estimates with associated standard errors of zero or extremely high standard errors (10 to 100 times larger than the estimate) were not considered. Total population size in each species was obtained as the sum of the estimated male and female population sizes from the chosen best-fitting model. Average capture probabilities for both species were obtained from estimated daily capture probabilities. When capture probability was time dependent, the initial, and final capture probabilities could not be cleanly estimated and were thus excluded from this calculation. Residence times in both species were calculated from survival probability as $-(\ln \varphi)^{-1}$ (e.g. Zimmermann *et al.*, 2005). One *A. adippe* and three *A. aglaja* individuals were removed due to missing information about the capture date, and one *A. adippe* and 18 *A. aglaja* individuals due to missing information about the sex. We calculated population densities by dividing estimated population sizes by the total area of potentially suitable sites (see above) and translated the values to population size per square kilometre.

Mobility patterns. As a measure of distance moved between recaptures, we analysed the shortest linear distance between consecutive captures of each individual using QGIS 2.18.25. We only included the distance between the first two capture events per individual in the analyses to avoid the risk of pseudoreplication, as high heterogeneity in mobility patterns among individuals can be assumed (Skórka *et al.*, 2013b). In each species, we pooled observed flight distances into distance classes and transformed the numbers of recaptures within each class into inverse cumulative proportions. We used these values to calculate dispersal kernels using both the inverse power function and the negative exponential function. In the inverse power function, the probability (P) of an individual moving a certain distance (D) is:

$$P = aD^{-n}$$

and in the negative exponential function, this probability equals to:

$$P = ae^{-kD}$$

where a is a scaling constant, and n and k are variables defining the effect of distance on dispersal, determining the shape of the curve. A Two-Way ANOVA was performed to evaluate if species identity or sex had an effect on the distance travelled. Since body size has previously been related to mobility (Öckinger *et al.*, 2010; Sekar, 2012; Kuussaari *et al.*, 2014), we explored potential differences in body size (wing span) between species by performing t -tests separately for each sex. We tested if distance covered between capture events in *A. aglaja* depended on wing size or sex by using a linear regression model. Since only 11 *A. adippe* butterflies were recaptured, this analysis was not performed on this species. Flight distances were \log_e -transformed in order to achieve normal distribution.

Behaviour. Separate Chi-squared tests were used to evaluate whether the distribution of displayed behaviour prior to capture (flying, territorial behaviour, mating, sitting, nectar feeding, sun basking) was independent of species identity. A post hoc test for significant deviances from expected frequencies in displayed behaviour was done by calculating P values from the adjusted residuals in the Chi-squared test (Beasley & Schumacker, 1995; MacDonald & Gardner, 2000) and evaluating significance against a Bonferroni corrected P value ($\alpha_{\text{adj}} = 0.05/6 \approx 0.0083$).

If not stated otherwise, all statistical analyses were performed in R 3.5.0.

Results

Abundance and population densities. During our study, we marked a total of 123 *A. adippe* and 1935 *A. aglaja* individuals. Both species occurred sympatrically within the study area, however, *A. adippe* only occupied about 19% of the area where *A. aglaja* was present. *Argynnis adippe* occurred in 39 (out of 12 000) hectare grids within the area, whereas 201 hectare grids were occupied by *A. aglaja*, 34 of which hosted both species (Fig. 1).

Population sizes and other population parameters were calculated in the program MARK using constrained linear models as implemented in the POPAN module. In the chosen best-fitting MARK-model for *A. aglaja*, catchability was time dependent, survival probability was group (i.e. sex) dependent, and the probability of entering the population was both time and group dependent. The modelled average capture probability in *A. aglaja* was 0.04, and survival probability was 0.83 in females and 0.81 in males, corresponding to residence times of 5.4 days (females) and 4.8 days (males). In *A. aglaja*, the average observed duration between first and last capture was 7.3 days for females and 5.8 days for males, respectively, while the maximum amount of time between first and last capture was 27 (females) and 28 days (males). Estimated population size was 8 044 (SE \pm 8 857) for females, and 11 107 (SE \pm 1 399) for males, i.e. a total estimated population size of 19 151 individuals, corresponding to a population density of 5 066 individuals per square kilometre. For *A. adippe*, in the chosen best-fitting model, both capture probability and the probability of entering the population were time and group (i.e. sex) dependent, while

survival probability was set to constant. The modelled average capture probability was 0.2 for females and 0.22 for males, and survival probability for both sexes was 0.65, corresponding to a residence time of 2.3 days. The mean number of days between first and last capture event was 2.7 days for females and 7.5 days for males, and the maximum was 5 days for females and 14 days for males. Estimated population size in *A. adippe* was 2 299 (SE \pm 5065) for females, and 780 (SE \pm 471) for males, i.e. total estimated population size of 3 079 individuals, corresponding to a population density of 814 individuals per square kilometre.

Female–male ratio was similar in both species with 31% females in *A. aglaja* and 34% females in *A. adippe*, which might be a result of slightly higher average capture probabilities in males (0.22) than in females (0.20), as found in *A. adippe*. Although intersexual comparison of catchability in *A. aglaja* would be interesting as well, estimating it would have led to over-parametrization of the statistical model, hence, in the chosen best-fitting POPAN model, capture probability was set to only time and not sex dependent. *Argynnis aglaja* was found during a longer period of the season, viz. 52 days (June 26 to August 17) compared to 46 days in *A. adippe* (July 2 to August 18) (Supplementary Fig. S3). The number of captures peaked in *A. aglaja* on July 6 for males and July 28 for females, and in *A. adippe* on July 6 for males and July 25 for females.

Mobility patterns. Out of 1 935 marked *A. aglaja* individuals, and 123 marked *A. adippe* individuals, 184 *A. aglaja* (9.5%), and 11 (8.9%) *A. adippe* were recaptured (Table 1). Two *A. adippe* and 44 *A. aglaja* individuals were recaptured more than once. The maximum flight distance recorded was 11.9 km in *A. aglaja* and 3.7 km in *A. adippe*. Fifteen individuals moved further than 1 km (two male *A. adippe*, 7 male and 4 female *A. aglaja* and for two *A. aglaja* the sex was not determined). In *A. adippe*, 50% of the individuals were recaptured within 114 m (102 for females and 149 for males), in *A. aglaja* within 49 m (49 for females and 48 for males; Table 1, Fig. 2). The majority of butterflies was rather sedentary with 80% of all recaptured *A. aglaja* individuals and 60% of *A. adippe* individuals being caught within 200 m from the point of their previous capture. Calculating dispersal kernels generated by the inverse power function resulted in the following equation for *A. aglaja*:

$$P = 51.34 (\pm 7.73) \times D^{-1.01(\pm 0.04)}$$

and for *A. adippe*:

$$P = 10.36 (\pm 1.87) \times D^{-0.6(\pm 0.04)}$$

Using the negative exponential function resulted in the following equation for *A. aglaja*:

$$P = 1.53(\pm 0.19) \times e^{-0.01(\pm 0.001) \times D}$$

and for *A. adippe*:

$$P = 1.06(\pm 0.11) \times e^{-0.004(\pm 0.0006) \times D}$$

Table 1. Frequency of marked and recaptured (RC) individuals in both sexes for *A. aglaja* and *A. adippe*. Maximum, mean, and median flight distances moved by *A. aglaja* and *A. adippe* for both sexes within the study area on central Öland, as well as percentage of distances longer than 1 km moved in each respective species and sex. Note that for some individuals the sex was not determined.

Species	Marked	RC	RC rate [%]	Mean dist. [m]	Median dist. [m]	Max. dist. [m]	Distances >1 km [%]
<i>A. aglaja</i>	1935	184	9.5	344	49	11 930	5.3
Female	604	55	9.2	303	49	5 310	5.1
Male	1312	126	9.6	305	48	11 930	4.3
<i>A. adippe</i>	123	11	8.9	563	114	3 650	15.4
Female	49	3	6.1	163	102	363	0
Male	72	8	11.1	713	149	3 650	20

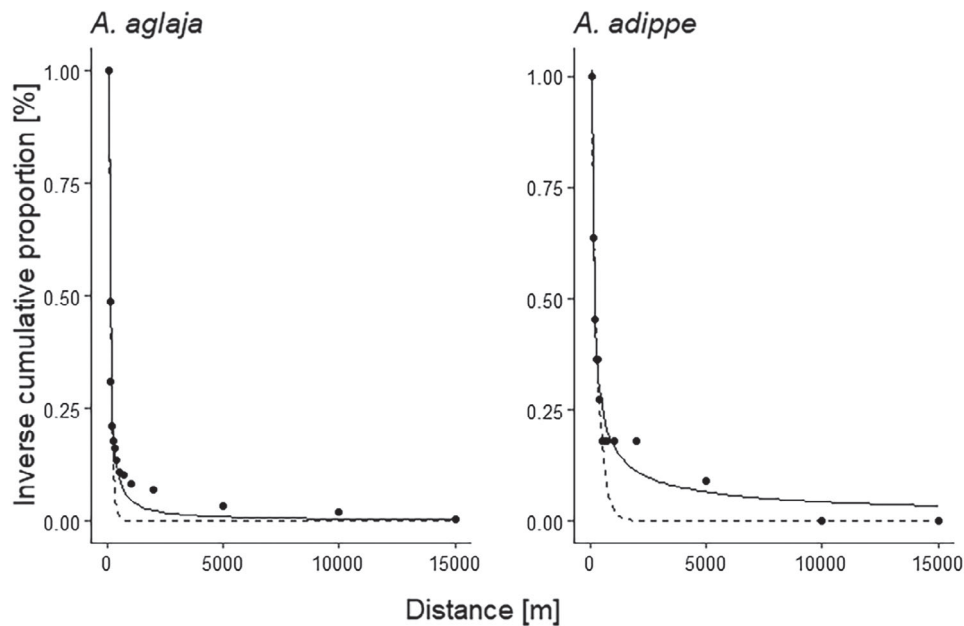


Fig. 2. Inverse cumulative proportion of individuals (dots) moving to or further than a certain distance in *A. aglaja* and *A. adippe*. Dispersal kernels generated by the inverse power function (solid line) and the negative exponential function (dashed line).

In both species, the inverse power function fitted the mobility data better (*A. aglaja*, $R^2 = 0.99$; *A. adippe*, $R^2 = 0.97$) than the negative exponential function (*A. aglaja*, $R^2 = 0.93$; *A. adippe*, $R^2 = 0.9$) (Fig. 2). From the inverse power function, the estimated probabilities of long-distance flights were 0.02 (*A. aglaja*) and 0.09 (*A. adippe*) for 3 km, 0.01 (*A. aglaja*) and 0.07 (*A. adippe*) for 5 km, and 0.01 (*A. aglaja*) and 0.04 (*A. adippe*) for 10 km. The difference in flight distance covered was no larger than 0.44 m (95% CI = 0.16–1.2) between the species, and 0.78 m (95% CI = 0.47–1.29) between the sexes, and there was no interactive effect of species identity and sex on flight distance either (Two-way ANOVA; effect of species identity, $F_{1,188} = 2.63$, $P = 0.11$; effect of sex, $F_{1,188} = 0.99$, $P = 0.32$; effect of species identity \times sex, $F_{1,188} = 0.24$, $P = 0.62$).

Argynnis adippe individuals were on average larger than *A. aglaja* (females: t test; $t_{578} = 10.67$, $P < 0.001$; males: t test; $t_{1123} = 11.28$, $P < 0.001$; Table 2). There was no association of distance moved between capture events with wing size or sex in *A. aglaja* individuals (regression, $R^2 = 0.01$, $F_{2,161} = 0.97$; effect of wing size, $b = 0.06$ (SE ± 0.08 , 95% CI = -0.09 to

Table 2. Maximum, mean, and median wing size in female and male *A. aglaja* and *A. adippe*. Wing size was measured as the longest straight-line distance from the wing base to the apex on the underside of the forewing.

Species	Mean wing size [mm]	Maximum wing size [mm]	Minimum wing size [mm]
<i>A. aglaja</i>	28.8	37.8	21.7
Female	30.3	35.5	25.7
Male	28.0	37.8	21.7
<i>A. adippe</i>	31.6	35.9	26.6
Female	33.1	35.9	28.7
Male	30.6	33.8	26.6

0.21), $P = 0.43$; effect of sex (male), $b = -0.15$ (SE ± 0.35 , 95% CI = -0.84 to 0.54), $P = 0.7$; Fig. 3).

Behaviour. The frequency of behaviour types (flying, territorial behaviour, mating, sitting, nectar feeding, sun basking)

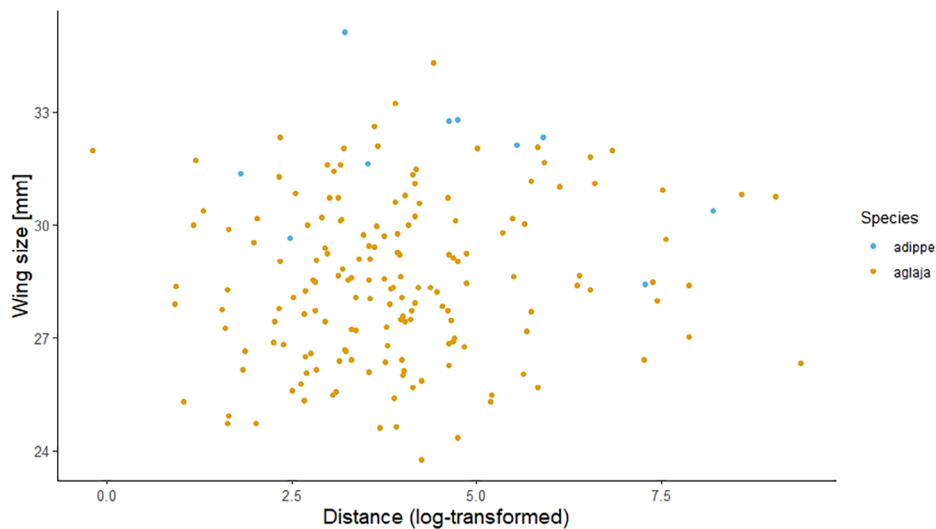


Fig. 3. Scatterplot visualizing the non-significant relationship between wing size [mm] and flight distance covered (log-transformed) in *A. aglaja* (orange) and *A. adippe* (blue). [Colour figure can be viewed at wileyonlinelibrary.com].

displayed by individuals prior to capture differed significantly between *A. aglaja* and *A. adippe* ($\chi^2 = 22.65$, $df = 5$, $P < 0.001$, Fig. 4). The displayed behaviour at capture deviated from expected frequencies between species on two activities, namely flying and nectaring. *Argynnis adippe* was significantly less likely to be found flying (Adjusted residual = -2.79 , $P = 0.005$) and significantly more likely to be found nectaring (Adjusted residual = 3.48 , $P < 0.001$). Female and male butterflies differed significantly in their behaviour in *A. aglaja* ($\chi^2_5 = 16.59$, $P = 0.005$). Males in *A. aglaja* were more often observed flying, while females were more frequently observed sitting. There was no difference in behaviour between the sexes in *A. adippe* ($\chi^2_5 = 1.75$, $P = 0.88$).

Discussion

Studying and comparing mobility and demographic patterns between *A. aglaja* and *A. adippe* on the Swedish island Öland, we found (1) differences in population structure, abundances, and mobility patterns between the specialist *A. adippe* and the relative generalist *A. aglaja*. (2) Differences in population size and density could be related to diverging mobility patterns and degrees of generalism, insofar as the specialist *A. adippe* was much less abundant than *A. aglaja* and formed less dense populations within the studied woodland landscape, while being more likely to engage in long-distance flight, pointing towards negative density-dependent dispersal. There was no intraspecific association of flight distance and body size. (3) We found no difference in mean flight distance between the two species, despite that they differed in observed behaviour types. (4) Although both species were rather sedentary, with $\sim 80\%$ of recaptures in *A. aglaja* and $\sim 60\%$ of recaptures in *A. adippe* occurring within 200 metres, we found the longest flight distances ever detected in an MRR-study in these species, 11.9 km for *A. aglaja* and 3.7 km for *A. adippe*.

Abundance and population densities. Estimated population densities on central Öland were lower for the specialist *A. adippe* than the relative generalist *A. aglaja*, confirming our hypothesis that a generally more common species would also be more abundant on a local scale. Whenever *A. adippe* occurred on a potentially suitable area, *A. aglaja* was present as well (except for one site), however, *A. adippe* was not observed on every site where *A. aglaja* occurred. Capture rates were more than 10 times higher for *A. aglaja* than for *A. adippe*, while recapture rates were similar for both species. This might reflect that *A. adippe* has more specific host plant and habitat requirements. For example, its larvae are restricted to *Viola* species, mainly *V. riviniana* and *V. hirta* (Eliasson *et al.*, 2005; Ellis *et al.*, 2019), while *A. aglaja* can also be found feeding on *Bistorta major* and rarely even on *Persicaria* spp., depending on geographic location (Forster and Wohlfahrt 1955; Higgins and Riley 1970; Fric *et al.*, 2005). Another factor potentially contributing to the divergent distribution between the two species might be temperature, as *A. aglaja* is able to breed in cooler habitats than *A. adippe* (Ellis *et al.*, 2010). Further, *A. adippe* is constrained to woodland and grassland habitats where *P. aquilinum* is present, while the relative generalist *A. aglaja* also inhabits chalk and limestone grassland, dry pastures, wetlands, coastal grassland, dunes, and scrub (Eliasson *et al.*, 2005; Ellis *et al.*, 2010). Additionally, it has been hypothesized that *A. adippe* requires large areas of woodland to maintain a viable population, which could further delimit the species' abundance and occurrence (Robertson *et al.*, 1995). For a specialist species, such as *A. adippe*, the quality of the landscape matrix might also be critical and possibly affecting population densities, while populations of common generalist species, such as *A. aglaja*, can be maintained even in more homogeneous landscapes (Ekroos *et al.*, 2010; Krämer *et al.*, 2012; Öckinger *et al.*, 2012).

Moreover, the higher abundance in *A. aglaja* might be due to that *A. aglaja* can develop in cooler microhabitats than *A. adippe*, therefore, its larvae can start foraging earlier in spring,

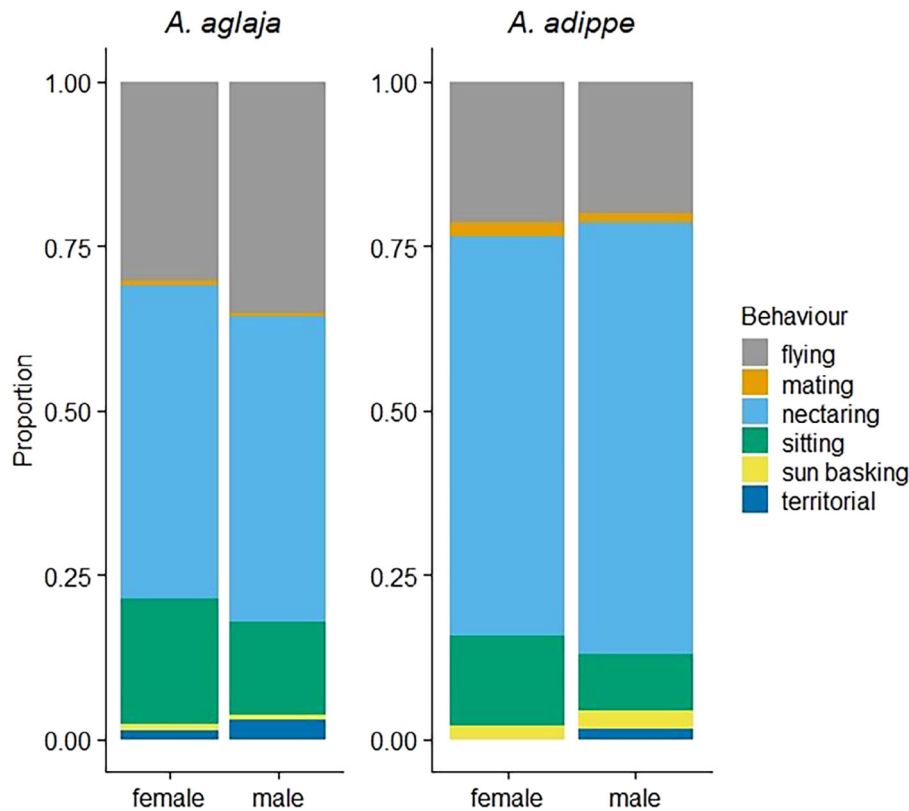


Fig. 4. Proportions of types of behaviours displayed prior to capture in female and male *A. aglaja* and *A. adippe*. [Colour figure can be viewed at wileyonlinelibrary.com].

before temperatures are high enough for *A. adippe*. Indeed, we observed that *Argynnis aglaja* emerged earlier in the season than *A. adippe*, but both species disappeared from the study sites at the same time. The peak dates of abundance, however, were very similar in both species (Supplementary Fig. S3). This might be indicative of a larger variability in the emergence date in *A. aglaja*, which could be a consequence of the species' tolerance for lower temperatures compared to *A. adippe*. Alternatively, a shorter active period of *A. adippe* imagoes could be another attribute pointing towards that *A. adippe*, being a specialist species, not only has particular requirements to its spatial habitat. Indeed, a study on divergent nectar plant usage between specialist and generalist butterflies in the UK showed that length of flight period was significantly positively associated with the degree of generalism, estimated as number of nectar plants used (Tudor *et al.*, 2004). However, since the overall observed abundance was higher in *A. aglaja*, a larger detected variability in the emergence date might also stem from a higher probability of encountering individuals earlier in the season.

Another factor contributing to the observed differences in population densities might be body size. *Argynnis adippe* was found to be significantly larger than *A. aglaja*, and might therefore have higher demands for nectar and larval food sources (Niven and Scharlemann 2005). This could further decrease population densities in the larger species. In general, estimated population densities on central Öland were lower than those reported in

previous studies of Argynniini species, such as *A. aglaja*, *Brenthis ino*, and *Speyeria idalia*, conducted in Czech Republic and Pennsylvania, US, respectively (Zimmermann *et al.*, 2005; Zimmermann *et al.*, 2009; Ferster and Vulinec 2010). The lower population densities detected in our study could be due to shorter and colder springs and summers in Sweden compared to the above mentioned studies, and thus, more adverse conditions for development. Like most butterfly species, *A. adippe* and *A. aglaja* are protandrous with males emerging earlier in the season than females (Fagerström & Wiklund, 1982), which was also evident in this study with the sex ratio changing towards females at the end of the sampling period (Supplementary Fig. S4).

Mobility patterns. Besides an association with niche breadth, population densities in the studied species were also linked to mobility patterns: while the rarer and in some parts of Europe declining *A. adippe* (van Swaay *et al.*, 2010) formed less dense populations than *A. aglaja*, *A. adippe* was more likely to perform long distance flights than *A. aglaja*, according to estimated dispersal kernels. This would hint at negative density-dependent dispersal in these species and corroborate estimated residence times, which suggest that *A. aglaja* spent more time in the study area than *A. adippe*. This is in contrast with reports of generalist butterfly species being more dispersive, while forming less dense local populations as opposed to specialist species

(Warren *et al.*, 2001). However, low-population densities might be indicative of low habitat quality, and this might be particularly critical for a specialist species, having very specific requirements to its habitat. Hence, we argue that, although specialists might generally be less dispersive, the ability to cover long-distance flights in order to find suitable habitat might be especially important for such species. Long-distance dispersal has also been reported for the specialist butterfly *Boloria aquilonaris* as a critical factor for habitat connectivity, in order to persist in a highly fragmented habitat (Baguette, 2003). This could at least in part explain the lower population densities along with higher probabilities of long distance dispersal in the specialist *A. adippe* compared to *A. aglaja*. It should be mentioned that the associated standard errors of estimated population sizes for females in both species were higher than the estimates, probably due to the small sample sizes. The interpretation of these results should therefore be considered with care. Despite this, we can state with confidence that *A. adippe* was less abundant in the study area than *A. aglaja*, and that the general found occurrence and mobility patterns are robust.

Regardless of differences in population densities and dispersal probabilities, the mean flight distance did not differ significantly between the two species. In *A. adippe*, the mean distance covered was 563 meters, and in *A. aglaja* 344 meters. However, low recapture rates together with low capture probabilities might have concealed a difference in mean flight distances between the studied species, and estimated dispersal kernels actually showed that *A. aglaja* was less likely to perform long distance flights than *A. adippe*. Other mobility studies on *Argynnis* or related species report lower mean flight distances than we found, e.g. 330 meters (females) and 200 meters (males) for *A. aglaja* in the Czech Republic (Zimmermann *et al.*, 2009), 49 meters (females) and 32 meters (males) for *Brenthis ino* in Germany (Weyer and Schmitt 2013), and 160 meters (females) and 230 meters (males) for *Boloria aquilonaris* in Finland (Gorbach 2011). Interestingly, despite the majority of individuals in this study being sedentary, we found, to our knowledge, the longest recorded flight distances in the two studied species in an MRR-study, 11.9 km for *A. aglaja* and 3.7 km for *A. adippe*.

Recapture rates were 8.9% for *A. adippe* and 9.5% for *A. aglaja*, which is lower compared with other MRR studies on *A. aglaja* in the Czech Republic, or on their Nearctic relatives *Speyeria idalia* and *S. diana* in the US (Kelly and Debinski 1998; Zimmermann *et al.*, 2009; Wells and Smith 2013). In principle, low recapture rates can be caused by a combination of high emigration and high mortality rates. However, it is nearly never possible to disentangle these two factors with certainty. Here we dealt with an open study system and therefore translated estimated survival to residence times within the study area. Low recapture rates might also imply low capture probabilities, which was the case in our study, i.e. 0.04 in *A. aglaja*, and 0.2 and 0.22 for females and males in *A. adippe*, respectively. This might reflect the short estimated residence times within the study area (5.4 and 4.8 days in *A. aglaja* for females and males, respectively, and 2.3 days in *A. adippe*). Since both studied species are able to cover distances of several kilometres in flight, they are potentially able to form open populations

stretching over large areas. Dispersal from one habitat patch to another over forested areas has even been reported for the less mobile nymphalid species *Euphydryas aurinia* within a similar study area on central Öland (Betzholtz *et al.*, 2007), and an MRR-study on this species on the Swedish island Gotland identified inter-patch movements of up to several kilometres through forest and other matrix types (Johansson *et al.*, 2019).

Butterflies can simplistically be divided into “sedentary” species, which form relatively closed populations and tend to stay within their natal patch, and “mobile” species, which can form open populations and likely visit many patches in heterogeneous landscapes during their imago stage (Cowley *et al.*, 2001b). Other assessments of butterfly mobility include rankings of butterfly experts by giving a “mobility index”, which would classify our studied species as relatively mobile (Dennis & Shreeve, 1997; Cowley *et al.*, 2001b; Komonen *et al.*, 2004). Depending on the species, flight distances above 500 metres—e.g. in *Maniola nurag*, and *M. jurtina* (Grill *et al.*, 2006)—up to several kilometres—e.g. in *Boloria aquilonaris* (Baguette, 2003)—are commonly considered long-distance movements in butterflies. In our study, most butterflies were recaptured within the same open or semi-open area and within a distance of ~200 metres from the point of first capture, which would render them rather sedentary. However, considering our low recapture rates and the species’ potential to cover long distances in flight, many individuals may have left the study area. We also found rather low capture probabilities, which means that the chances of recording movements, including long-distance flights, were slim.

Although body size is commonly associated with dispersal capacity, besides butterflies also in grasshoppers, beetles, and flies (Feener Jr 1987; Roff 1991; Levy & Nufio, 2015), our data suggested no intraspecific association of wing size or sex with distance flown between capture events. However, in our study such associations might have been masked by low recapture rates. On the other hand, body size might not always be a good predictor of mobility, for example, a study on *Melitaea cinxia* in the Åland Islands, Finland, revealed no difference in the distances moved between males and females, despite significant differences in morphology (e.g. wing size, wing loading) between the sexes (Breuker *et al.*, 2007).

Behaviour. *Argynnis aglaja* was more active and seemed to spend more time on the wing compared to *A. adippe*, while *A. adippe* was more often nectar feeding compared to *A. aglaja*. This did not confirm our hypothesis that more active behaviour types indicate general higher mobility, but again, such an association might have been missed due to low recapture rates. On the other hand, the activity detected only represents a snapshot in time, hence, it might not necessarily reflect the individuals’ actual prevalent behaviour.

Conclusion

The outcome of our study implies a complex relationship between mobility, population density, distribution area,

and niche breadth. As expected, we found that distribution ranges and niche breadth were positively correlated with local abundance in the studied *Argynnis* species. However, contrary to what is commonly reported, we found that dispersal probabilities were negatively associated with distribution ranges and the degree of generalism in these species, with the specialist *A. adippe* being more likely to engage in long-distance flight. Since specialist species are restricted to a certain, very particular set of environmental and ecological factors, they might have to rely on engaging in long distance flights just to arrive at a suitable habitat patch, and thereby not necessarily expanding their distribution range. Taking the risk of entering the surrounding matrix in order to find a potentially suitable, new habitat might therefore be crucial for *A. adippe*.

Although we detected the longest recorded flight distances in an MRR-study so far in these species, the majority of recaptured butterflies seemed to be rather sedentary in open and semi-open areas within the studied woodland landscape. However, together with low recapture rates and low estimated residence times, this might in part reflect that many individuals moved outside our study area, indicating that they use large habitats. This could have important implications for conservation, as it seems that the in some parts of Northern Europe endangered *A. adippe* uses extensive areas of suitable habitat within a forest matrix to form stable populations. To increase our understanding of the ecology in these butterflies and to aid management, further studies on density-dependent mobility in these species in different landscapes would be worthwhile. Our study emphasises the importance of regarding a whole set of species attributes, such as movement and distribution patterns, local abundances, and niche breadth, as well as how these traits influence each other in order to draw conclusions about how a species or population might react to environmental changes.

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Author contributions

DP, AF, MF, and PEB conceived the study. DP, AF, MF, and YY collected field data. DP, and CT analysed the data. DP, and AF wrote the first draft. All authors contributed to the final version and approved the submitted manuscript.

Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Supporting Information

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

Supplementary Figure S1 Examples of habitats for *A. aglaja* and *A. adippe* within the studied woodland landscape on central Öland.

Supplementary Figure S2 Wing size measurement as longest straight-line distance from the wing base to the apex on the underside of the forewing, here in *Argynnis aglaja*.

Supplementary Figure S3 Frequency of capture events of *A. aglaja* (orange) and *A. adippe* (blue) per day on central Öland. A separate y-axis (right) was used for *A. adippe* for better visualization.

Supplementary Figure S4 Histogram showing how the sex ratio changed throughout the season in *A. aglaja* and *A. adippe*.

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