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DEMOGRAPHY OF A COMMON BUTTERFLY ON HUMID GRASSLANDS: *ARGYNNIS AGLAJA* (LEPIDOPTERA: NYMPHALIDAE) STUDIED BY MARK-RECAPTURE

ABSTRACT: Much of the research into the demography of butterflies conducted in Europe during the last few decades focused on rapidly declining or, on the other hand, expanding species, whereas species with stable trend tend to be neglected by researchers. *Argynnis aglaja*, a widely distributed inhabitant of semi-natural grasslands, represents a suitable model for studying patterns of landscape persistence of not-yet-threatened grassland insects. Using mark-recapture method conducted for one season on humid meadows in Western Bohemia, Czech Republic, we show that this large-bodied species is capable to form large and dense populations, reaching densities of over 250 individuals per hectare. The adults were relatively long-living, an average female longevity (11.8 d) was over twice as high as an average male longevity (4.6 d), with maxima being 22 (a male) and 30 (a female) days. The prolonged female lifespan is beneficial for a species that do not emerge with fully-matured eggs and oviposits singly over large areas. Modelling mobility, well-approximated by an inverse-power function, predicted that about one individual in a thousand would cross the distance of 1000 meters. We conclude that the satisfactory conservation status of *A. aglaja* stems from its capability to reach high local densities combined with a good dispersal power.

KEY WORDS: butterfly ecology, conservation, grasslands, mark-recapture, population size, dispersal, seminatural meadows

1. INTRODUCTION

Throughout Europe, habitat loss and fragmentation, brought about by intensification of agriculture and forestry as well as by the abandonment of traditional land use, accelerate the decline of biodiversity, which also affects the representative groups of butterflies. One fifth of European butterflies are endangered on the continental scale (Van Swaay and Warren 1999), the situation is much worse within smaller regions (Maes and Van Dyck 2001, Konvička *et al.* 2006, Wenzel *et al.* 2006). In contrast, some mainly generalist species are expanding their ranges as a result of climate warming (Roy *et al.* 2001, Hill *et al.* 2002). A genuine concern of the scientific community is reflected in increasing numbers of studies on butterfly ecology, ranging from single-species studies to monitoring of populations and communities.

Much of the recent efforts focuses on endangered butterflies inhabiting rare or declining habitats (*e.g.* Bulman *et al.* 2007, Eichel and Fartmann 2008) or, in contrast, on currently expanding species profiting from the climatic change (Hill *et al.* 2006, Merrill *et al.* 2008). This leaves out many species whose distribution remains stable, although some

may be changing their status in subtler ways (cf. Gaston and Fuller 2007). Detailed studies in Britain disclosed that two such butterflies, *Polyommatus icarus* (Rottemburg, 1775) (León-Cortés *et al.* 1999) and *Lycaena phlaeas* (Linnaeus, 1761) (León-Cortés *et al.* 2000), have declined by over 75 per cent of their populations compared to the beginning of 20th century. Numbers of farmland butterflies in Western Europe declined by one third, compared to situation a decade ago (Van Swaay and Van Strien 2005). These observations point to the need of collecting basic ecological information on selected representatives of the still-common species, particularly those with endangered close relatives, as understanding life history traits linked to persistence *versus* declines is indispensable for efficient conservation.

The dark green fritillary, *Argynnis aglaja* (Linnaeus, 1758) (Nymphalidae: Argynnini) represents a suitable model of a relatively common butterfly, inhabiting a wide range of biotopes from wet bogs through mesic meadows to dry pastures. Its distribution is stable in Central Europe (*e.g.* Benes *et al.* 2002, Reinhardt *et al.* 2007). Two of its close European relatives, *A. adippe* (Denis and Schiffermüller, 1775) and *A. niobe* (Linnaeus, 1758), have declined across the continent (Warren 1995, Benes *et al.* 2002, Spitzer *et al.* 2009). While *A. aglaja* has attracted a minimum interest from researchers, its North American relatives, such as *Speyeria idalia* (Drury, 1773) or *S. mormonia* (Boisduval, 1869), have become models for butterfly ecological research in North America (*e.g.* Boggs 1987, Swengel 1997, Swengel and Swengel 2001, Fleishman *et al.* 2002) (*Speyeria* and *Argynnis* are in fact monophyletic: Simonsen 2006, Simonsen *et al.* 2006). Several more distant *A. aglaja* relatives (*Proclossiana eunomia* (Esper, 1799) and *Boloria aquilonaris* (Stichel, 1908)) are also being intensively studied (*e.g.* Baguette and Néve 1994, Baguette *et al.* 2003, Schtickzelle *et al.* 2002, Schtickzelle *et al.* 2006).

In this paper, we (a) provide basic demography characteristics of a population of *A. aglaja*, based on a one-season study of adults within a region with high adult density and applying the mark-recapture method (b) describe basic dispersal characteristics of the

population and (c) discuss how this species is surviving in modern landscapes.

2. METHODS

2.1. Study system

Argynnis aglaja distribution ranges from N. Africa across Europe and temperate Asia to China and Japan (Tolman and Lewington 1997). This relatively large (wingspan 50–60 mm) butterfly remains widely distributed in Central Europe. The life cycle is univoltine, adults occur from late June until August, eggs are laid singly, and larvae feed solitarily on violets (*Viola* spp.) and bistort *Bistorta major* (Linnaeus, 1753) (Lepidopteren Arbeitsgruppe 1987, Weidemann 1995), the latter being used at the study site (Fric *et al.* 2005).

The study was carried out in the vicinity of Karlovy Vary, Western Czech Republic (50°9'N, 13°2'E, altitude 650 m), on a hilly piedmont of the Doupovské Mts. The landscape is a mosaic of both semi-natural and improved grasslands, pastures, ponds, woodlots, and scrubs. The semi-natural hay meadows and pastures constitute a stronghold for several declining butterflies (Hula *et al.* 2004, Zimmermann *et al.*, 2005). We selected a network of 30 such meadows, separated by ponds, shrubby hedges, and woodlots, covering the total area of 28 ha, identical to that studied in Zimmermann *et al.* (2005). These meadows are managed by mowing once to twice a year, but less accessible or waterlogged parts, varying in extent from year to year, are temporarily left uncut. The centroids of the 30 fragments (mean area = 0.9 ha, SD = 0.64 ha), distinguishable by prominent landmarks, were used for analysing the mobility of butterflies.

2.2. Mark-recapture

We marked adult butterflies from 22 June, when the first individual appeared on wing, to 17 August, 2006. Each day, weather permitting, two to five persons visited all the meadow sections, captured as many butterflies as possible, and marked them with unique numbers. Sex and position of capture were noted before releasing each individual on its

capture point. We also recorded their behaviour prior to capture, distinguishing flight, patrolling (searching flight distinguished in males only), perching (settled individuals occasionally chasing other flying objects, males only), basking, resting, egg-laying, mating, and nectaring, the latter recorded with the nectar source used.

2.3. Demography

Daily population sizes, N_t , were estimated within the framework of the constrained linear models (Lebreton *et al.* 1992; application for butterflies: Schtickzelle *et al.* 2002, Baguette and Schtickzelle 2003). We used the MARK package (White and Burnham 1999) and applied the Jolly-Seber method, POPAN parameterisation, suitable for open populations with births, deaths, emigration, and immigration.

The program uses daily capture histories for all individuals captured at least once, and iteratively fits sets of generalised linear models to the data, estimating the daily values of three primary parameters: the residence probability Φ_i (a probability to survive until next marking, note that it combines mortality and emigration), catchability p_i , and the proportional probability of entering the population, $pent_i$. These primary parameters can differ between sexes (*e.g.* $p(g)$ for different catchability), their responses to time expressed in marking days, can be factorial (t), linear (T) or polynomial (T^2), and there can be either additive (*e.g.* $g+t$) or multiplicative (*e.g.* $g * T$) time * sex interactions. Derived parameters, estimated from values of the primary parameters, are daily births B_t , daily population size N_t , and total population size N_{tot} . See Williams *et al.* (2002) for details.

The program successively computes models varying in responses of the parameters and selects the most parsimonious ones (those offering the best compromise between model precision and complexity) using the Akaike information criterion (AIC) (Akaike 1974, Burnham and Anderson 1998).

Average values of residence Φ' and catchability p' were obtained in MARK by defining the best-fitting models with the respective parameters not dependent on time. Comparing models in which these parameters differed

and not differed between sexes, *i.e.* $\Phi(g)$ vs. $\Phi(\cdot)$, allowed direct comparison of sexes for residence and catchability. Average residence was converted to residence time ('longevity') as $-(\ln \Phi')^{-1}$.

2.4. Dispersal

We used the inverse power function (IPF) to model the probabilities of movements to distances beyond those covered by the marking (Hill *et al.* 1996, Fric and Konvička 2007). For all butterflies captured more than once, the probability density I of movements to distances D equals:

$$I_{\text{IPF}} = C \cdot D^{-n} \quad (1)$$

The parameters C and n are estimated by plotting the logarithm of cumulative fractions of individuals moving specific or greater distances ($\ln I$) against linearised expressions of the distances, *i.e.* $\ln I = \ln C - n(\ln D)$. We compared slopes and intercepts of the resulting linear regressions using t-tests (Zar 1996).

3. RESULTS

3.1. Adult behaviour

A. aglaja is a strong and fast flier: we often observed individuals crossing several dozen meters during one bout or crossing such barriers as woodlots by ascending above the treetops.

The prevailing mate-locating behaviour of males was patrolling, with males flying back and forth over grasslands, actively searching for females ($n = 629$). In 12 cases only, we observed settled males attacking flying objects, an activity classifiable as perching. Females behaved more cryptically, the prevailing behaviours were flying, resting, and nectaring (Fig. 1).

Use of nectar plants was very similar for both sexes (Fig. 2). The prevailing nectar sources were *Cirsium* spp. (Miller, 1754) (a half of all plant visits in both sexes), *Betonica officinalis* (Linnaeus, 1753), *Centaurea jacea* (Linnaeus, 1753), and *Trifolium* spp. (Linnaeus, 1753).

We recorded 13 mating events, occurring on freshly cut sward ($n = 10$), in shrubs

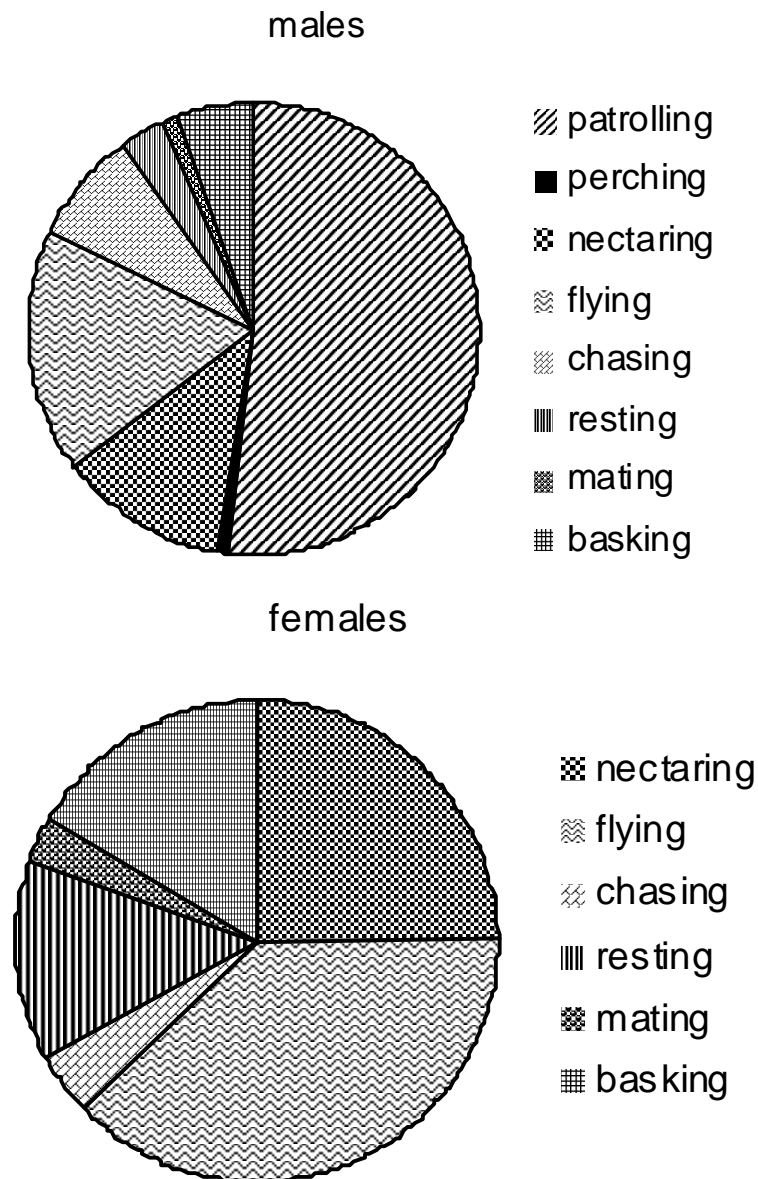


Fig. 1. Types of behaviour (%) prior to capture, recorded during a mark-recapture study (22 June – 17 August, 2006) of *Argynnis aglaja* butterfly. The percentages are based on 1212 (males) and 411 (females) observations of behaviour prior to capture.

($n = 2$), and even on a tree branch (1 occasion). Majority of matings occurred 5–20 cm above ground, the highest position was 160 cm. Egg-laying was difficult to observe. A female typically flew slowly above the vegetation, then settled, and crawled back and forth on the foliage, attempting to lay eggs. We repeatedly observed bending of abdomen, and in eight cases, we actually found a singly laid

egg. The substrates were bistort leaves ($n = 1$), *Alchemilla* sp. (Buser, 1906) ($n = 4$), *Potentilla erecta* ((L.) Raeusch., 1797) ($n = 2$), and a dry grass tuft ($n = 1$). In many cases, the egg laying was not terminated, indicating that a substrate selection occurred during the abdomen bending phase. All successfully laid eggs were located close (< 0.5 m) to a bistort plant.

Table 1. Summary of mark-recapture data obtained during a study of population of *A. aglaja* butterfly.

	Individual captured	Individual recaptured	Proportion recaptured	Capture events	Max. residence
Males	890	323	36.3 %	1213	22 days
Females	366	55	15.0 %	421	30 days
Total	1256	378	30.1 %	1634	

Table 2. Summary of best-supported Jolly-Seber model and models with time-constant residence and catchability, used for estimated demographic parameters and population size in *Argynnis aglaja*.

Models	AIC	Δ AIC	Parameters	Estim. males (\pm SE)	Estim. females (\pm SE)
Best-supported model					
$\Phi(g+t) p(g+t) pent(g+T^2)$	3 642.6	0.0	95	4 250(\pm 1542)	3 130(\pm 509)
Time-constant models					
$\Phi(g) p(g+t) pent(g+T^2)$	3 712.0	69.5	55	4 600(\pm 295)	2 160(\pm 296)
$\Phi(.) p(g+t) pent(g+T^2)$	3 742.5	99.9	54	4 570(\pm 288)	2 720(\pm 304)
$\Phi(g+t) p(g) pent(g+T^2)$	3 863.3	220.8	52	2 990(\pm 204)	1 810(\pm 193)
$\Phi(g+t) p(.) pent(g+T^2)$	3 918.6	276.1	51	4 110(\pm 276)	2 810(\pm 384)

Model parameters: Φ = residence, p = catchability, $pent$ = proportion of entering.

Parameter responses: (.) – not depending on sex or time; (g) – sex dependent; t – responding to time in a factorial manner; T – responding to time in a linear manner; T^2 – responding to time in a domed polynomial manner.

3.2. Demographic parameters

We marked 1 256 individuals and obtained 378 recaptures (Table 1). The first male appeared 7 days earlier than the first female (22 vs 29 June). The greatest numbers of males were captured during the first week of July, two weeks after the beginning of the adult flight. Numbers of females increased less rapidly than those of males; the greatest numbers appeared in late July.

The best-fitting MARK model (Table 2, Fig. 3) revealed that residence and catchability depended on a marking day in a factorial way, with additive effect of sex ($g+t$). The recruitment ($pent$) followed a domed pattern, with peak daily values for males higher than those for females. The curves of daily population sizes revealed a strong protandry; note that the first few estimated values for males were unrealistically high for males, possibly due to low daily catches early in the flight period. The peak of male numbers was separated from the peak of female numbers by two weeks, and the prolonged 'tail' of the estimates was due to survival of some butterflies, mainly females, until mid-August. The estimates of the total population size were 4252 (\pm 1541 SD) for males and 3126 (\pm 509 SD) for females (*ca*

7000 individuals), corresponding to densities of 150 males and 110 females (or 260 individuals) per hectare.

The models with residence and catchability constant in time performed much worse, in terms of AIC values, than the best model (Table 2). However, these time-invariable residence and catchability models performed better if the two parameters differed between sexes. Thus modelled capture probability (constant in time, differing between sexes) was twice higher for males (0.573) than for females (0.262). Similarly, the residence modelled as constant in time and differing between sexes was higher for females (0.919) than for males (0.805), corresponding to a longer female lifespan (11.8 d vs 4.6 d) (see Table 1 for maximum residence values).

3.3. Mobility

The sexes did not differ in frequencies of movements among meadow fragments ($\chi^2 = 1.86$, d.f. = 1, $P = 0.17$), but differed in mean and median distances, which were both higher in females (Mann-Whitney U: $Z = -4.60$, $P < 0.0001$) (Table 3).

Fitting the mobility with the inverse power function resulted in the equations:

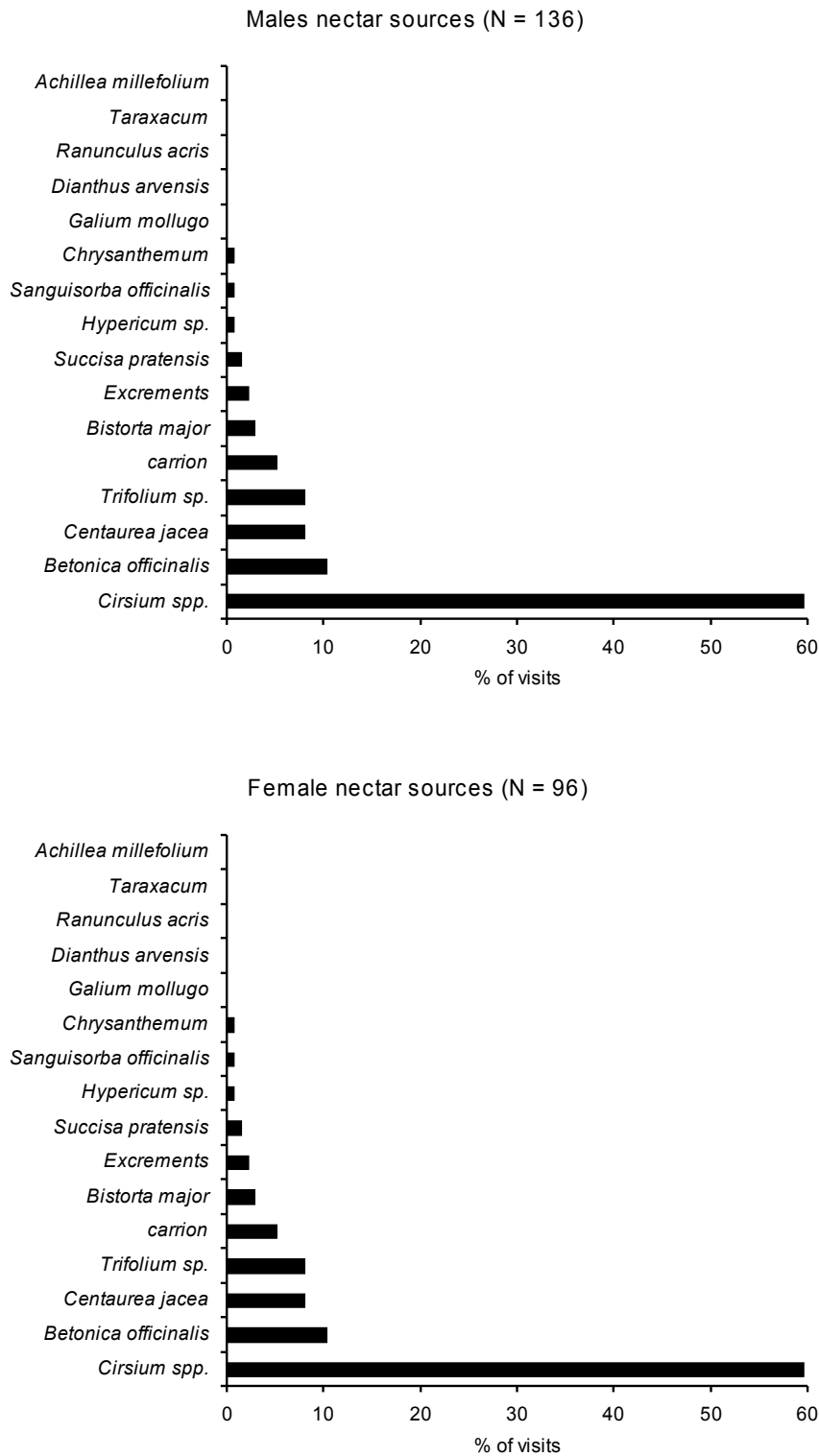


Fig. 2. Use of nectar plants by males and females of *Argynnis aglaja*, recorded during mark-recapture study (22 June – 17 August, 2006), based on 157 observations for males and 364 observations for females.

Table 3. Summary of mark-recapture data used for analysing the mobility of *Argynnis aglaja* butterfly.

	Patch-to-patch movements	Mean distance (\pm SD)	Median distance	Maximum single move	Maximum total distance
Males	198	200 m (\pm 241)	130 m	1050 m	1440 m
Females	39	330 m (\pm 353)	470 m	1120 m	1340 m

$$\text{males: } \ln I = -3.44(\pm 0.161) - 1.59(\pm 0.156) \times \ln D \quad (2)$$

$$\text{females: } \ln I = -2.16(\pm 0.227) - 1.08(\pm 0.198) \times \ln D \quad (3)$$

where I is the probability density of movements to distance D .

Data fitting was highly significant for both males ($F = 109.6$, d.f. = 1, 23, $P < 0.0001$, $R^2 = 0.83$) and females ($F = 29.4$, d.f. 1, 19, $P < 0.0001$, $R^2 = 0.61$). The two regressions did not differ ($t = 0.386$, 44 d.f., $P > 0.1$), and we constructed a single common regression:

$$\ln I = -3.08(\pm 0.189) - 1.47(\pm 0.181) \times \ln D \quad (4)$$

From this equation (with $R^2 = 0.72$), the estimated probabilities of long-distance flights were 0.01 for 3 km, 0.004 for 5 km, and 0.001 for 10 km. Given that there were *ca* 7000 individuals within the study system, and that semi-natural humid grasslands are still rather common in the landscape, the butterfly inhabited the meadows as an interconnected system.

4. DISCUSSION

4.1. Demographic patterns

The non-declining butterfly *Argynnis aglaja* inhabiting wet meadows of Western Bohemia, Czech Republic, forms populations comprising of thousands of adults. The individuals frequently move across the sampled area of 28 ha, their dispersal rates ensure that for a local population of *ca* 7000 individuals about 70 adults will cross 3 kilometres and seven adults will move as far as 10 kilometres. Hence, the species forms open population systems over large areas of land.

Among temperate Argynnini, similar demographic data exist for two non-declining and two endangered species. The non-declin-

ing ones are represented by *Speyeria mormonia*, studied by Boggs (1987) in the Rocky Mountains, Colorado, USA; and *Brenthis ino* (Rottemburg, 1775) studied by Zimmermann *et al.* (2005) within the same system as *A. aglaja*. The endangered ones are represented by *Proclissiana eunomia*, with detailed MRR results from Belgian Ardennes (Schtickzelle *et al.* 2002, Mennechez *et al.* 2003, Baguette *et al.* 2003), Finland (Baguette *et al.* 2003, Petit *et al.* 2001) and France (Nève *et al.* 1996); and *Boloria aquilonaris*, studied also in Belgium (Mousson *et al.* 1999, Baguette and Schtickzelle 2003).

We obtained rather high recapture rates for a strong flier occurring in a rather high population density. The rates were higher in males, probably due to more conspicuous habits (*i.e.* patrolling mate-locating behaviour). Swengel and Swengel (2005) reported a strong male bias in the North American relative *Speyeria idalia*, and attributed it to a more cryptic lifestyle of females.

A. aglaja females exceeded males in average residence, and hence adult life span. The average male longevity was close to those found earlier for *B. ino* (6.9 days; Zimmermann *et al.* 2005), *P. eunomia* (7.5 days; Schtickzelle *et al.* 2002) and *S. mormonia* (4.9 days; Boggs 1987). For females, however, only the detailed studies of *P. eunomia* (Schtickzelle *et al.* 2002) revealed greater longevity for females (8.9 days) than for males; whereas female longevities of *B. ino* and *S. mormonia* were mere 4.5 (Zimmermann *et al.* 2005) and 1.6 days (Boggs 1987). Zimmermann *et al.* (2005) explains, for the case of *B. ino*, that the female longevity appeared low due to a premature termination of marking, when many females were still on wings. The present study of *A. aglaja* covered the August 'tail' of female residence, giving more realistic longevity estimates.

The prolonged lifespan of *A. aglaja* females agrees with what is known about the

life cycle of closely related American species. Females of *S. mormonia* emerge from pupae with undeveloped ovaries and require a period of adult feeding to mature their eggs (Boggs 1997). Such ‘income-breeding’ (as opposed to ‘capital-breeding’: Tammaru and Haukioja 1996) requires that each *Speyeria* (and, likely, *A. aglaja*) female has to live for about a week to begin with oviposition. This, together with the habit of laying eggs singly, selects for the long female lifespan while maintaining nectar intake (Boggs 1988). Males, in contrast, strive to inseminate as many fresh females as possible early in the flight period, whereas residence late in the flight period does not provide additional benefits.

The regression functions used to predict long-distance *A. aglaja* dispersal did not differ between sexes. Still, males exhibited a lower mean and median distance (Table 3) and a steeper (although not significantly) slope of

the regression. These indices of lower mobility may arise as a by-product of a shorter life span because, everything else being equal, a longer-living animal will disperse further. A propensity for long-distance flights late in lifetime seems to be common in butterflies (e.g. Warren 1987, Bergman and Landin 2002, Boggs *et al.* 2006, Konvička *et al.* 2008), although in our case the procedure of marking within a bounded area limited our chances to detect rare long-distance flights (cf. Baguette 2003).

A demographic variable comparable with observations on related species is adult density. Within the identical area, *A. aglaja* densities reported here (260 ind. \times ha⁻¹) were much higher than densities of *B. ino* estimated just two years earlier (60 ind. \times ha⁻¹; Zimmermann *et al.* 2005) and still higher than those estimated concurrently in 2006 (188 ind. \times ha⁻¹; unpublished). The two other species that

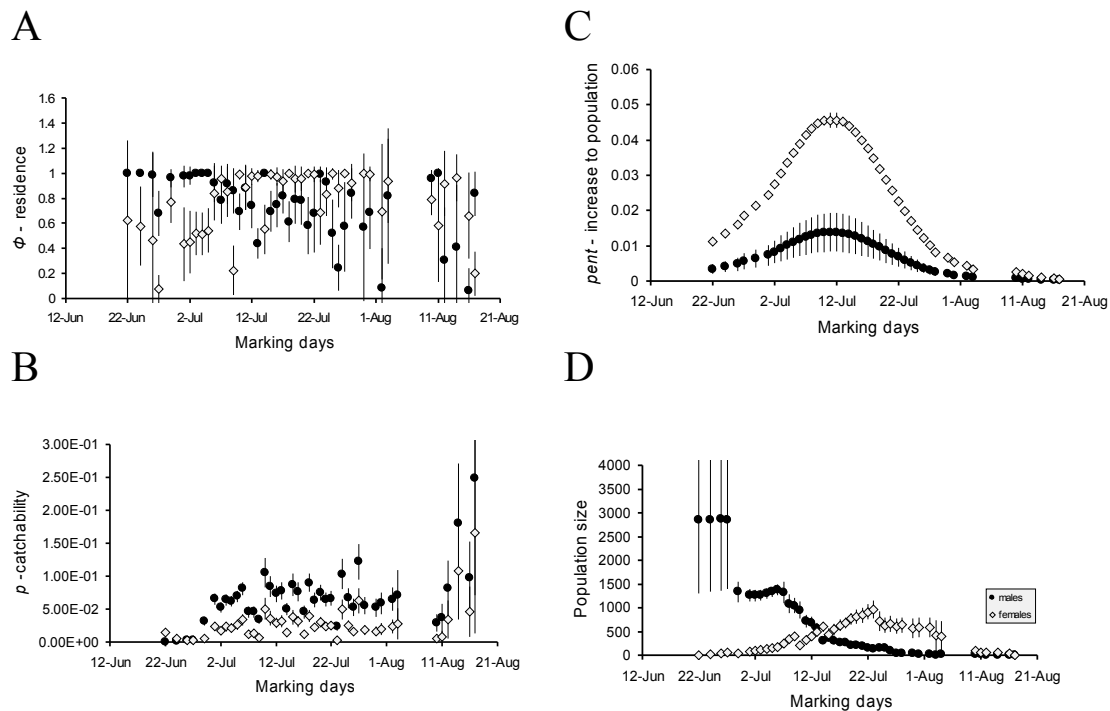


Fig. 3. Daily values of demographic parameters from a population of *Argynnis aglaja*, subject to a mark-recapture study. A. – the primary parameters residence (Φ); B. – catchability (p); C. – proportional recruitment ($pent$); and D. – daily population size. All parameters are based on model $\Phi(g+t) p(g+t) pent(g+T^2)$, see Table 2 for details.

we studied in the same system and year, the fritillary *Boloria selene* (Denis and Schiffermüller, 1775) and the checkerspots *Euphydryas aurinia*, also occurred in lower numbers (110 and 40 ind. \times ha⁻¹, respectively). The high densities of *A. aglaja* appear counterintuitive, because the butterfly is the largest of the four syntopically studied species and one would assume that larger species may require larger areas to sustain a population of a given size. Clearly, the availability of resources is more important here than mere area size. For the related *Speyeria mormonia*, Boggs (1987) observed a higher maximum density (450 ind. \times ha⁻¹) than we did, but the *S. mormonia* numbers also varied from 164 ind. \times ha⁻¹ to 712 ind. \times ha⁻¹ among three sites and three years.

4.2. Persistence of *A. aglaja* in human-dominated landscapes

The traits contributing to the favourable conservation status of *A. aglaja* include laying of eggs singly, which diminishes the risk of brood loss, a prolonged female lifespan, which allows enough time for oviposition, and a good dispersal propensity, which combines with high local densities to ensure a sufficient gene flow across landscapes. These traits, found to various degrees also in other temperate Argynnini, contrast with those existing in another intensively studied group of temperate butterflies, Melitaeini checkerspots, whose habit to lay eggs in masses exposes them to the risk of losing entire broods (e.g. Freese *et al.* 2006, Liu *et al.* 2007, Eichel and Fartmann 2008). Going into more detail, there are notable differences among Argynnini species co-occurring on humid meadows of temperate Europe (e.g. Sawchik *et al.* 2003). Thus, *Brenthis ino* develops on a broad range of host plants that may grow in various biotopes, from wetlands to calcareous steppes (e.g. Zimmermann *et al.* 2005). The much-studied *Proclissiana eunomia*, which shares the bistort host with *A. aglaja*, is strictly monophagous and requires sites in a late successional stage with prominent sedge tussocks (Schtickzelle *et al.* 2007). *P. eunomia* is absent in some otherwise suitable regions due to historical constraints, but once reaching them, it is ca-

pable of rapid expansions (Nève *et al.* 1996, 2009).

In terms of host plants range, *A. aglaja* stands in the middle between the generalist *B. ino* and the strictly specialized *P. eunomia*. Besides feeding on *P. bistorta*, *A. aglaja* can develop on multiple species of violets (*Viola* spp.). The bistort is much bulkier than violets, possibly supporting more larvae per unit area. On the other hand, it is restricted to humid grasslands in C. Europe and has retracted to hilly regions due to land drainage (Kubat 2002), whereas violets still occur widely, as various species utilize different habitats. Although *A. aglaja* formed huge densities at our study site, it is usually visibly less abundant, occurring in a handful of individuals per site. It is tempting to hypothesize that the sites with *P. bistorta* act as population sources, producing high local densities and enough colonists for smaller violet-dependent colonies. The testing of this hypothesis will require quantifying *A. aglaja* numbers according to a habitat type, assessing if individuals from a single population can develop on both bistort and violets, and measuring a gene flow among sites differing in host plant availability (cf. Williams *et al.* 2003).

The broader host range must provide *A. aglaja* with an advantage compared to the two much rarer congeners occurring in temperate Europe, *Argynnis adippe* and *A. niobe*. These species are monophagous on violets and display narrower habitat requirements, the former thriving at abandoned scrubby sites, including coppices (Warren 1995, Fox *et al.* 2006), and the latter requiring shortly grazed turf (Hafner 2005). It has long been known that *A. adippe* and/or *A. niobe* reach lower local densities than *A. aglaja* (Settele *et al.* 1999, Six 2000) due to more precise requirements for the physiological state of their host plants (Fartmann and Herman 2006, Salz and Fartmann 2009). The combination of less bulky hosts and more specific habitat requirements results in lower adult densities. A link between habitat specialisation and vulnerability has been detected among American representatives of *Speyeria* varying in degrees of specialisation (Swengel 1997, Swengel and Swengel 2001).

Our results originated from one of the best-preserved grassland regions in the

Czech Republic, with finely-structured habitat mosaics supporting a number of specialised grassland species (Zimmermann *et al.* 2005). Nevertheless, the wide range of detected oviposition substrates and a good dispersal propensity reveal that *A. algaja* is quite opportunistic when it comes to habitat needs. Pöyry *et al.* (2005) and Davies *et al.* (2007) reported that the butterfly thrived under intermediate conditions, at sites that were neither too heavily grazed/mowed, nor abandoned. A potentially limiting factor, in cases when machine hay mowing removes plant biomass over larger areas, may be a scarcity of nectar, particularly because insufficient nectar intake decreases lifetime fecundity in income-breeding fritillaries (Boggs and Ross 1993, O'Brien *et al.* 2004). Managing semi-natural grasslands in a mosaic-like manner enhances *A. aglaja's* local densities, contributing to the interconnection among its populations over wide landscapes.

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