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Inter-annual variation in adult demography, but no sex bias in a large lowland population of the threatened Clouded Apollo *Parnassius mnemosyne* butterfly

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Abstract
The Clouded Apollo, *Parnassius mnemosyne* is a charismatic West Palaearctic butterfly, threatened in some European countries and listed in Appendix IV of the Habitats' Directive. We investigated a large lowland population of the species inhabiting a complex of irregularly coppiced light forest and adjacent wet meadows in the anthropogenic landscape in the valley of the Narew river in NE Poland. A mark-release-recapture (MRR) method was used over 4 years to estimate population size, adult catchability, daily survival and lifespan. The beginning and length of the flight period (which lasted 4–6 weeks) differed over the years and was clearly related to weather conditions (temperature, sunshine) in April, i.e. the most important period for larval development. The seasonal population size varied from 555 to 942 adults. In contrast to some previous studies, the sex ratio turned out to be well balanced, although the catchability of males was significantly higher than that of females in each year. The quality of the wings deteriorated during the season in both sexes, but it was generally better in the case of females, which indicates that they are less active. Inter-seasonal variation in the lifespan (6.36–12.45 days) is more difficult to interpret, but it is worth noting that individuals lived the longest in the coldest and least sunlit flight period. The temporal fragmentation index (i.e. the ratio of flight-period length to adult lifespan) also varied (3.37–5.97) but was generally relatively low, which suggests that there is no threat of reduction of the effective population size at the moment. Nevertheless, the investigated population may be at risk of decline due to the observed intensification of meadow use and especially the possible conversion of grasslands into cornfields.

Keywords: *Flight period*, *life span*, *mark-recapture*, *population size*, *sex ratio*

Introduction

Butterflies are a model group of insects for studies of adult demography and dispersal. Their daily activity and usually conspicuous behaviour make them especially convenient subjects. A large amount of data can be obtained with the quite simple and cheap mark-release-recapture method, usually consisting of drawing a unique number or code on a wing (Haddad et al. 2008; Nowicki et al. 2008; Kral et al. 2018).

Among the parameters which can be inferred from such studies are estimates of adult numbers and their longevity. Studies of European butterflies indicate that their average lifespan varies from 2 to 15 days, showing variation among sites and seasons (Bubová et al. 2016). Intra-specific variation may also concern the difference between the two sexes, and some studies indicate that the lifespan of females is longer than that reported for males (Sielezniew et al. 2019).

As far as vulnerable species are concerned, knowledge on population size is even more important. Most species show high temporal fluctuations related to seasonal weather conditions and habitat quality as well as survival of prematures (Wilson &

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Roy 2009). Parasitoids which could decimate premature instars contribute to this instability (Shaw et al. 2009). Population dynamics may also be related to some species-specific traits such as diet specialisation, mobility, length of flight period, habitat area, and distance to the edge of the species' distribution (Franzén et al. 2013; Nowicki 2017). Species with larger fluctuations generally face higher extinction risks (Hanski 2005).

Local abundance is an important factor in the dynamics, genetics, and evolution of populations (Gyllenberg et al. 1997). The effect of population size may be altered by a distorted sex ratio, e.g. by enhancing the level of competition among individuals of the prevalent sex (Casula & Nichols 2003). According to Fisher's principle (Hamilton 1967) one may expect that males and females are present in a butterfly population in the same numbers, but cases of extraordinary sex ratios are also reported. A bias may be primary, e.g. the ratio of eggs of different sexes is different from 1:1 or there may be differences in survival rates between male and female prematures (Frey & Leong 1993; Underwood & Shapiro 1999). Infection with certain strains of *Wolbachia* could also be the cause of sex ratio distortion, and the most well-known examples of female-biased populations have been affected by this male-killing bacterium (Dyson & Hurst 2004; Sakamoto et al. 2011).

However, in natural adult butterfly populations, male-biased sex ratios are most often observed (Ehrlich et al. 1984). Capture-recapture models (Nichols 1992) can help to distinguish whether differences in abundance are not just artefacts of sampling arising from the different "catchabilities" of males and females in the studied area (Stoks 2001). In the case of butterflies, the latter phenomenon usually follows sex-related differences in behaviour, and males are more conspicuous, especially when using a patrolling strategy to find mates. Hence, they are recorded and captured more often than females (Frey & Leong 1993; Casula & Nichols 2003; Zimmermann et al. 2011; Čelik et al. 2012).

Typical contradictions concerning sex ratio are related to representatives of the charismatic genus *Parnassius*, and some data analyses indicate that surpluses in abundance of males are not apparent but real (Brommer & Fred 1999; Matter & Roland 2002; Vlasanek et al. 2009). One of the most intensively studied species is the Clouded Apollo *Parnassius mnemosyne*, which is an interesting research object because of its conservation status as well as its life history. Larvae hatch in early spring, and they develop remarkably quickly to produce adults locally even as early as April (Pásztor et al. 2022).

The Clouded Apollo, despite its wide Eurosiberian range, is considered as near threatened in Europe and listed in Appendix II of the Bern Convention, as well as in Appendix IV of the Habitats' Directive (Van Swaay et al. 2010). In Europe, it is reported from 32 countries and in 28 of them it is considered as a species of conservation concern (Maes et al. 2019). Habitat loss, i.e. the disappearance of traditionally managed flower-rich meadows and pastures accompanied with open deciduous forest or open grasslands, is probably the main threat, as suggested by studies in Finland and Sweden (Kuussaari et al. 2015; Johansson et al. 2017). On a continental scale, *P. mnemosyne* is also potentially threatened by climate change (Settele et al. 2008), which could be one of the reasons for the recent decline of the Clouded Apollo in the Italian Alps (Cini et al. 2020). On the other hand, in the north (e.g. in Estonia), warming has possibly contributed to species expansion (Liivamägi et al. 2013).

In the present paper, we studied the demography of a large lowland population of *P. mnemosyne* for 4 years, which differed significantly in weather conditions. Each year we aimed to estimate the abundance and sex ratio, as well as the lifespan of adults, and to look for the possible relationships of these traits with temperature and insolation.

Materials and methods

Study species

The Clouded Apollo, *Parnassius mnemosyne* (Linnaeus, 1758) is a West Palaearctic butterfly associated with sparse woodlands, clearings, wooded meadows and forest steppes of the temperate vegetation belt. In Central and Southern Europe it occurs in mountain and submontane regions while in the northeast it inhabits lowlands (Tolman & Lewington 2009; Kudrna 2011). Poland could be a typical example of this distribution type, with two main areas of *P. mnemosyne* occurrence, i.e. the Carpathians and the lowlands in the north-eastern part of the country. Isolated populations occur in the Sudety mountains and in Central Poland (Gromek et al. 2021). Genetic studies have revealed the existence of several spatially segregated lineages in Europe, indicating postglacial recolonization from different refugial areas (Gratton et al. 2008).

The Clouded Apollo is a univoltine species, which flies from late April to August depending on locality and season (Tolman & Lewington 2009). It is not specific towards nectar plants and can adjust its foraging to varying resource availability, although it shows some inter-specific variation in preferences (Szigeti et al. 2019, 2020). Males use a patrolling strategy when looking for mates. During copulation, a sperm plug (sphragis) is deposited on the female abdomen by a male to prevent subsequent matings (Vlašánek et al. 2009). Females usually lay their eggs in the vicinity of larval food plants i.e. *Corydalis* spp. (*C. solida, C. cava* and *C. intermedia*), since in the flight period they are already mostly dried up as typical geophytes (Bergström 2005). Caterpillars overwinter in egg shells to emerge in early spring when they develop very quickly, moulting three times, and finally pupate in dried spun tree leaves. The transition zone between deciduous light forest and extensively used grasslands is preferred for development (Habel et al. 2022).

Study site

We conducted our study on a lowland site of *P. mnemosyne* localized near Tykocin (53°13′N; 22° 50′E, 105–108 m a.s.l.) in the Narew Valley (NE Poland), within the Natura 2000 Site "Ostoja Narwiańska" PLH200024. The investigated population was part of a metapopulation system consisting of about 20 occupied patches, of which the focal site was the largest, and well known for at least 25 years. The current landscape was created in the 1970s when this section of the Narew river was regulated and former swamps were converted into grasslands. The inhabited biotope was heterogeneous, and its central part was an elongated fragment of raised land stretching from west to east, 570 m long and 50–100 m wide. This area of about 4 ha was covered by light deciduous forest (mostly oaks, limes, hornbeams and aspens) with some small clearings, surrounded by wetter hay meadows (usually mowed twice a year). The forest was irregularly coppiced, several larger trees were usually cut down every year during the winter time. The only larval food plant of *P. mnemosyne* at the site, i.e. *Corydalis solida*, was patchily distributed and locally very abundant. Caterpillars could be found in April, mostly in sun-exposed patches. Adult butterflies were most often observed along the forest edge and in the clearings, as well as in meadows adjacent to the forest, usually up to about 50 m from the forest boundary (Figure 1).

Data collection

We sampled the population through a mark-release-recapture (MRR) study over 4 years (2017, 2019–2021), on 17–21 occasions (74 in total). Each year the sampling covered the entire flight period of the focal species, and the site was visited every second day on average if the weather was favourable (i.e. dry and not very cloudy or windy), between 9 am and 5 pm CEST. One or two people spent about 2–4 hours on the site during each sampling day. Butterflies were captured with an entomological net, marked on the underside of their hind-wings with unique identity numbers (Figure 2) using a fine-tipped waterproof pen, and then immediately released at the place of capture. Date, time of each (re)capture and ID number of each butterfly were recorded, as well as sex and for females also the presence/absence of a mating plug (sphragis). Recaptures of individuals on the same day were not recorded. Additionally, in two seasons (2019 and 2021) the wing wear of each individual was assessed on a 4-point scale (0 = fresh, 1 = the least worn, 2 = moderately worn, 3 = heavily worn).

Analysis

We analysed our data with the Jolly-Seber model (Arnason & Schwarz 1999) using Program MARK, version 8.0 (White & Burnham 1999). The model represents a well-established standard for estimating population size in open populations, and it has been

Figure 1. The study site of *P. mnemosyne* in the Narew river (NE Poland): a view at the peak of the flight period in late May (on the left) and in late April i.e. when most caterpillars complete their development (on the right).

Figure 2. Examples of marked *P. mnemosyne* on the study site in the Narew river (NE Poland): a male (on the left) and a female with a mating plug (sphragis).

frequently applied in butterfly studies (Schtickzelle et al. 2002; Nowicki and Vrabec 2011; Osváth-Ferencz et al. 2017). Based on the lowest value of the Akaike Information Criterion corrected for small sample size (AIC_c) (Hurvich & Tsai 1989), the model variant $\varphi(.)p(s + t)B(s{*}t)$ turned out to perform the best for each year. This best-performing model assumed a constant (and equal for both sexes) survival rate (φ), but differences as far as other parameters were concerned, such as sex-dependent and time-varying (thus differing between capture days) recruitments of new individuals into the population (*B*), and sex-dependent and time-varying capture probabilities (*p*) with a constant difference between sexes. The model was used to obtain the estimates of daily numbers of males and females as well as their seasonal population sizes. Subsequently, we estimated the total population size as the sum of the male and female population sizes estimated from the model. Based on survival estimates we calculated the mean adult lifespans as $e = (1 - \phi)^{-1} - 0.5$ (Nowicki et al. 2005). For comparative purposes, we also derived mean capture probabilities for males and females across the entire season. Additionally, we calculated the temporal fragmentation index, i.e., ratio of flight period length to adult lifespan, which is considered as one of the indicators of species vulnerability (Bubová et al. 2016).

Weather data for the characterization of the sampling seasons were acquired from the Białystok weather station located approximately 23 km south-east of the study site and run by the Polish Institute of Meteorology and Water Management - National Research Institute (IMGW-PIB).

Results

Sampling years differed significantly as far as the phenology of *Parnassius mnemosyne* was concerned and there were also substantial weather variations (Table I). In 2019, the first butterflies were already on the wing on May 3, while in 2021 they emerged nearly 3 weeks later. Then, the flight period lasted from only 4 weeks in 2017 to six in 2020. Overall, 1,421 individuals (1,042 males and 379 females) were captured and marked in four seasons (302–398 in each one). The sex ratio of marked

Table I. General information for the study years. Weather conditions in the flight period refer to daily means recorded between 8 a.m. and 5 p.m., i.e. the period of butterfly activity in favourable conditions. Weather conditions in April (i.e. the month most important in the context of larval development) refer to daylight time. Data were acquired from the IMGW-PIB Białystok.

	Flight period (duration)			Flight period (daily means)		April (daily means)	
Year	Start	End	Days	Temperature (°C)	Sunshine (%)	Maximum temperature (°C)	Sunshine (h)
2017	18 May	14 June	28	19.74	64	11.48	5.66
2019	03 May	09 June	38	18.13	58	15.56	9.75
2020	08 May	18 June	42	17.11	55	13.84	8.52
2021	21 May	21 June	32	20.28	67	11.75	5.28

individuals was strongly male biased (2.8:1) and ranged from 2.4:1 in 2017 to 3.3:1 in 2020. The presence of sphragis was recorded in the case of 85.4% females, with relatively small inter-year variability (Table II).

About 50% of the marked individuals were recaptured at least once. The proportion of recaptured individuals differed somewhat between years (0.4–0.6) and was substantially higher (1.7–3.1 times) for males than for females (Figure 3). Correspondingly, the average capture probability was 2–2.9 higher for males than for females in all years (Figure 4).

The maximum duration between captures of an individual reached 22 days for males and 25 days for females in 2020 (Figure 5). The mean number of days between the first and last captures ranged between 5.65 in 2017 to 8.89 days in 2020, and in all years except 2020 was longer for males than for females (Table III). The estimated population size of adults ranged between 555 individuals in 2017 and 942 in 2019. The estimated sex ratio was fairly well balanced in all seasons, with a slight predominance of males in three of the years and females only in 2019 (Table IV) The distortion was not significant in any year (X^2 test, P = 0.73–0.85). The estimated figures were 2–3 times lower compared to direct observations, i.e. proportions of marked individuals.

The wing condition of captured individuals decreased continuously during the flight period in both of the seasons in which this assessment was made. In the case of females, wings were generally of better quality compared to males throughout the studies and even in the final weeks they were given mostly 0 or 1 (Figure 6).

The daily survival rate obtained with the Jolly-Seber model varied between 0.854 and 0.923, which corresponded to an estimated adult lifespan of 6.36–12.45 days (Table V). Taking into consideration the recorded flight periods in particular years, the temporal fragmentation index was estimated at 3.37–5.97.

Discussion

Variation concerning both the timing and length of the flight period is not surprising when compared with other observations of *P. mnemosyne*, e.g. from long-term studies in Finland (Kuussaari et al. 2016),

Table II. Summary of mark-recapture surveys conducted.

Year	Sampling occasions	Number of marked butterflies			Recorded sex ratio (M:F)	Percentage of females with sphragis
		males	females	both sexes		
2017	19	213	89	302	2.39	85.4
2019	21	282	116	398	2.43	84.3
2020	17	296	89	385	3.33	89.8
2021	17	251	84	336	2.99	82.1

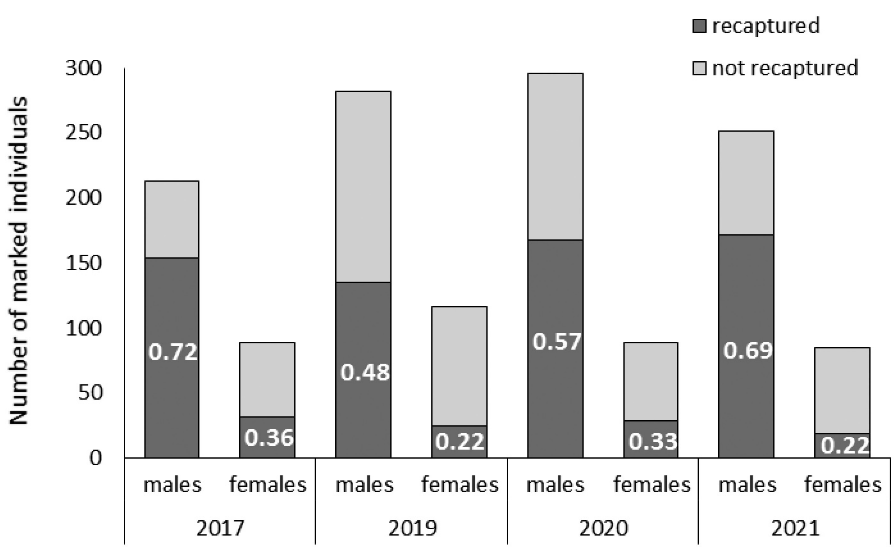

Figure 3. Sample sizes and proportion of recaptured individuals of both sexes, in four years.

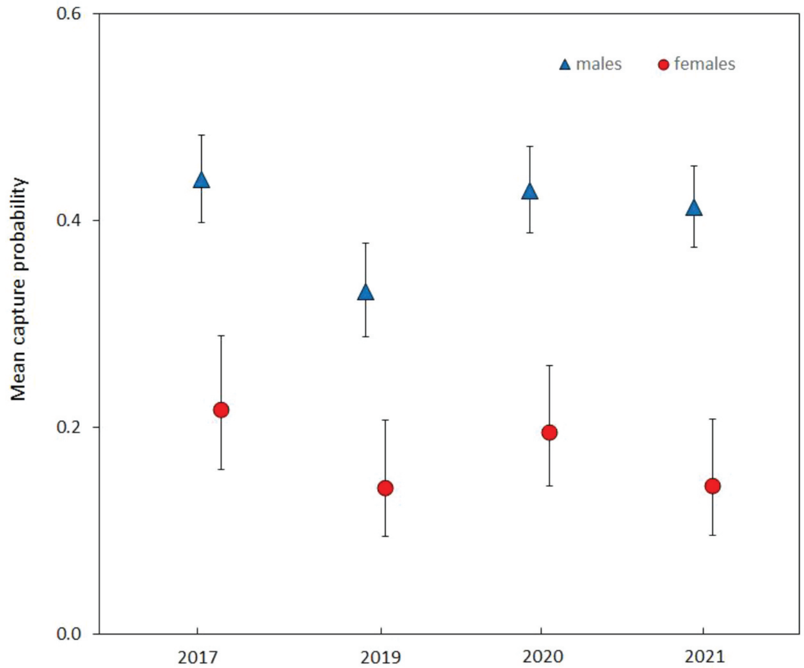

Figure 4. Mean capture probability in the four sampling years derived for males (triangles) and females (dots) as estimated with the Jolly-Seber model. Error bars represent 95% confidence intervals. Significant intersexual differences were detected for all years.

and can be easily explained by weather conditions. In 2017 and 2021, when butterflies were on the wing for only about 4 weeks, mean temperatures and sunshine percentages were higher compared to 2019 and 2020, when the appearance of the species was extended. The beginning of adult emergence was clearly earlier in years with warmer and more sunny conditions in early spring, i.e. the relevant time for larval development. Analyses of long-term data for 20 univoltine butterfly species indicate that temperature in the months immediately preceding adult emergence has the strongest relationship with phenology (Gutiérrez & Wilson 2021). Phenological shifts related to weather conditions are generally well-documented, especially in the context of global warming, and some life history traits as well as habitat types may influence specific responses (Altermatt 2010, 2012; Brooks et al. 2017, Fric et al. 2020; Zografou et al. 2021).

Variation in the duration of the flight period recorded in our study was similar to that observed by Pásztor et al. (2022) for a small population in Hungary over seven seasons (26–45 days). Even greater phenological shifts and variation in the duration of the flight period were reported for montane populations (Adamski et al. 2019).

Adult population size was relatively stable when compared to some other butterfly species (e.g. Nowicki et al. 2009). Long-term observations over 25 years suggest that *P. mnemosyne* has been numerous on the site every year. In our study, the maximum abundance was recorded in 2019, when the weather conditions for the quick development of caterpillars were probably the best. Larvae are thermophilic, switching between feeding and basking. Weather may also act indirectly by affecting the interactions between prematures and parasitoids (Wilson & Roy 2009), but in the case of *P. mnemosyne*, data on natural enemies of this kind are lacking (Shaw et al. 2009), which could be related to difficulties in finding larvae (Vlasánek et al. 2017).

Butterfly populations are sensitive to weather, which affects numbers and flight behaviour. Generally, their activity increases with temperature and decreases with cloudiness, which can translate into dispersal abilities (Cormont et al. 2011; Kuussaari et al. 2016). Relationships between weather and numbers are usually more complicated, and often concern previous seasons and/or not only the conditions during the flight period but also those experienced during larval development, and sensitivity may vary across distribution ranges (Mills et al. 2017). Case studies on the alpine *Parnassius smintheus* indicate that snow cover in early winter is the best predictor of annual adult population change (Roland et al. 2021).

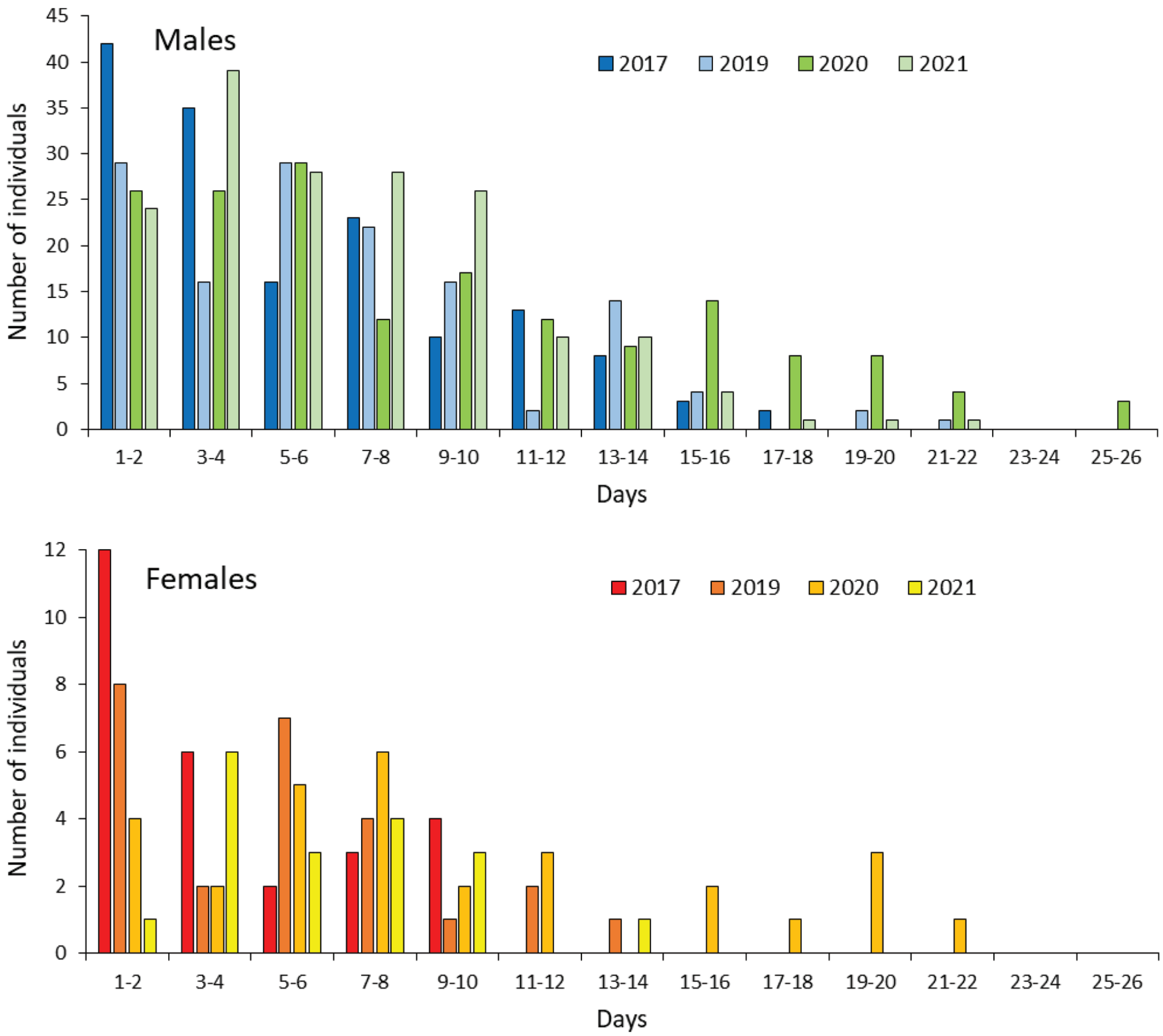

Figure 5. Distribution of recaptured individuals according to maximum temporal distance between the first and the last capture.

Table III. The mean numbers of days between the first and last captures in the four sampling seasons.

Year	Males	Females	Both sexes
2017	5.81	4.91	5.65
2019	6.70	5.20	6.46
2020	8.82	9.31	8.89
2021	6.84	6.22	6.78

A combination of climate and interspecific interactions also affects longevity. Estimation of lifespan in our studies showed considerable inter-seasonal variation. Previous assessments concerning *P. mnemosyne* also suggest similar variation (5–11 days), but it is worth noting that the estimates were for different sites (Konvička & Kuras 1999, Bubová et al. 2016). In the case of our studies, the most puzzling was 2020, when adults lived on average twice as long as in the previous year. Both mean temperatures and sunshine percentages were the lowest during the flight period in 2020, but no correlation could be found when only the four studied years were taken into consideration.

Little is known about factors affecting adult mortality, which could explain differences in adult longevity among the years. During our studies, only a few cases of spider predation were recorded. Adamski (2013) suggests that ants can be important predators of *Parnassius* butterflies. Adults are active only in sunny weather, and they sit to rest on plants almost immediately when the sun hides behind the clouds. Therefore, they can be attacked by ants

Table IV. Estimated population sizes for the four investigated seasons; the values in parentheses represent 95% confidence intervals.

	Estimated population size N ± SE (95% CI)			
Year	Males	Females	Total	Estimated sex ratio (M:F)
2017	297 ± 13 (275–325)	258 ± 17 (227–295)	555 ± 22 (516–600)	1.151
2019	464 ± 22 (427–512)	478 ± 31 (422–544)	942 ± 38 (873–1022)	0.971
2020	394 ± 15 (369–429)	375 ± 26 (328–431)	469 ± 30 (714–833)	1.051
2021	355 ± 15 (330–388)	336 ± 16 (307–368)	691 ± 24 (651–736)	1.057

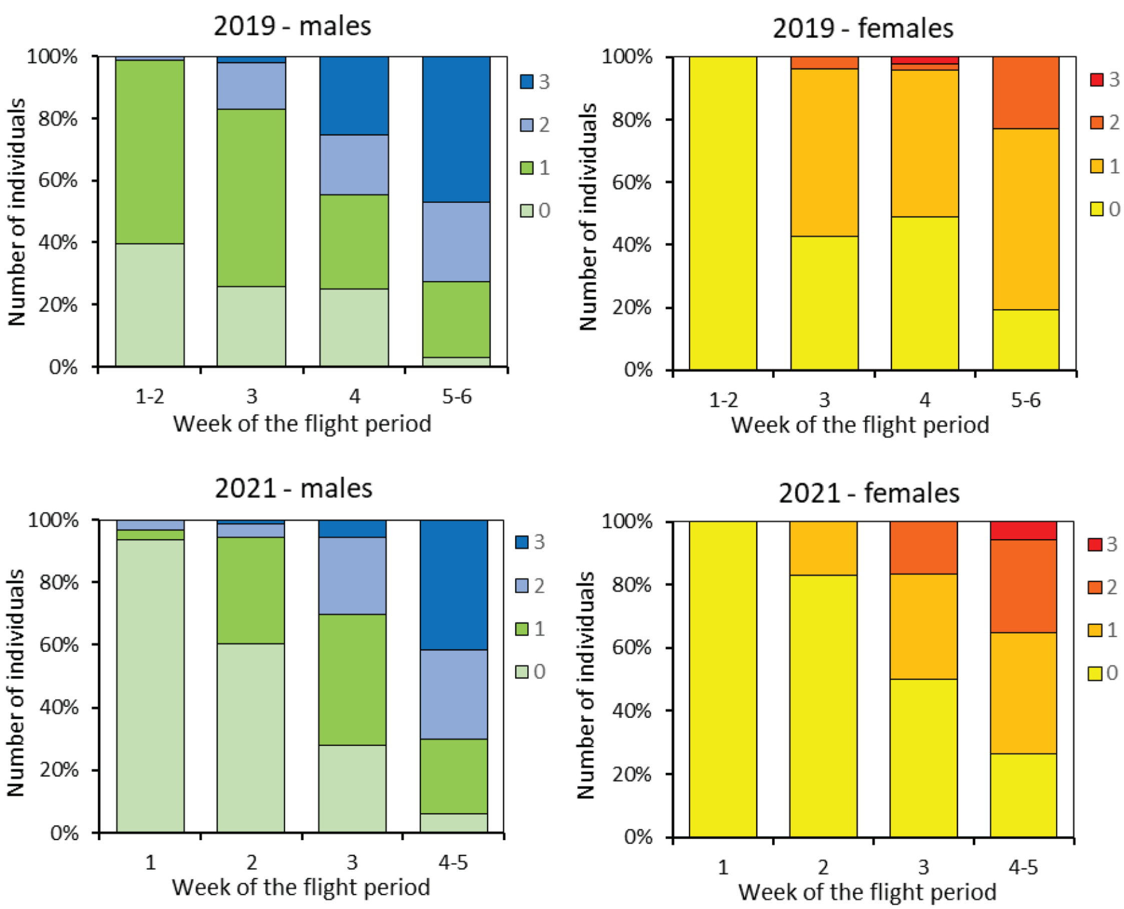

Figure 6. Wing wear of captured individuals (recaptures included) in two investigated years. Colours of bars correspond to wing wear on a 4-point scale (0 – very fresh, 1 - the least worn, 2 - moderately worn, 3 - heavily worn). Data for weeks 1–2 and 5–6 in 2019 and for weeks 4–5 in 2021 were pooled, due to very few individuals being captured in the beginning/end of the flight period.

Table V. Estimates of daily survival rate and lifespan for the four investigated seasons; the values in parentheses represent 95% confidence intervals.

Year	Daily survival rate ± SE (95% CI)	Estimated lifespan in days ± SE (95% CI)
2017	0.869 ± 0.011 (0.846–0.888)	7.11 ± 0.63 (5.99–8.46)
2019	0.854 ± 0.011 (0.832–0.874)	6.36 ± 0.52 (5.44–7.46)
2020	0.923 ± 0.007 (0.907–0.936)	12.45 ± 1.23 (10.28–15.11)
2021	0.895 ± 0.010 (0.875–0.913)	9.04 ± 0.88 (7.49–10.93)

while resting. *Formica* spp. are common on the presently-studied site, especially near trees, i.e. where most adults emerge. The pressure from ants is probably lower in surrounding open grasslands, so the most affected are adults emerging from pupae on cloudy days and waiting for conditions enabling flight. However, our anecdotal observations suggest that individuals often successfully spend nights near ant hills, so the impact of this kind of pressure is not clear. Butterflies basking in the early morning could also be prey to small mammals as is indicated for *Pieris* butterflies showing similar colouration (Kingsolver 1987). Little is known about the impact of birds. The beak-mark frequency can be used to estimate the pressure of birds (Shapiro 1974; Ota et al. 2014). However, in the case of the present studies, clear symptoms which could be attributed to such events were not recorded, and no direct observations were made either. The question of wing colouration of *P. mnemosyne*, which could be an aposematic signal, remains open (Lyytinen et al. 1999).

Konvička and Kuras (1999) found male-biased sex ratio of captured individuals in a population studied in the Czech Republic. Our data are only partially consistent with those findings. While we marked far more males than females and the mean capture probability was twice as high for males, our estimates clearly indicate no bias in real numbers of individuals of both sexes. However, studies carried out in the Czech Republic by Vlasanek et al. (2009) designed especially to eliminate possible biases show that males are really more abundant (a 1.6 bias towards males). A very similar ratio (1.5–1.6) is reported from two sites in Hungary (Meglécz et al. 1999). Vlasanek et al. (2009) suggest that these phenomena could be related to larval development, but it has not been confirmed (see Vlasánek et al. 2017). Moreover, data concerning the congeneric Apollo butterfly *P. apollo* based on captive breeding indicate no bias in sex ratio (Adamski 2004).

The better detectability of males is not surprising taking into consideration their conspicuous patrolling behavior. Females just after emergence are probably not very active, since at least 85% of them had already mated (as proved by the presence of sphragis) when they were captured for the first time. In fact, the actual proportion of females that mated soon after emergence is likely to be even higher, as a very recent research indicated that in some cases previous copulation is marked with some inconspicuous structures (that might have been overlooked in our field study) rather than with a typical sphragis (Gór et al. 2023). Ovipositing females could also be difficult to detect in the turf, especially since during the flight period vegetation is relatively high. The higher catchability of males is typical for butterflies (see e.g. Zimmermann et al. 2011; Sielezniew et al. 2019). The reverse pattern is rare and may occur for less conspicuous species inhabiting biotopes dominated by tall herbs and young trees, where patrolling males flying low could be more difficult to detect (Sielezniew & Nowicki 2017).

We also found that the quality of wings in males deteriorated much more than in females. The most likely explanation is related to the fact that they spend a higher proportion of time flying than females. Pásztor et al. (2022) assessed phenotypic senescence using different measurements, i.e. the body mass and thorax, and found that their values decreased in both sexes. A steeper decline was observed in the case of females, and it was suggested that the females may use more nutrients from muscle breakdown for reproduction than males. Therefore, wing quality probably better reflects flight activity, and this is why females are generally 'less worn'.

The Clouded Apollo is a relatively long-lived butterfly in its adult stage. Some individuals may live for up to 3 weeks, so for the most of the flight period. The calculated values of the temporal fragmentation index showed some variability but were relatively low compared to previous studies on both *P. mnemosyne* and the congeneric relative *P. apollo*. Species of conservation concern are rather characterized by higher values of this index and, on average, a shorter adult lifespan (see review by Bubová et al. 2016).

The investigated population is potentially one of the largest in the region and therefore seasonal fluctuations are not really a threat to it. The current coppicing management of the breeding habitat, i.e. light deciduous forest with *Corydalis*, seems to be optimal for the butterfly, because it creates the microhabitats preferred for larval development (Välimäki & Itämies 2005). Some concerns may be related to the surrounding meadows. The use of fertilizers contributes to the reduction of wildflowers, which constitute nectar resources for the focal butterfly, and some of them are cut during the flight period. However, its relatively early emergence makes the butterfly relatively unaffected by this factor. The Clouded Apollo is the most common butterfly species in the end of May at the site. Most meadow species cannot survive the twice yearly mowing, which is the typical local mowing regime. In the future, possible further threats may be related to the conversion of meadows into corn fields, as observed in the area.

Unfortunately, *P. mnemosyne* is listed only in Appendix IV of the Habitat Directive, and thus it is not a target of conservation actions within Natura 2000 sites. Hence, appropriate management of meadows seems to be the most important measure for species preservation. Mowing should be delayed until the end of the flight period, i.e. mid-June, and the use of fertilizers should be excluded at least in places neighbouring the breeding habitats of *P. mnemosyne*. Extensive grazing would likely be a more favourable alternative use (Johansson et al. 2017). Finally, some measures should be also taken to prevent possible deforestation of the forest sites occupied by *P. mnemosyne*.

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