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ORIGINAL PAPER

Demographic insights into *Lopinga achine* populations in alluvial forests: implications for conservation in non-grazed woodlands

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Abstract Butterflies inhabiting open forests are declining across Europe, but the knowledge on their population ecology is still limited. The *Lopinga achine* is an endangered species, occupying open forests that are typically maintained by extensive forest grazing or coppicing. Previous studies on the ecology of *L. achine* were restricted to certain geographical areas, habitat and management types, thus their conclusions may not be transferred to all parts of Europe. To inform conservation strategies for this species, we investigated populations in non-grazed alluvial forests in western Hungary and gathered demographic and movement data using capture-mark-recapture. We marked 165 butterflies in Alsószölnök and 130 in Szakonyfalu, with more males than females in both populations. Total population sizes were estimated at 311 (95% CI 257–398) in Alsószölnök and 264 (95% CI 196–386) in Szakonyfalu, with 1.43 and 1.11 male ratios, respectively. In Alsószölnök, apparent survival declined over the season, and male recapture probability increased with age. Most individuals moved less than 150 m, but four males dispersed more than 1,000 m between the sites. We obtained robust estimates of population size and survival in *L. achine*, providing a baseline for future demographic, behavioural, and conservation-management studies. Although population sizes were low compared with other European studies, their national conservation value remains high.
Implications for insect conservation Targeted habitat management should focus on maintaining a semi-open forest structure, we propose bark girdling primarily on non-indigenous tree species. The distance between suitable habitat patches should not exceed 100 m.

Keywords Woodland brown · Lepidoptera · Capture-mark-recapture · Population size · Movement · Őrség National Park

Introduction

In recent decades, European butterfly populations have suffered severe declines primarily due to a combination of habitat loss, deterioration of habitat quality and climate change (Bubová et al. 2015; Habel et al. 2019; Warren et al. 2021). Much research effort has been focused on the relationships between land-use intensity, landscape structure and butterfly diversity in agricultural areas (e.g. Ekroos et al. 2010; Börschig et al. 2013; Perović et al. 2015; Habel et al. 2019, 2022 rösi et al., 2022), but insect decline in forest ecosystems has also been demonstrated (Staab et al. 2023). Woodlands are among the most species-rich habitats for butterflies in Europe and numerous species inhabiting open forests are threatened or endangered (Van Swaay et al. 2006). In the last twenty years, the red list status of such species have considerably deteriorated in some parts of Europe (e.g. in Baden-Württemberg, Germany: Ebert et al. 2005; Steiner and Trusch 2025). However, the ecology of open forest butterflies is still relatively understudied (but see e.g. Hinneberg et al. 2023; Habel et al. 2025).

There is a growing body of evidence that the temperate forest biome in Europe was dominated by light woodland during the Last Interglacial period (Pearce et al. 2023, 2025). After the decline of herbivore megafauna, diverse human activities such as coppicing, pollarding and forest

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grazing maintained light woodlands until the 20th century (Peterken 1996; Vera 2000; Rupp 2013). Nowadays, prevailing management practices retain European temperate forests in succesional stages with closed canopy, high stock of timber and low species richness of producers and consumers (Hilmers et al. 2018). In these modern forests, only clear-cuts (Viljur and Teder 2016) and nature conservation oriented management practices such as coppicing and forest grazing can provide suitable habitat for open woodland butterflies (Benes et al. 2006; Fartmann et al. 2013; Dolek et al. 2018).

Canopy openness is a crucial determinant of woodland butterfly assemblages, primarily due to its positive effect on the availability of nectar sources, larval host plants and sunlit patches (Schmitt et al. 2024). Increased light penetration promotes a richer and more diverse understorey vegetation, which supports both adult foraging and oviposition (Ohwaki et al. 2017).

The woodland brown butterfly (*Lopinga achine* (Scopoli, 1763) strongly depends on open forests and its populations are declining in Central Europe. Previous studies on the ecology of *L. achine* examined its populations in coniferous forests in Sweden (Bergman 1999, 2001; Bergman and Landin 2001, 2002; Bergman and Kindvall 2004; Lindman et al. 2013; Johansson et al. 2025), coniferous and mixed forests in Germany (Streitberger et al. 2012) and oak dominated forests in the Czech Republic (Konvička et al. 2008). They all concluded that the habitat of *L. achine* had been maintained primarily by forest grazing, and grazing intensity is a crucial factor influencing population size (Johansson et al. 2025). In Hungary, *L. achine* occurs in mesic broadleaf woodlands: sessile oak-hornbeam or pedunculated oak-hornbeam forests and riverine ash-alder woodlands (Scherer and Horváth 2016; Sum 2017). Although several local populations have been discovered recently (Sáfián et al. 2012; Sáfián et al. 2016; Sum 2017; Scherer 2021), at the country level, the species is declining (Sáfián et al. 2012). Since forest grazing was prohibited in Hungary for many decades (until 2017), open forests are either in a transitional stage of succession after forestry management (e.g. clear-cut) and/or are maintained by hydrological conditions (e.g. high ground water level).

Due to the diversity of suitable habitats and possible management practices, the effective conservation of *L. achine* requires a deeper understanding of local population dynamics. This is particularly important for populations inhabiting riverine ash-alder woodlands, which remain relatively understudied across Europe. In butterflies, population size and adult sex ratio are key demographic parameters that determine effective population size, reproductive potential (Adamski 2004; Sielezniew and Nowicki 2017), and also shape mating patterns (Wedell et al. 2002). The spatial behaviour is crucial to determine the habitat use, habitat connectivity, population viability and they guide the habitat management as well (e.g. O'Neil and Montgomery 2018; Evans et al. 2020). In this study, we investigated two populations of *L. achine* in Western Transdanubia, Hungary. We used capture-mark-recapture method with the aim to estimate daily and total population sizes, sex ratio and residence time, and to reveal within-habitat movement patterns and dispersal between the two populations. We aimed to provide a robust baseline for future monitoring on the effects of habitat improvement efforts.

Materials and methods

Study species

Lopinga achine is in near threatened status in Europe (Van Swaay et al. 2025) and is one of the most endangered and strictly protected butterflies in Hungary (13/2001. (V. 9.) KöM Decree). Its geographic range extends across Europe, from northern Iberia to southern Scandinavia, and through temperate forest zones of Asia to Japan (Kudrna et al. 2015). The larvae of *L. achine* feed on various host plants, including *Brachypodium* species, grasses (*Poaceae*), and sedges (*Carex* species) (Bergman 2000; Lindman et al. 2013). In Hungary, the species currently occurs in the western and southwestern regions – including the Dráva Basin, Zala Hills, and Alpokalja – as well as in the northeastern part of the country (Aggtelek Karst and Szatmár Plain forests) (Kemencei and Patalenszki 2021). The primary host plants are *Brachypodium* species in the Aggtelek Karst (Sum 2017) and *Carex brizoides* in the Szatmár Plain and western Hungary (Scherer and Horváth 2016; Deli 2021). In the Őrség National Park, the species inhabits open riparian ash-alder woodlands (Sáfián et al. 2012; Scherer and Horváth 2016). The butterfly prefers semi-shaded forests with higher host plant densities (Horváth and Scherer 2018, 2021).

Lopinga achine is univoltine, with adults flying from late May to early July in Hungary, depending on late spring weather. Butterflies spend the night in tree canopies and descend to the understory in the morning. They mainly fly over host plant patches, rarely settling on the ground or on the undergrowth. Females drop their eggs individually over host plant stands, where they fall on the ground. The larvae develop in summer and autumn, overwinter at ground level in dense vegetation, resume feeding in spring, and pupate shortly afterwards (Bergman 1996).

The closed populations of *L. achine* usually constitute metapopulation structure with a relative low number of dispersing individuals (Bergman and Landin 2001; Konvička et al. 2008). However, long-distance movements are essential for the long-term persistence of the species' populations due to the successional nature of its habitats (Bergman and Kindvall 2004). Earlier studies found that distance of movements of females increased after they had laid most of their eggs, but males do not move more with increasing age (Bergman and Landin 2002). The sex ratio generally weighted toward the males (Bergman and Landin 2002; Konvička et al. 2008), but the ratio of dispersing individuals between the sexes is not completely clear, previous studies represented contrasting results (Bergman and Landin 2001; Konvička et al. 2008).

Study area

The survey was conducted in two sites of *L. achine* within the Őrség National Park: the Szakonyfalu Valley and a parallel valley west of it, located between Alsószölnök and Kétvölgy (Fig. 1). The two valleys are separated by a north-south ridge about 310–320 m high, covered with sessile oak-hornbeam forests and beech (*Fagus sylvatica*) woodlands with Scots pine (*Pinus sylvestris*). Both sites were characterized by grassland habitats until the 19th century (Arcanum Adatbázis Kiadó 2025).

The Szakonyfalu Valley, shaped by a small stream originates south from the village of Kétvölgy and flows northward, joining the Rába River. The extent of the whole potential habitat for *L. achine* is approximately 34 hectares, but one third is currently less suitable for the species due to the high canopy closure. The survey focused on the known occurrence of the species (2 km long valley section). The surveyed section lies 250–260 m a.s.l. The streambed is meandering, 2–4 m wide, and 1–2 m deep. Water levels fluctuate dramatically, ranging from almost complete dryness to valley-wide flooding. The typical vegetation is alluvial forest with black alder (*Alnus glutinosa)* as dominant tree species, scattered with ash (*Fraxinus excelsior*) and white willow (*Salix alba*). Small sections are dominated by hornbeam (*Carpinus betulus*), and some areas feature spruce (*Picea abies*). The upper canopy is not entirely closed, and the shrub density is various, mainly consisting of elderberry (*Sambucus nigra*), hazel (*Corylus avellana*), and blackberry (*Rubus fruticosus* agg.). The herbaceous layer is well-developed, with *Carex brizoides* occasionally forming dense stands (Fig. 2a). The valley also hosts small populations of protected species like spring snowflake (*Leucojum vernum*) and ostrich fern (*Matteuccia struthiopteris*).

The Alsószölnök study site is in a tributary valley of the Szölnök stream, which originates northwest of Kétvölgy and flows northward, joining the Szölnök stream southwest of Alsószölnök. Similarly to Szakonyfalu, one third is characterized by higher canopy closure, making it less suitable for *L. achine*. The survey focused on the known occurrence site of the species, a 2-km-long valley section at an elevation of 255–270 m a.s.l. The stream within this area is 1–2 m wide and shallow and generally exhibits low water levels. Vegetation here is similar to that of Szakonyfalu. However, the otherwise closed forest is more frequently interrupted by small open patches and sedge stands resulting in a broader extent of suitable habitat for *L. achine*.

Sampling method

We carried out a capture-mark-recapture (CMR) survey between 8 and 26 June 2016, with nine sampling sessions in Alsószölnök and eight in Szakonyfalu. Each day only one site was sampled. Suitable habitats within both study sites were thoroughly walked by one person every second day (as weather permitted) and individuals were caught using butterfly nets. Sampling was conducted under suitable weather conditions (temperature > 20 °C, without rain and strong

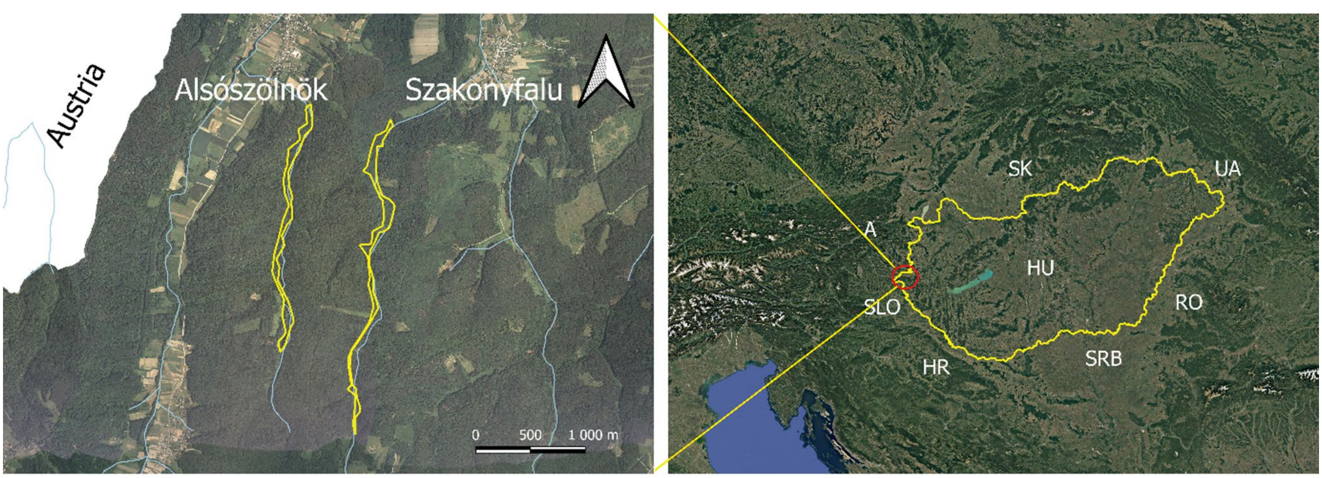

Fig. 1 Location of study sites in Hungary, South from Alsószölnök and Szakonyfalu settlements. Yellow line indicate the distribution area of *Lopinga achine* individuals (left). Basemaps: FÖMI orthophoto 2005 (left) and Google Maps Satellite (right)

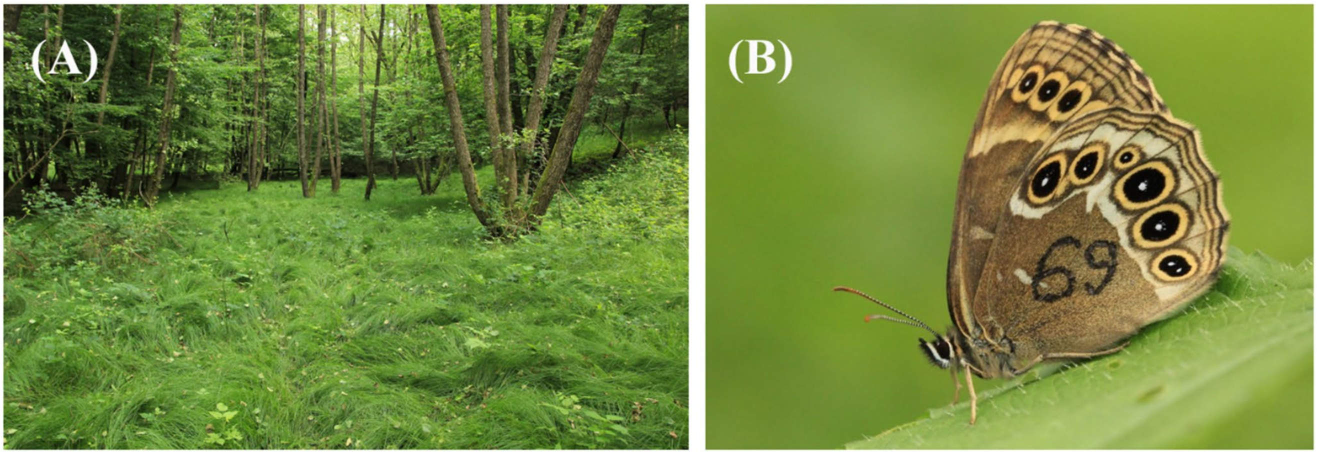

Fig. 2 **A** Typical habitat of *Lopinga achine* in alluvial forests with *Alnus glutinosa*; the ground vegetation has high cover of *Carex brizoides*. **B** *Lopinga achine* female with the individual number on the underside of hindwing. **A** © Bálint Horváth; **B** © Zoltán Scherer

wind) between 10:00 and 16:00, because outside of this period butterflies stayed in the canopy due to shading from surrounding hills and forests, thus inaccessible for capture.

Butterflies were marked using black permanent markers, with individual identification numbers written on the underside of the hindwings (Fig. 2b). GPS was used to record capture locations (accuracy ± 10 m). Recaptures occurring within 10 m of the initial capture location were considered to have a movement distance of 0 m. The sampling site, time of capture, sex and condition of the wings (fresh, intact, worn, or heavily worn) were additionally recorded using the Epicollect5 app. After marking and data collection, butterflies were released immediately.

Capture-mark-recapture analysis

To visualize the number of marked butterflies, we plotted the cumulative number of marked individuals during the sampling period for each sex and site. We used the 'RMark' package (Laake 2013) within the R 4.3.3 statistical software (R Core Team 2024) and the MARK 9.0 program (White and Burnham 1999) for model fitting.

Data were analysed using the Cormack-Jolly-Seber (CJS) model (Pledger et al. 2003) and the Jolly-Seber (JS) model (Jolly 1965; Seber 1965). The CJS model assumes that all marked individuals have equal probability of survival and equal capture probability, and it has two parameters, apparent survival (*Phi*) and recapture probability (*p*). The JS model assumes that survival probability and capture probability are equal for all (marked and unmarked) individuals. We used the 'POPAN' parameterisation of the JS model which estimates apparent survival (*Phi*), capture probability (*p*), probability of entry into the population (*pent*), and superpopulation size (*N*). This model also provides derived estimates of gross and daily population sizes. Before model fitting, we carried out goodness-of-fit (GOF) tests to check model assumptions of the CJS model using the R2ucare package (Gimenez et al. 2018).

Our aim was to perform an exploratory modelling, i.e. to search as large part of the model space as possible to reveal relationships between some covariates (sex, age and time) and the demographic parameters (Doherty et al. 2012). Therefore, we did not aim to find one single most supported model, but rather applied multi-model inference. Although we built only biologically reasonable models, the number of all possible parameter combinations for the JS model was still quite high, thus we used a multi-stage model selection (Bromaghin et al. 2013; Morin et al. 2020) and multi-model inference to reduce model selection uncertainty (Burnham and Anderson 2002).

First we built CJS models separately for the Alsószölnök and Szakonyfalu populations, as well as for males and females (four datasets in total). The CJS model parameters (*Phi* and *p*) were allowed to vary as constant, fully time-dependent, monotonically time-dependent, or age-dependent. 'Constant' models estimate one parameter value for all sampling intervals/occasions, while fully time-dependent models estimate one parameter value for each sampling interval/occasion. In the other two models, parameters can change linearly either with time (day of the sampling period), or age (time since marking). Thus, for each dataset, we could build 16 CJS models with different parameterisations. As we analysed the two sites and two sexes separately, we did not need to involve site and sex as covariates in the models, which largely reduced the model space.

We applied an automated AICc-based model selection where the model with the lowest AICc was considered as most supported. Those models that could not estimate all parameters were excluded from the model selection. The outcome of the CJS model selection informed us in the building of JS models. To assess the relative importance of covariates, we summed the weights of models containing each covariate for each parameter (Burnham and Anderson 2002).

In the second step, we built JS models, where age-dependence is not applicable. For each dataset separately, we built models with only those covariates which were supported in the CJS model selection. For example, if CJS models could estimate *Phi* only in those models where it was constant, then we built JS models only with constant *Phi*. For probability of entry we used the linear and quadratic terms of time as covariates. After model selection, we calculated model-averaged parameter estimates. In the third step, we used the covariates of models from the second step with ΔAICc<2 to build models with sex-dependent parameters as well on the pooled data of males and females (but for the two sites separately). Thus we could directly test if demographic parameters were different between males and females. Furthermore, since we had better data on males (more captures and recaptures, see Results) we aimed to get more robust parameter estimates by pooling the sexes. Since we found large differences between the raw capture data of males and females, and protandry is a widely known phenomenon among butterflies (e.g. Schtickzelle et al. 2002; Zimmermann et al. 2005; Nowicki et al. 2005; Örvössy et al. 2013), we used sex-dependent probability of entry in the models. We provide the model-averaged estimates of parameters and the summed weights of models containing each covariate. When model-averaged estimates of survival were constant, we calculated mean residency time using $(1-Phi)^{-1}-0.5$ (Nowicki et al. 2005).

Movement analysis

Investigation of the full complexity of movement trajectories would require data-intensive movement analyses, which were not feasible with our CMR dataset, because movement paths were not directly observed. Therefore, we calculated the largest net displacement (LND) as the Euclidian distance between the two furthest capture locations of each butterfly specimen (Weyer and Schmitt 2013; Hinneberg et al. 2023). Distances were computed in QGIS 3.34.2 (QGIS Development Team 2019). We disregarded the relief of the sites; consequently, the movement distances are possibly slightly underestimated.

Boxplot charts were used to visually assess distributions of LND and the interquartile range (IQR) across populations and sexes. For visualization, we applied the 'qqbetweestats' function from the 'ggstatplot' package (Patil 2021) within the R statistical software environment.

We performed a Pearson's correlation test between LND and the corresponding number of days to check if butterfly movement followed a random walk (Turchin 1998; Hovestadt and Nowicki 2008). We fitted a linear model to log1p-transformed LND as response variable, and the corresponding time length (number of days), sex and their interaction as explanatory variables ($n=104$). Then we applied an automated AICc-based model selection and model averaging using the 'MuMIn' package (Bartoń 2023). Diagnostic plots suggested that the assumptions of a linear model were violated due to some individuals with 0 m LND, thus we repeated the analysis by omitting these individuals ($n=97$). Since there is some evidence on that butterflies follow different movement rules within habitat patches during routine movements and between habitat patches during dispersal in the matrix (e.g. Van Dyck and Baguette 2005; Delattre et al., 2010), we repeated the analysis (correlation tests and linear modelling) by omitting the four dispersal events. All statistical tests were run with $\alpha=0.05$.

Results

Descriptive statistics

In Alsószölnök, 110 males and 55 females, in Szakonyfalu, 79 males and 51 females were marked. A total of 59 butterflies were recaptured in Alsószölnök, and 38 individuals were recaptured in Szakonyfalu. A higher proportion of males than females was recaptured (Table 1).

The cumulative number of marked individuals showed a clear saturation trend for males in both populations, while no such trend was observed for females (Fig. 3). Additionally, the number of marked males increased sharply during the first two sampling sessions and then plateaued, whereas female captures were initially low, gradually increasing, and remaining relatively high at the end of the sampling period (Fig. 3).

Table 1 Number of marked and recaptured individuals, the proportion of recaptured individuals, and number of sampling days

Population	Sex	Number of		Proportion of recaptured individuals		Sampling days
		Marked ind.	Recaptured ind.			
Alsószölnök	females	55	15	0.273	0.358	9
	males	110	44	0.400		
Szakonyfalu	females	51	11	0.216	0.292	8
	males	79	27	0.342		

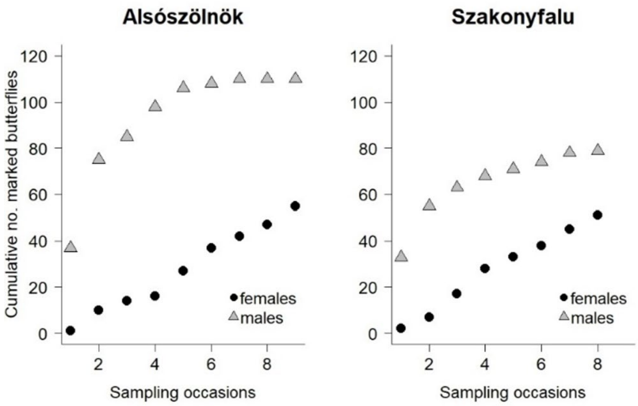

Fig. 3 The cumulative number of marked male and female butterflies in the investigated populations

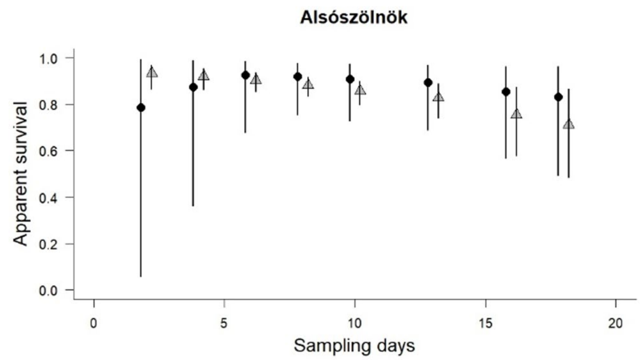

Fig. 4 Model-averaged estimates of apparent survival probability (±95% CI) from JS models on the pooled dataset in Alsószölnök (grey triangles – male; black dots – female). Sampling day 1 is 8 June

Cormack-Jolly-Seber model

The overall GOF-tests showed no violations of the CJS model assumptions (Supplementary Material 1). Model parameters were non-estimable in some models, these were omitted from the model selection. For all datasets, we found more than one models with ΔAICc < 2 (see model selection results in Supplementary Material 2). In three of the four datasets, both apparent survival (φ) and recapture probability (p) were constant in the most supported models and summed model weights were also highest for the constant models (Supplementary Material 2). In Alsószölnök, male survival declined linearly with the progress of the flight period and recapture probability increased with age in the most supported model. For this dataset, time-dependent survival was highly supported (sum of model weights = 0.937), while age-dependent recapture probability was moderately supported (sum of model weights = 0.591) (Supplementary Material 2).

Jolly-Seber models

We built 6 JS models for each dataset in the separate analysis, and 150 and 60 models for the pooled datasets in Alsószölnök and Szakonyfalu, respectively. In general, confidence intervals of parameter estimates were larger for females than males, and larger in the analysis for the separate than for the pooled dataset (Table 2, Supplementary Material 2) We found no major differences in parameter estimates between sexes, except for probability of entry (see below).

Apparent survival rate was similar for males and females, although it showed a stronger decline with progress of the flight period for males in Alsószölnök (Table 2; Fig. 4). In the separate analysis in Alsószölnök, survival was constant for females and time-dependent for males. Thus in the pooled analysis, we had to build both time-dependent and constant models, which resulted in larger confidence intervals for females than in the separate analysis (see Supplementary Material 2). In the pooled analysis, the summed model weight for time-dependent survival was 0.934, which is a relatively strong support, while it was 0.636 for sex-dependent models. In Szakonyfalu, only constant survival models were tested (see above) and the model weights did not support sex-dependency (Supplementary Material 2). These model-averaged estimates of survival translates into 20.3 days and 17 days of mean residency for females and males, respectively.

Capture probability decreased with progress of the flight period for both sexes in Szakonyfalu and for females in Alsószölnök, however, the confidence intervals of sexes and sampling occasions largely overlap (Table 2; Fig. 5). By

Table 2 Model-averaged parameter estimates (with 95% CI) of the Jolly-Seber models for the separate and the pooled datasets. Parameter estimates marked with * are shown in figures

Dataset	Population	Sex	φ	p	Pent	N
Separate	Alsószölnök	Female	0.913 (0.757–0.972)	Declined with time	Declined with time	130 (90–212)
		Male	Declined with time	Increased with time	~0	181 (152–229)
	Szakonyfalu	Female	0.973 (0.39–0.99)	Declined with time	Declined with time	125 (81–235)
		Male	0.948 (0.816–0.987)	Declined with time	~0	134 (105–192)
Pooled	Alsószölnök	Female	Changed with time *	Declined with time *	Declined with time *	128 (100–174)
		Male	Declined with time *	Declined with time *	~0	183 (157–224)
	Szakonyfalu	Female	0.952 (0.794–0.990)	Declined with time *	Declined with time *	125 (84–197)
		Male	0.943 (0.853–0.979)	Declined with time *	~0	139 (112–189)

the end of the flight period, capture probability tended to be lower in Szakonyfalu than in Alsószölnök (Fig. 5). Model weight sums did not indicate any sex-dependence or time-dependence in Alsószölnök. In the Szakonyfalu population, time-dependence was moderately supported (Supplementary Material 2).

The probability of entry was estimated to zero in all models for males. This means that our sampling highly likely started at the peak of the flight season and practically no new individuals entered the population during the sampling period. For females, probability of entry slightly declined during the sampling period in Szakonyfalu, while it was rather constant in Alsószölnök (Fig. 6).

Size of the superpopulation was estimated very similar between sexes in Szakonyfalu, while in Alsószölnök male population size was higher. The confidence intervals overlap both between sexes and between sites (Table 2). Estimates on daily population size showed that sex ratio was strongly male-biased in the beginning of the sampling period. In Alsószölnök, the number of males declined sharply to almost zero by the end of the flight period and the number of females increased up to the 6th sampling occasion when it reached a plateau (Fig. 7). In Szakonyfalu, the difference between the daily numbers of females and males was smaller (Fig. 7).

Movement and dispersal

Altogether 104 individuals (29 females and 75 males) were involved in the movement analysis. The LND parameter showed a skewed distribution as most individuals moved over very short distances. The IQR ranged from 30 m to 123 m for females and from 29 m to 111 m for males. Only three female LNDs and nine male LNDs covered a wider range (303–1249 m). The five longest movement distances were recorded by males, four of which occurred between the two populations (Fig. 8). The IQR ranged from 24 m to 97 m in Alsószölnök and from 34 m to 155.5 m in Szakonyfalu (both sexes involved) (Supplementary Material 3).

All the four dispersal flights were made by males first captured in Alsószölnök (Fig. 9) The moves between the two study sites took 7–11 days, i.e. so many days elapsed between two consecutive captures (one in Alsószölnök, the next in Szakonyfalu). We note that LNDs (and the corresponding number of days elapsed) of these individuals may be higher, because three of these individuals were also recaptured before and/or after the dispersal event.

The correlation between LND and the number of days elapsed was significant when dispersing individuals were included ($r=0.32$, $p=0.0008$, $n=104$), but it was not significant when they were omitted ($r=0.18$, $p=0.07$, $n=100$). The linear model showed that none of the explanatory

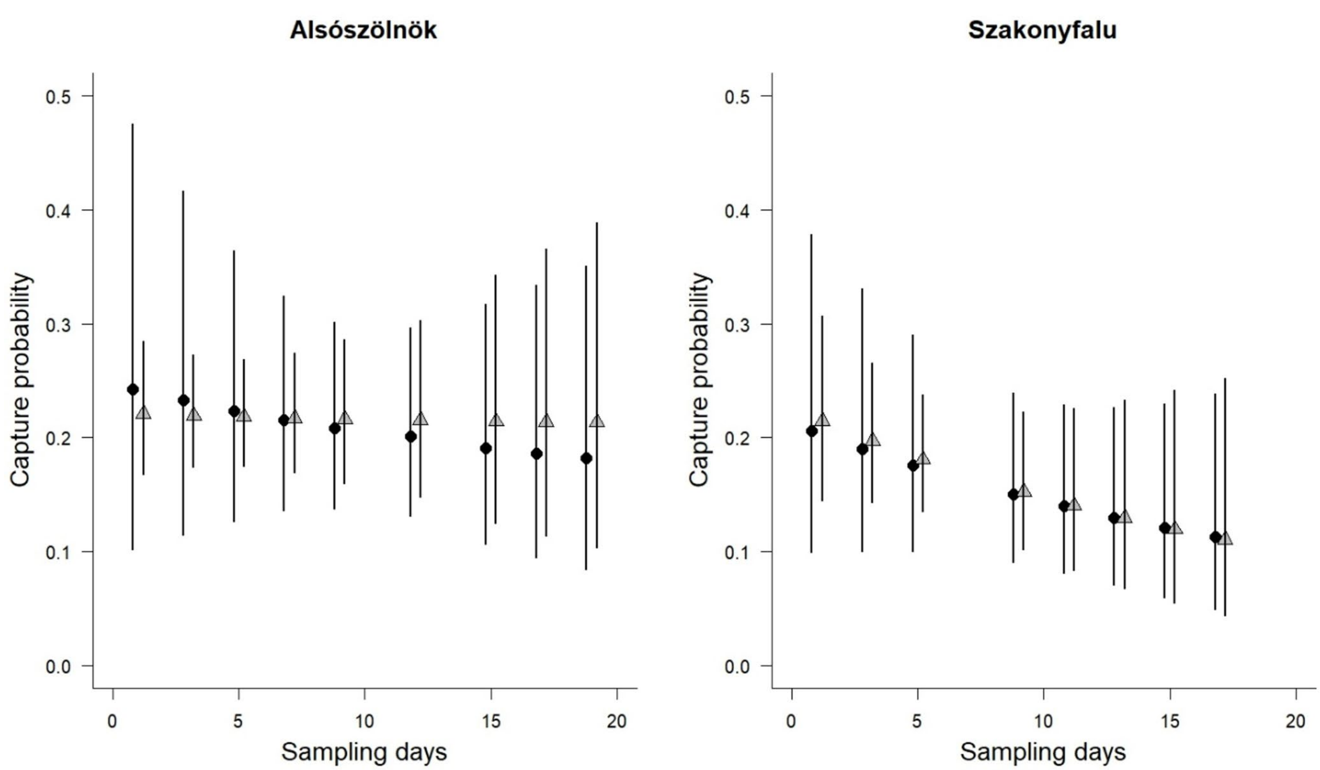

Fig. 5 Model-averaged estimates of capture probability (±95% CI) from JS models on the pooled dataset (grey triangles – male; black dots – female). Sampling day 1 is 8 June in Alsószölnök and 9 June in Szakonyfalu

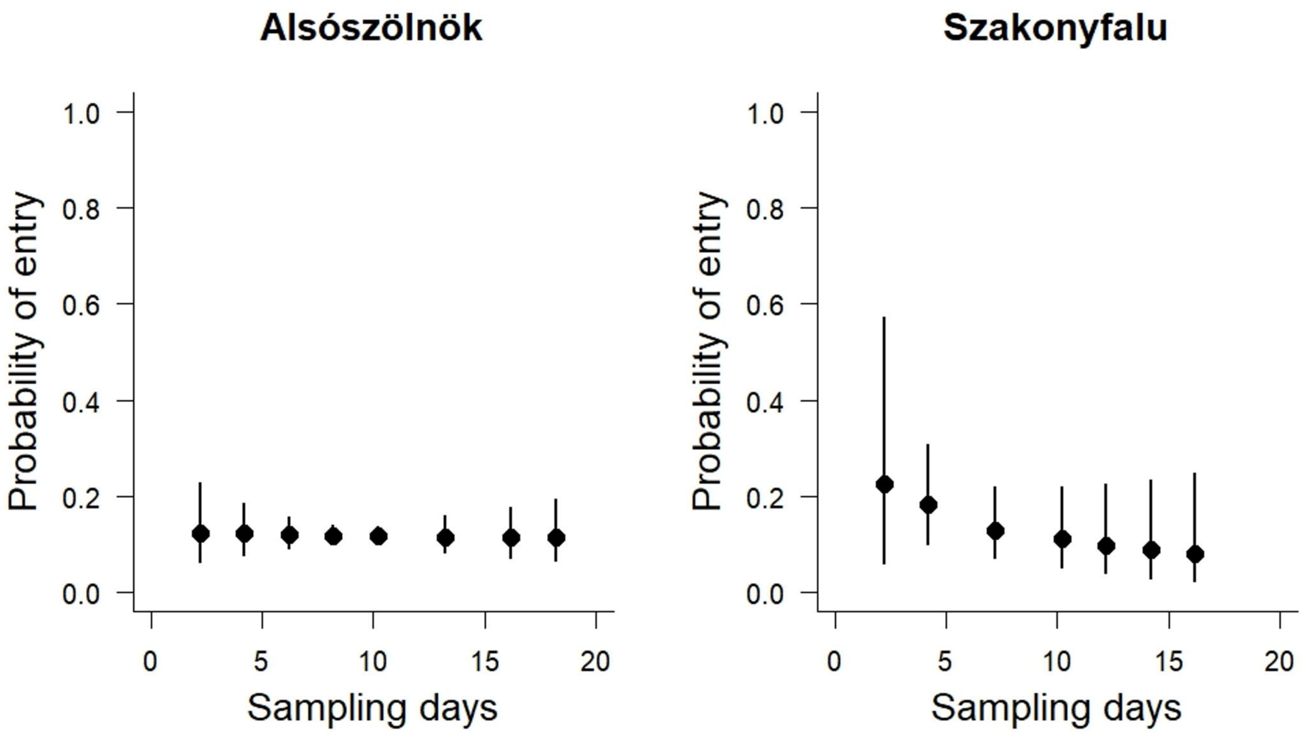

Fig. 6 Model-averaged estimates of probability of entry (±95% CI) of females in the two populations

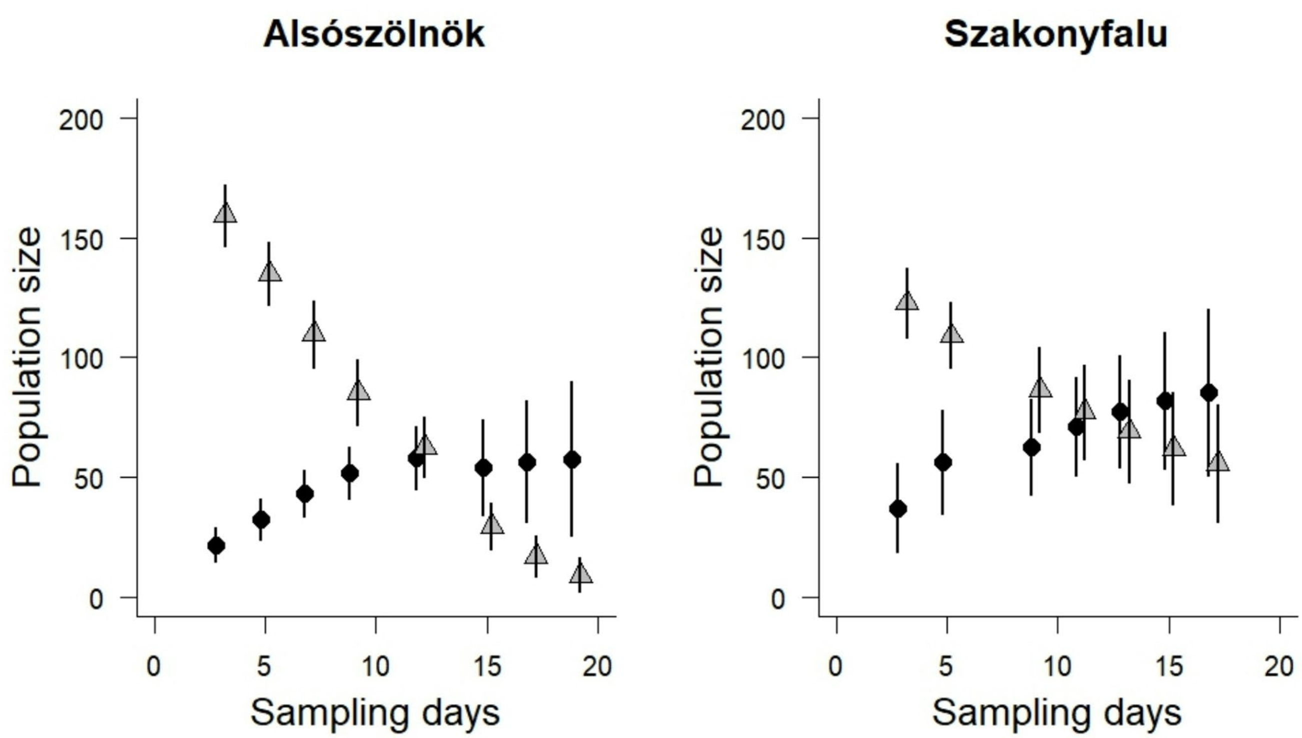

Fig. 7 Model-averaged estimates of daily population size (±SE) of both sexes (grey triangles – male; black dots – female). Sampling day 1 is 8 June in Alsószölnök and 9 June in Szakonyfalu

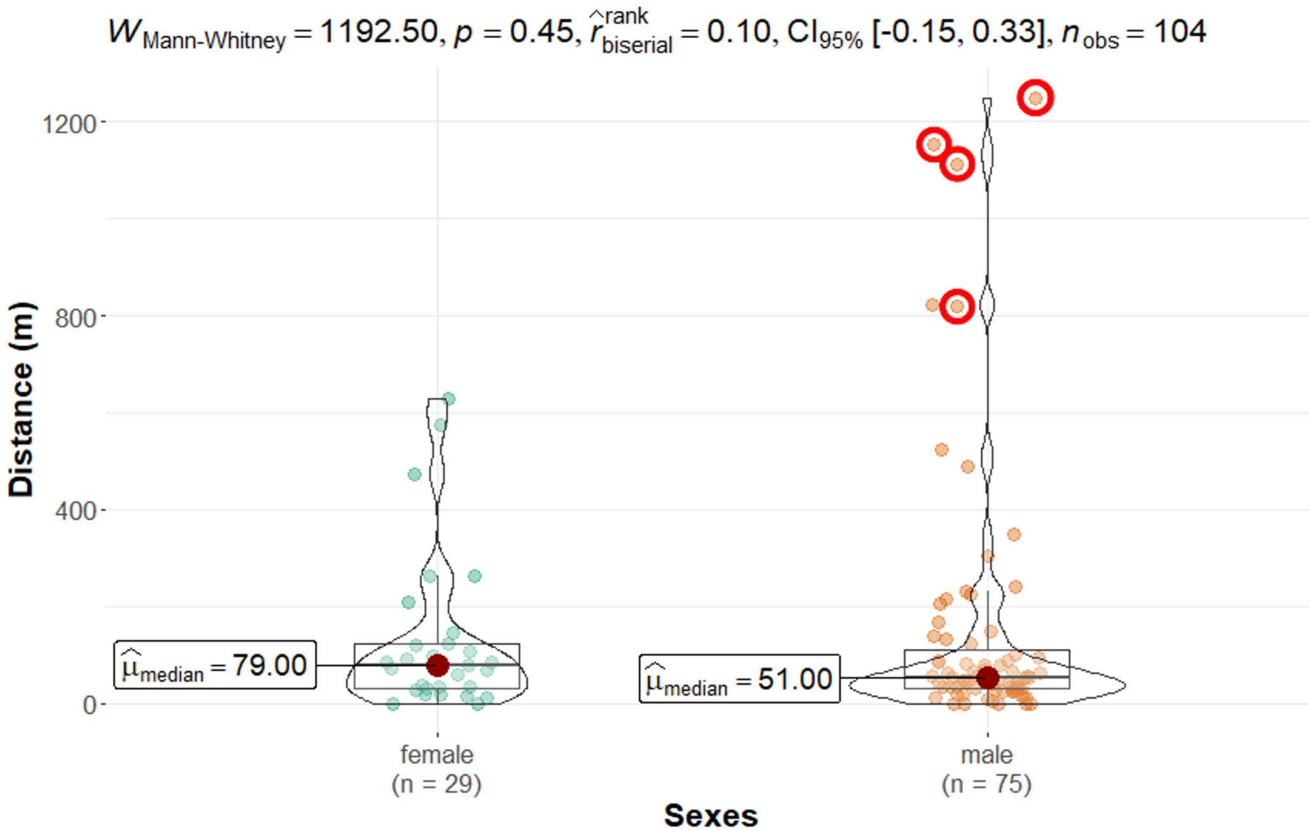

Fig. 8 Largest net displacement distances of *L. achine* sexes on box-plots. Quantiles for females: Q1:0–30, Q2:30–79, Q3: 79–123, Q4:123–630. Quantiles for males: Q1:0–29, Q2:29–51, Q3: 51–111, Q4: 111–1249. Inter-quartile range for females: 30–123; males: 29–111. Red circles mark the dispersal events between the populations

variables had any significant relationships with LND when dispersers were excluded, but the number of days showed a significant positive relationship with LND when dispersers were included (Fig. 10). We found no significant differences between male and female LNDs.

Discussion

Demography

Conservation efforts of rare species must be based on reliable estimates on their population demography (Sutherland et al. 2004). Despite the fact that our sampling did not cover the whole flight period of the studied *L. achine* populations, we could make some conclusions that may be valuable for future studies and conservation efforts. In most cases, the best supported CJS models estimated constant apparent survival and recapture probabilities. This is likely due to the fact that we could not collect sufficient data to uncover more complex patterns (e.g. ageing), because the capture histories were not long enough (see e.g. Sielezniew et al. 2020). Moreover, females marked during the last three sampling occasions were never recaptured. Daily sampling covered approximately three hours and was conducted by a single person. We suggest that both sampling intensity and the length of sampling period should be increased in future CMR studies on *L. achine*. We conclude, that a relatively high proportion of recaptured individuals (0.22–0.4) alone is not sufficient to explain or uncover all details of demographic processes, but the number of recaptures per individuals and the length of capture histories are also important.

We found no sexual differences in apparent survival. This may be because male and female survival were indeed equal, or (more likely) because our sampling could not collect sufficiently long capture histories. We note that in single site studies, such as ours, emigration and mortality cannot be distinguished. Therefore the mean residency time that we calculated from the apparent survival rates is a product of true survival and probability of non-emigration. Our estimates on apparent survival are relatively high compared to earlier studies on this species (Bergman and Landin 2002). When sexes were analysed separately, apparent survival rate of males showed a decline with the progress of the flight period in the Alsószölnök population, and models including time-dependent survival received the highest support in the

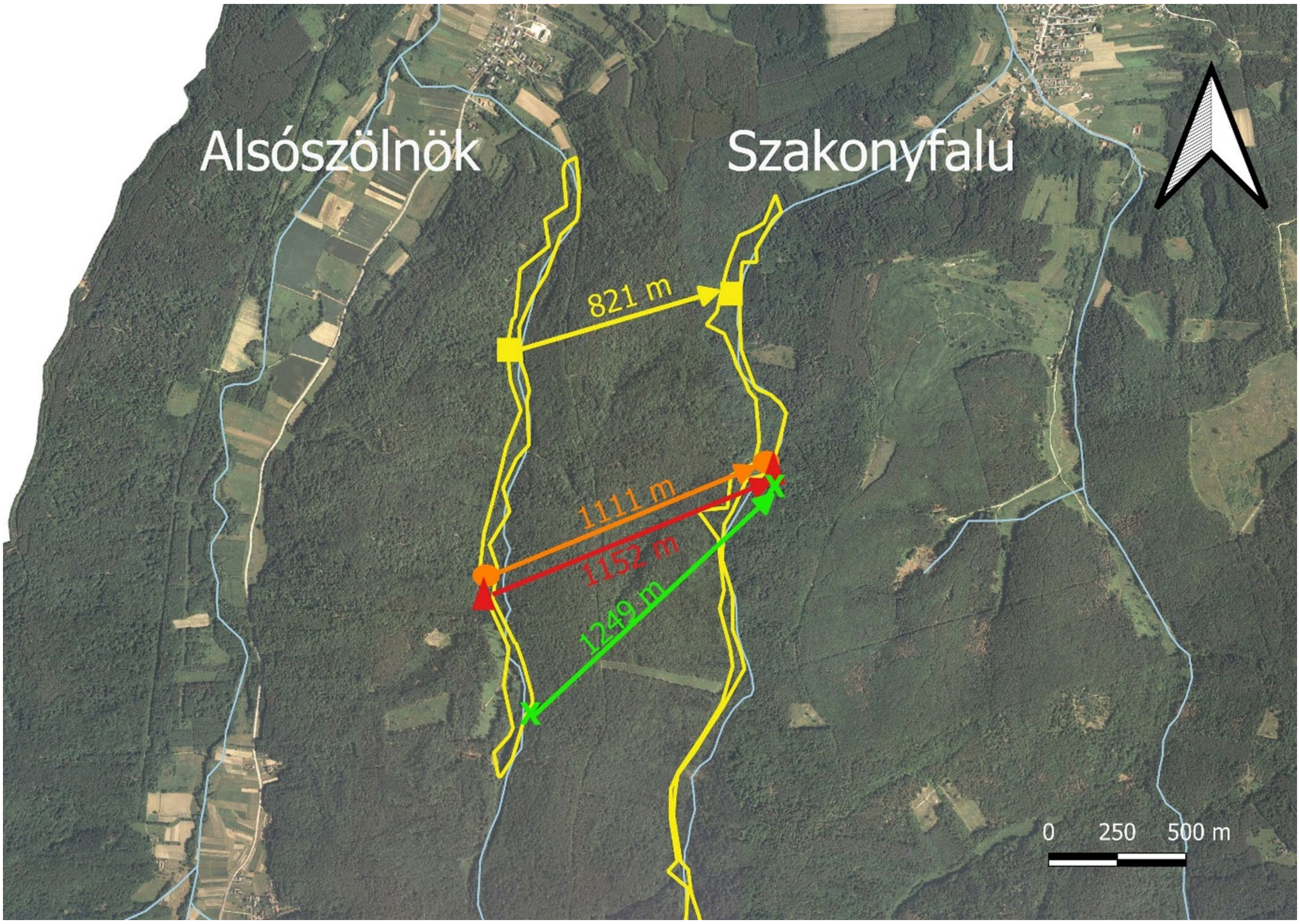

Fig. 9 Dispersal events and their directions between the study sites. Symbols indicate the individuals of marked specimens. Two individuals were recaptured twice after dispersal

pooled analysis as well. In case of males, survival declined with time which can indicate either a decline in true survival and/or an increase in dispersal probability. As the models with age-dependent survival were not highly supported, the increasing mortality cannot be explained with ageing. Thus we suppose that emigration propensity might have increased with progress of the flight period. In case of females, survival showed a non-linear pattern in time with lower estimates and large confidence intervals for the first two sampling intervals, which is likely due to that in this population no females were recaptured until the fourth sampling occasion.

We also found no significant sexual differences in recapture probability. However, when sexes were analysed separately, male recapture probability increased with age in the Alsószölnök population in the most supported model and model weights also supported an age-dependent recapture probability. We suppose that older individuals might be weaker flyers and hence more easily catchable, but this needs further investigations in the future. In the Szakonyfalu population, capture probability of the JS model showed some decline with time for the pooled dataset. The reasons are unknown, changing behaviour with age, weather conditions or a hidden decline in sampling intensity may all cause such patterns. These issues must be addressed in future studies.

Despite covering only about two-third of the flight period, total population size estimates were relatively robust. We highlight that we certainly underestimated population size due to the limited sampling period. We did not find differences in population sizes between males and females in Szakonyfalu, in spite of that higher number of males were marked. We suppose that this is mostly due to that we had a sparse dataset and parameter-poor models were more supported in the model selection, because survival and capture probability did not differ between the sexes (see above). In Alsószölnök, male population size was estimated almost 50% higher than female, but the confidence intervals still overlapped (Table 2). In comparison to other CMR studies on *L. achine* (e.g. Bergman 2001; Konvička et al. 2008), both the estimated superpopulation size and daily population sizes were relatively low in our study. Bergman (2001)

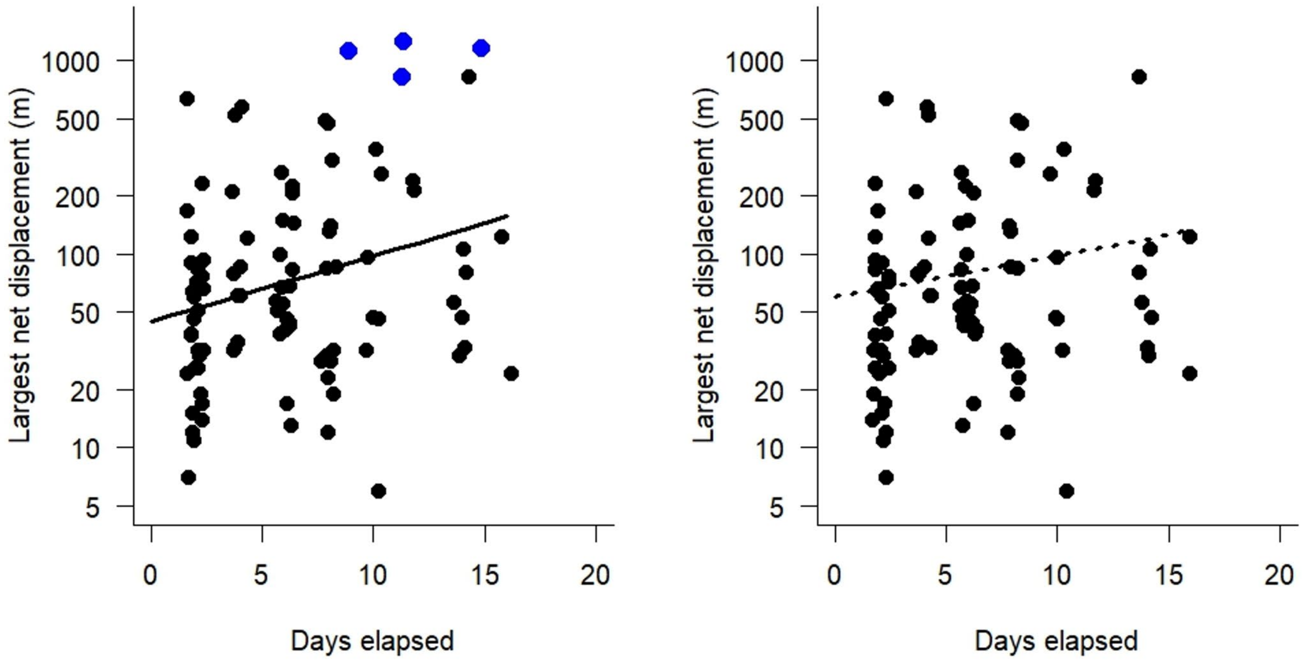

Fig. 10 Largest net displacements (LND) on a log-scale in relation to the elapsed time. Each dot symbolizes one individual. Dots are slightly jittered along the x-axis for better visibility. On the left panel, the four blue dots indicate LND of the four dispersing males, the continuous black line shows the model-averaged predicted mean. On the right panel, the dotted line also shows model-averaged prediction, but it indicates that the effect of time was not significant

demonstrated a clear effect of canopy closure on population size and density, with the most favourable canopy cover ranging between 70 and 85%. Canopy cover below 65% and above 90% created unfavourable light conditions for the species. In the Alsószölnök sampling site, canopy cover varied, with an average closure of 64% (SD = 0.16) (based on the dataset of Őrség National Park Directorate, see Supplementary Material 4), which may have been less favourable for *L. achine* compared to the conditions in the Swedish study. However, direct comparison between the demographic parameters of our study populations and those in Sweden maybe inappropriate due to the substantial geographical, climatic and habitat differences. Canopy closure data were not available for the sampling site of Szakonyfalu, however, the stand characteristics closely resemble those of the Alsószölnök study site.

Our estimates on daily population sizes and the cumulative numbers of marked individuals suggested a clear protandry with males emerging probably quite synchronously, which may have resulted in the largely male-biased sex ratio in the beginning of the flight period. Females seemed to have a more extended emergence period and they were still on the wing when males already had disappeared (see Geyer and Dolek 2013). These estimates suggest that our sampling started around the peak of males when some females were also already on wing. Our results on the change of sex ratio during the season are in line with that of Konvička et al. (2008), as they also observed a male-biased sex ratio in the beginning of the flight season that turned into female-biased at the end of the sampling.

We did not directly test for differences between sites, but the JS models estimated very similar population sizes. Based on these estimates we can claim that the populations had a minimum of 311 (95% CI: 257–398) and 264 (95% CI: 196–386) individuals at Alsószölnök and Szakonyfalu, respectively (see Table 2). An interesting difference between the sites was that the estimated daily number of males declined below 10 in Alsószölnök, while it was still above 50 in Szakonyfalu at the last sampling day. It may demonstrate an asynchrony between the two studied populations, which might help ensure the long-term survival of the species (Bergman and Kindvall 2004; Jangjoo et al. 2016). Asynchronous metapopulation dynamics can reduce extinction risk: if one population becomes small or declines, immigration from a neighbouring population may prevent extinction by increasing the number of individuals and maintaining gene flow (rescue effect). Alternatively, the strong male-biased sex-ratio in Alsószölnök in the first half of the sampling period might have induced a positive density-dependent dispersal of males which could result in the declining apparent survival and the very low male abundance by the end of the season that our most supported model estimated. The fact that all the four observed dispersal flights were performed by males from Alsószölnök to

Szakonyfalu may support this explanation. Further studies should address these issues, possibly incorporating the estimation of dispersal rates between sites (e.g. Baguette et al. 2011; Nowicki and Vrabec, 2011).

Future studies should aim for longer sampling periods, ideally from the first observed individuals until the last (late May to early July in Hungary). Extended sampling could provide more accurate estimates of daily population size and insights into female dispersal at the end of the flight period, sex ratio, and the time lag between male and female peaks. The observed patterns in this study were similar to those reported for *Coenonympha oedippus* in the Hanság region, Hungary (Ambrus et al. 2016.), where males nearly disappeared by the end of the flight period, while a few females survived for a longer time. However, continued sampling during the late flight period is often inefficient due to low abundance. Our findings were different from those of other open-forest butterfly species. For example, daily population size of males was higher during the whole flight period in case of *Limenitis reducta*, although total population size was equal for the sexes (Hinneberg et al. 2023). In a population of clouded Apollo (*Parnassius mnemosyne*) Vlasanek et al. (2009) found that the numbers of females and males declined simultaneously by the end of the flight period. The similarities between *L. achine* and *C. oedippus* might attributed to their phylogenetic relationship, similar life histories (e.g. grass-feeding, overwintering larvae), and habitat requirements (humid, nutrient-poor, weakly disturbed). Further research is needed to clarify these patterns and refine our understanding of their life histories.

Movement and dispersal

Our results showed that the majority of LNDs was surprisingly short, i.e. below 130 m. However, the longest LNDs within a sampling site ranged up to 630 m for females and 812 m for males. The lack of any linear relationship between time and distance of LNDs within sites indicates that butterfly movement did not follow a random walk at the spatial scale of the habitat patches (Hovestadt and Nowicki 2008). These results together suggest that most *Lopinga achine* individuals might have had a home range in our study sites, although more detailed individual movement paths would be necessary to reveal such patterns (see e.g. Kőrösi et al. 2008). Similar movement distances were reported by Bergman and Landin (2002), who identified significant differences between sexes, and by Konvička et al. (2008), whose results – like ours – showed no significant difference between male and female movements. At a larger spatial scale, when LNDs of the four dispersing individuals were included, we found a weak positive correlation between time and distance. However, it does not necessarily mean that individuals moved randomly, but that random walk as a null-model could not be rejected at this scale.

Dispersal ability is another key factor for the long-term persistence of the *L. achine* populations. Owing to successional habitat changes, imagoes must escape unsuitable environments by relocating to adjacent suitable habitats (Johnson 2000; Bergman and Landin 2002). Furthermore, gene flow also plays a vital role in maintaining butterfly metapopulation structures (e.g. Ugelvig et al. 2012). In our study, we recorded four dispersal events between the two sites, all involving males with distances ranging from 797 to 1249 m. Similarly, Konvička et al. (2008) reported more dispersing males, than females, whereas Bergman and Landin (2002) did not observe a clear sex-based difference. In our study, the low number of dispersal events between the populations does not allow us to make conclusions, therefore we only propose two potential explanations for the observed pattern: (i) males dispersed more frequently than females, and/or (ii) the detection probability of male dispersal was higher, at least during our sampling period. Dispersal of male butterflies might be driven by high male and low female density enhancing male-male competition. Female dispersal may occur later in the season, caused by intraspecific competition for suitable oviposition sites (Plazio et al. 2020). Our data are not sufficient to distinguish between these alternatives, however, they demonstrate obvious dispersal between the populations, which requires further investigation.

Conservation implications

The *L. achine* populations of Western Hungary have not been previously investigated. Our study provided the first quantitative results to support nature conservation efforts. The estimated superpopulation size and the daily population sizes in our study sites were lower than in other European studies on *L. achine* (Konvička et al. 2008), but our sampling did not cover the whole flight period, thus these are minimum estimates of the total population size for the entire flight season. However, when qualitatively compared to species-specific transect count reports (e.g. Sum 2017; Scherer 2021), the populations of the investigated sites are amongst the populations with the highest densities in Hungary. Consequently, they present high conservation value considering its near threatened status in Europe (Van Swaay et al. 2025), and strictly protected status in Hungary.

Based on some historical maps (Arcanum Adatbázis Kiadó 2025), the study sites had been covered by meadows and had been mowed or grazed until the end of the 19th century, after which forest structure developed mostly through spontaneous succession until the middle of the 1900's years. The current forest stands exhibit moderate canopy closure likely reflecting the mid-stage forest succession. Grazing has not influenced the present habitat structure (cf. Bergman 2001; Bergman and Kindvall 2004), since due to its long-term prohibition in forests it is not part of habitat management practices in Hungary. Due to changes in livestock farming and landscape structure over the past few decades in the study region, forest grazing is unlikely to take place in the near future at the study sites. Consequently, maintaining *L. achine* habitats is feasible through extensive and targeted forest management that considers the specific habitat requirements of the species (Streitberger et al. 2012; Geyer and Dolek 2013).

The distribution of *L. achine* adults within the study sites clearly overlapped with the foodplant patches delineating the most suitable parts of the valleys. Extending the suitable habitat of the butterfly is a conservation priority at the Őrség National Park, aiming to increase both the density and population size of *L. achine*. Our results provided valuable data for habitat improvement initiatives. The results of the movement analysis indicated that distances between existing and newly created habitat patches should not exceed 100 m to be reachable during routine movements. However, the four observations of dispersal between populations suggest that a spontaneous colonization of newly created habitat patches would even be possible slightly beyond 1 km.

Considering conservation efforts within the study sites, we recommend reducing shading in areas where canopy closure approaches 100%, for example by using bark girdling primarily on non-indigenous species and on understorey trees. This may help ensure an optimal light regime for *L. achine* and its local foodplant (*C. brizoides*). Bark girdling on native tree species is recommended only in the absence of non-indigenous and non-native species. Moreover, the resulting dead wood provides valuable habitat for many forest organisms, such as larval substrates for saproxylic insects and foraging sites for woodpeckers. It is not certain that *C. brizoides* will successfully colonize newly created gaps, as other forest plant species (e.g. *Rubus fruticosus*, *Urtica dioica*) are strong competitors. To ensure the presence of *C. brizoides* in these patches, we recommend vegetative propagation – the method tested and verified by the local national park directorate.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Competing interests The authors declare no competing interests.

Ethical approval All authors declare that we did not collect threatened species during the study, and all individuals were carefully returned into their habitat.

Consent to participate Not applicable.

Consent for publication All authors declare that we agree to publish this manuscript in the Journal of Insect Conservation.

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