

Factors affecting survival and dispersal of the comma butterfly in a high mountain deciduous forest habitat

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Summary

Factors affecting survival and dispersal of the comma butterfly in a high mountain deciduous forest habitat. Population and community dynamics of butterflies are relatively well known in Europe thanks to citizen science and academic efforts to cover large spatio-temporal scales. However, there are still gaps of knowledge about which life-history traits have a large influence on the dynamics of particular species and the ecological factors that influence those traits. We conducted a capture-recapture demographic study on the comma butterfly *Polygonia c-album* in a high mountain deciduous forest. We estimated daily survival in breeding adults caught while foraging on thistles and we calculated the probability of dispersal between two close sites. Thistle growth was enhanced by nitrification in cattle grazing in the study area. Local survival was higher for males (0.920, 95% CI: 0.851–0.959) than for females (0.869, 95% CI: 0.799–0.917). Short-range dispersal mostly occurred in absence of wind. Light winds and high levels of solar radiation likely enhanced foraging activity. In contrast with findings in most butterfly demographic studies, recapture rates were significantly higher in females than in males, likely due to the latter moving each afternoon to establish territories along sunny forest edges away from the foraging habitat. Further demographic studies are needed to assess the effects of climate stochasticity and habitat transformation caused by changes in extensive cattle grazing on the population dynamics of the comma butterfly.

Key words: Capture-recapture, Pyrenees, Comma butterfly, Survival, Wind, Dispersal

Resumen

Factores que afectan a la supervivencia y la dispersión de la mariposa c-blanca en un hábitat de bosque caducifolio de alta montaña. Las dinámicas de las poblaciones y las comunidades de mariposas son relativamente bien conocidas en Europa gracias a la ciencia ciudadana y a los esfuerzos académicos para abarcar grandes escalas espaciotemporales. Sin embargo, todavía se desconocen las características del ciclo biológico que influyen en la dinámica de determinadas especies y cuáles pueden ser los factores ecológicos que inciden en estas características. Realizamos un estudio demográfico de captura-recaptura de la mariposa c-blanca *Polygonia c-album* en un bosque caducifolio de alta montaña. Estimamos la supervivencia diaria de los adultos reproductores y la probabilidad de dispersión de los individuos capturados entre dos sitios cercanos mientras se alimentaban de cardos, cuyo crecimiento se ve favorecido por la nitrificación provocada por el ganado que pasta en la zona de estudio. La supervivencia local fue mayor en los machos (0,920, IC 95%: 0,851–0,959) que en las hembras (0,869, IC 95%: 0,799–0,917). La dispersión de corto alcance ocurrió principalmente en ausencia de viento. Los vientos ligeros y los altos niveles de radiación solar probablemente incrementaron la actividad de búsqueda de alimento. Al contrario de lo que se observa en la mayoría de los estudios demográficos sobre mariposas, las tasas de recaptura fueron significativamente más altas en las hembras que en los machos, lo que probablemente se deba a que los últimos se alejan cada tarde del hábitat de alimentación para establecer territorios a lo largo de los bordes soleados del bosque. Se necesitarían más estudios demográficos para evaluar los efectos de la estocasticidad climática y la transformación del hábitat causada por los cambios en el pastoreo extensivo del ganado en la dinámica poblacional de la mariposa c-blanca.

Palabras clave: Captura-recaptura, Pirineos, Mariposa c-blanca, Supervivencia, Viento, Dispersión



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Introduction

In butterflies, capture mark–recapture techniques (CMR) consist of marking the wings of a subset of a population before their release and later recapture. The proportion of marked individuals in the re–sampling is then determined. Butterflies were one of the commonest organisms on which, in the late 1950s, CMR models were first applied (Ehrlich and Davidson, 1960). Since then, the technique has been in common use to estimate population density in many butterfly species (Brussard and Ehrlich, 1970; Bergman and Landin, 2002; Osváth–Ferencz et al., 2017). The CMR approach also allows researchers to estimate demographic parameters such as survival and dispersal (parameters that are crucial to understanding the demographic drivers of population and metapopulation dynamics in butterflies) and to study how ecological and climate factors may influence these parameters (Hill et al., 1996; Hanski et al., 2000; Wahlberg et al., 2002; Schtickzelle et al., 2006). Most CMR butterfly studies, however, have focused on species with relatively low mobility, that is, species structured in meta–populations with limited dispersal between habitat patches (Hanski, 1999). In this work, we instead focused on a highly mobile species, the comma butterfly (*Polygonia c–album*), for which no previous CMR is available to our knowledge.

The comma butterfly (*Polygonia c–album*) is a polyphagous species whose larvae can feed on plants from several taxa (e.g. Urticaceae, Cannabaceae, Salicaceae, Betulaceae, and Grossulariaceae) (Nylín, 1988). In its southern European range, multivoltine populations seem more specialized in common nettle (*Urtica dioica*) than univoltine northern European populations. This is likely because late generations of the former populations avoid deciduous trees and shrubs because their nutritious quality deteriorates rapidly as the season progresses (Nylín et al., 2009). The species is known to exploit various habitats, likely thanks to the high mobility of adults and its open population structure (Stefanescu, 2007). Nevertheless, knowledge of the demographic parameters of the species and the environmental factors that may drive this butterfly's dynamics are scarce.

Here we carried out the first demographic study on the comma butterfly in a Pyrenean population in the upper altitudinal range of the species. We estimated survival, sex–ratio and dispersal between two study patches. We tested the effects of sex on survival and those of wind and sunlight radiation (cloudiness) on dispersal and recapture probabilities as these two variables are known to strongly influence the activity patterns of insects, especially in mountainous areas (Heinrich, 1993; Nève et al., 1996).

Material and methods

Study area and study species

El Catllar is a small valley (ca. 1,000 ha) in the eastern Pyrenees. Altitude ranges widely, from 1,170 m a.s.l. at the lowest parts to 2,693 m a.s.l. at the highest

summit. The two study sampling patches (Pletó and Cabanes) are at the same altitude (ca. 1,450 m a.s.l.), and consist of pasture meadows of 0.81 and 0.32 ha, respectively, 196 meters apart (using the centroids), and surrounded by deciduous forests (mainly silver birch, ash and oak trees; fig. 1). Due to the impact of a herd of cows, nitrophilous vegetation is common in the meadows, especially common nettle (*Urtica dioica*) and woolly thistle (*Cirsium eriophorum*), two important plant species for the comma butterfly. Common nettle is the main host plant for this butterfly in the area, and a wide range of wild flowers and sap exudates constitute the trophic resources of adults. In the study area, in particular, wounds caused by the weevil *Larinus sturnus* in woolly thistles produce sap exudates that are highly attractive to comma adults. These exudates are also visited by other butterflies, such as the red admiral (*Vanessa atalanta*), the white admiral (*Limnitis camilla*), the purple emperor (*Apatura iris*), and the speckled wood (*Pararge aegeria*).

The comma butterfly overwinters as an adult and has two generations a year in the study area of El Catllar. The first generation (corresponding to the offspring of wintering adults, which reappear and breed in March–April) begins to emerge in June and reaches its maximum abundance in July. Individuals belonging to this generation are reproductively active, and they give rise to the second generation of adults, which emerge in September and enter hibernation until the following spring. Reproductive males show strong territorial behaviour and each afternoon they establish and defend territories along sunny forest edges.

Here we regularly sampled the two patches with large stands of woolly thistles (fig. 1), and systematically captured comma butterflies feeding on the thistle exudates. Visits to the patches were made between July 21, when thistle exudates became first available, and August 20, 2020, when the flowering season of thistles was over.

Sampling occurred every week from Monday to Thursday, with two daily sessions of two hours each, one in the morning and one in the afternoon. Each day, the weather conditions (cloudiness and wind) were also recorded in a weather station set up the Cabanes patch (see below).

Individuals were caught with a butterfly net and the wings were marked with an individual numerical code using a permanent fine–tipped marker. A total of 88 individuals were caught during the 20 sampled days. We recorded the sex and wing wear status of each individual, and used this as a proxy to estimate the age of the breeding adult (on a categorical scale from 1 to 5, from youngest to oldest). The capture–recapture study was performed almost exclusively with individuals of the first annual generation, as just one fresh butterfly from the second (diapausing) generation was captured towards the end of the sampling period. The analysis thus allowed us to study the behaviour of reproductively active individuals towards the second part of their life.

Environmental variables

Wind was recorded each sampling day using a categorized Beaufort scale of intensity (from 1 to 5),

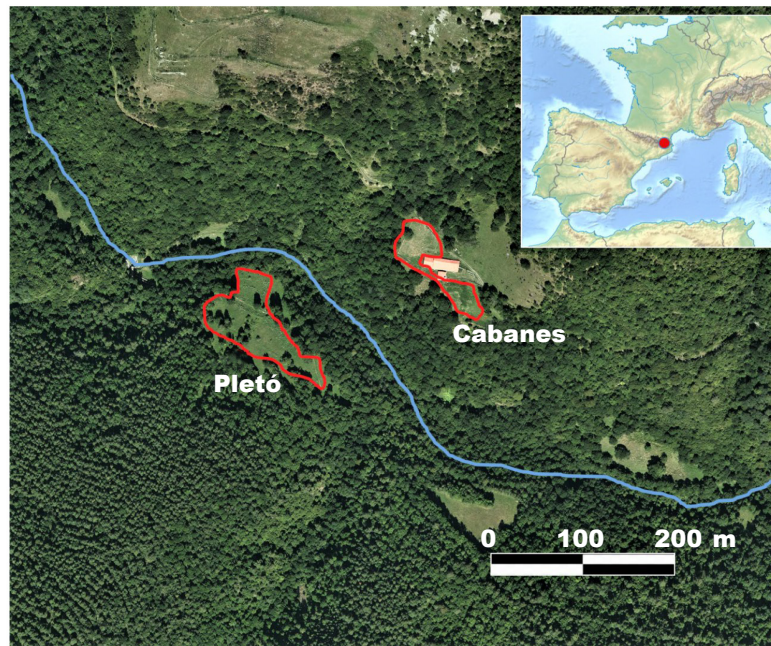


Fig. 1. Map of the study area at El Catllar, a high small valley in the eastern Pyrenees, showing the two study patches (red contours) where we studied the demography of the comma butterfly. The blue line shows the stream crossing the area. The two patches have ca. the same altitude above sea level.

Fig. 1. Mapa de la zona de estudio en El Catllar, un pequeño valle alto en el Pirineo oriental, en el que se muestran los dos sitios de la zona de estudio (contorno rojo) en los que se estudió la población de la mariposa c–blanca. La línea azul representa el curso de agua que atraviesa la zona. Los dos sitios están situados a la misma altura sobre el nivel del mar.

and for certain analyses and when this information was available, we used wind velocity (in km/h), which was measured in an automated Campbell weather station at the Cabanes patch. Cloudiness (daily mean sunlight radiation in w/m^2) was also recorded at the station. Mean cloudiness over the study period was $211.3 w/m^2$ (median = 228.1 , range = 97.8 – 291.0). This variable was categorized on a scale of 1 to 5 to include in the capture–recapture analysis (see below).

Analysis of demographic parameters

To estimate demographic parameters such as daily survival, and probability of dispersal between sites, we used multi–event capture–recapture modelling (Pradel, 2005). This approach holds two levels of capture–recapture data: the field observations, called 'events', encoded in the capture histories, and the 'states' defined to match the biological questions, which can only be inferred. Since the study system was open, mortality could be separated from permanent emigration outside the study site, and thus our estimates should be considered as local parameters. Nevertheless, we assumed that the potential bias for permanent dispersal was similar throughout the study period. Models were fitted in the program E–SURGE (Choquet et al., 2009b).

Individuals were classified into two groups based on their sex. Our models included four biological states: individual alive at patch 1 (AS1); individual alive at patch 2 (AS2); individual recently dead (RD); and dead (D), this last state being non–observable. The initial state in our models was always AS1 or AS2. Transitions between states were modelled in a two–step approach, i.e. survival probability and probability to disperse. In each capture–recapture occasion (t) we considered four possible events: Individual not seen (noted 0); individual seen alive at patch 1 (noted 1); individual seen alive at patch 2 (noted 2); individual found recently dead (noted 3). Mean life expectancy was calculated as $-1/\ln(\text{daily survival})$ (Seber, 1982).

We tested for differences between sexes in daily survival probability. We also assessed factors affecting dispersal probabilities; we tested models assuming constant, sex and site–dependent dispersal probabilities and the potential effect of wind and cloudiness on those probabilities. We tested for time–varying and constant probabilities for recapture probabilities and an effect of environmental covariates (wind and clouds).

Model selection relied on QAICc, i.e. the Akaike Information Criterion corrected for overdispersion and small sample sizes (Burnham and Anderson, 2002). Since there is no goodness–of–fit test (GOF–test)

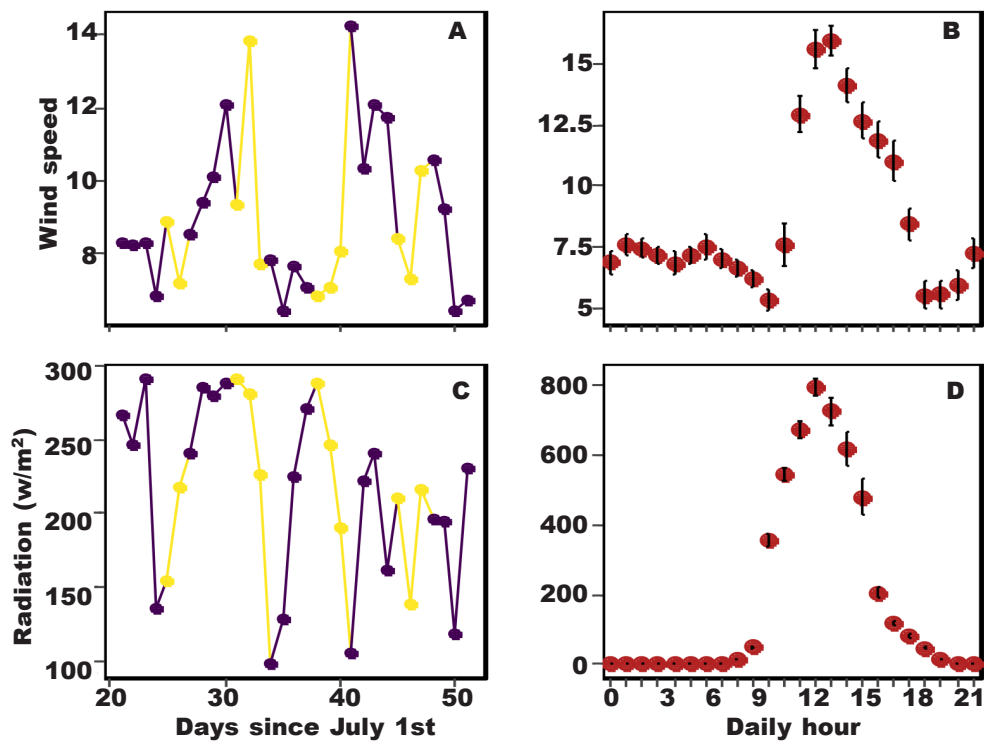


Fig. 2. Features of wind speed dynamics (in km/h) at the study site: A, mean wind speed on each sampled day ($N = 20$, in purple); B, average (and SE) of wind speed for each daily hour considering the 20 sampled days; C, mean solar radiation in each sampled day ($N = 20$, in purple); and D, average (and SE) of solar radiation for each daily hour considering the 20 sampled days. For wind speed and solar radiation, we show the continuous values for the whole month; thus yellow lines represent days when we did not capture comma butterflies in the study area.

Fig. 2. Características de la dinámica de la velocidad del viento (en km/h) en la zona del estudio: A, promedio de la velocidad del viento todos los días del estudio ($N = 20$, en morado); B, promedio (y DE) de la velocidad del viento cada hora durante los 20 días del estudio; C, promedio de la radiación solar todos los días del estudio ($N = 20$, en morado); y D, promedio (y DE) de la radiación solar cada hora durante los 20 días del estudio. Respecto de la velocidad del viento y la radiación solar, mostramos los valores continuos de todo el mes, de forma que las líneas amarillas representan los días en los que no se capturaron mariposas c-blanca en la zona de estudio.

available for these multi-event models, we assessed the fit of a multi-site model without recoveries (Jolly Movement type models, JMV) using U-care software (Choquet et al., 2009a).

Results

Wind and sunlight radiation varied throughout the study season and both variables showed a marked daily pattern with peaks at the central hours of the day (fig. 2).

The wing wear state indicated that the majority of individuals caught corresponded to the final part of the first generation (94.3% predominance of categories 3–5). Only two fresh individuals of the dark morph (corresponding to the second overwintering genera-

tion) were found, on August 10 and 11, respectively. Of these two individuals, one was marked, but the other escaped before being captured.

While sex ratio between males and females was almost totally balanced at Cabanes (0.96, Fisher exact test $p = 1.000$), the ratio was more male-biased at the Pletó patch, although differences were not statistically significant (1.87, Fisher exact test $p = 0.195$) (table 1). Considering the two patches together, the sex ratio was slightly male-biased (1.32).

When looking at the number of recaptures by sex, results showed that 64% and 66% of males and females were never recaptured. While males showed a larger number of single recaptures, females had a higher number of multiple recaptures than males, with a single female recaptured on up to eight different sampling occasions (fig. 3). From the

Table 1. Number of comma butterflies caught during summer 2020 at each study patch considering their sex.

Tabla 1. Número de mariposas c–blanca capturadas durante el verano de 2020 en cada sitio de la zona de estudio teniendo en cuenta su sexo.

Patch	Sex	
	Males	Females
Cabanes	22	23
Pletó	28	15

33 individuals that were recaptured at least once, 27% were found in the patch other than that where they were marked (i.e. individuals that dispersed between the two patches). Even though the number of individuals caught in Cabanes and Pletó was similar (45 and 43 respectively), dispersal was less frequent in the former than in the latter (33% and 66% of all dispersal events respectively). We recorded a single case of a butterfly dispersing to the other patch and

later dispersing back to the patch where it was initially captured. Our GOF test did not detect any departure from the JMV models (males = 25.176, $p = 0.155$; females = 7.961, $p = 0.925$). Table 2 shows a list of all the models fitted to the data.

The probability of recapture was almost constant throughout the study period, likely due to the standardized sampling protocol. Nevertheless, the best models also showed that the probabilities of recapture decreased with cloudiness and wind intensity (fig. 4). All four best models showed an effect of sex and patch on recapture probabilities: females showed a higher recapture probability than males (mean and 95% CI: 0.249 (0.138–0.402) and 0.120 (0.066–0.209) respectively), and this probability was higher in Pletó than in Cabanes.

The models that best explain our observations all reveal an effect of wind on the probability of dispersal (models 1 to 4 in table 2). When the wind was stronger, the probability of dispersal decreased (fig. 5). We did not detect an effect of sex on dispersal probabilities, but one of the best models (model 2, see table 2) included an effect of sex on daily survival, with males showing higher survival (0.920, 95% CI: 0.851–0.959) than females (0.869, 95% CI: 0.799–0.917). These estimates give an average life expectancy for a breeding adult of ca. 12 and 7 days for males and females, respectively. The mean probability of daily survival was estimated at 0.894 (95% CI: 0.849–0.927).

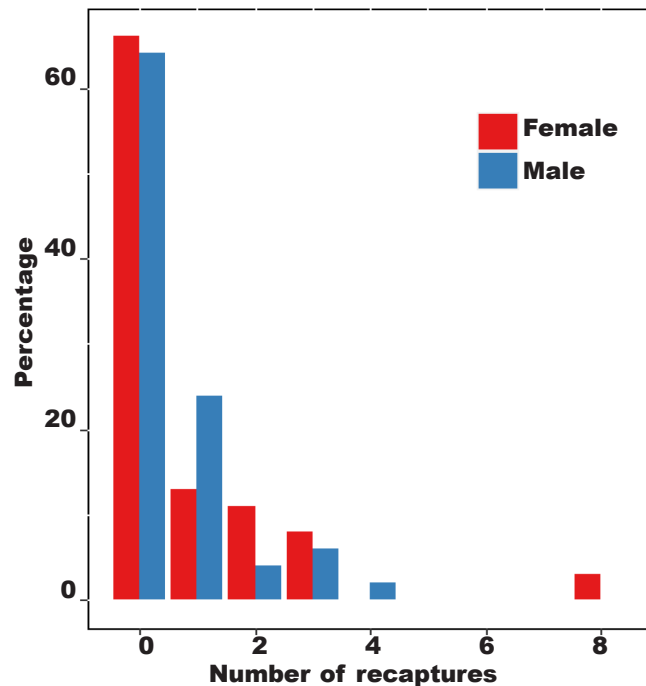


Fig. 3. Percentage of the number of recaptures of comma butterflies in the study area of El Catllar for each sex during our study ($N = 50$ for males and $N = 38$ for females).

Fig. 3. Porcentaje de recapturas de mariposas c–blanca en la zona de estudio de El Catllar de cada sexo durante el estudio ($N = 50$ para los machos y $N = 38$ para las hembras).

Table 2. List of models built to tests biological hypotheses about survival and dispersal in the comma butterfly in the study area of El Catllar (eastern Pyrenees): IS, initial state for the first capture; ϕ , adult survival; D, dispersal between patches; p, probability of recapture; np, number of identifiable parameters; Dev, deviance of the model; QAICc, corrected AIC for small sample sizes; W, weight of each model according to QAICc value; Δ AIC, difference of QAICc value from the best model; . constant; + additive factors; t, time varying; sex, different value for each sex; wd, effect of the wind; c, effect of cloudiness; patch, effect of patch. (The best four models, Δ AIC < 2, are shown in bold).

Tabla 2. Lista de modelos elaborados para comprobar las hipótesis biológicas sobre supervivencia y dispersión de la mariposa c–blanca en la zona de estudio de El Catllar (Pirineo oriental): IS, estado inicial de la primera captura; ϕ , supervivencia de los adultos; D, dispersión entre sitios; p, probabilidad de recaptura; np, número de parámetros identificables; Dev, desviación del modelo; QAICc, AIC corregido para tamaños muestrales pequeños; W, peso de cada modelo según el valor de QAICc; Δ AIC, diferencia del valor de QAICc respecto del mejor modelo; . constante; + factores aditivos; t, probabilidad cambiante en el tiempo; sex, valor diferente para cada sexo; wd, efecto del viento; c, efecto de la presencia de nubes; patch, efecto del sitio. (Los cuatro mejores modelos, Δ AIC < 2, se indican en negrita).

Model	IS	ϕ	D	p	np	Dev	QAICc	W	Δ AIC
1	to	.	wd	patch+c+sex	8	554.825	571.869	0.25	0.00
2	to	sex	wd	patch+c+sex	9	553.450	572.764	0.16	0.90
3	to	.	wd	patch+wd+sex	8	555.723	572.766	0.16	0.90
4	to	.	wd	patch+sex	7	558.105	572.911	0.15	1.04
5	to	.	wd+patch	patch+c+sex	9	554.821	574.135	0.08	2.27
6	to	sex	wd	patch+c	8	557.325	574.369	0.07	2.50
7	to	.	.	patch+c+sex	7	561.094	575.900	0.03	4.03
8	to	.	.	patch+c	6	563.650	576.250	0.03	4.38
9	to	.	.	patch+sex+wd	7	561.991	576.797	0.02	4.93
10	to	.	.	patch+sex	6	564.373	576.973	0.02	5.10
11	to	.	c	patch+c+sex	8	560.268	577.312	0.02	5.44
12	to	.	.	patch	5	567.067	577.492	0.01	5.62
13	to	.	.	.	4	574.917	583.199	0.00	11.33
14	to	.	t	patch+c+sex	23	678.502	733.477	0.00	161.61

Discussion

We provide the first demographic estimates for the comma butterfly in a high mountain deciduous forest, towards the upper range of its altitudinal distribution. The estimates of local daily survival, sex ratio and recaptures are similar to those estimated for other butterfly species (table 3). Our estimates of life expectancy from survival probabilities should be taken with caution: our sampling started when thistles produced sap exudates and butterflies took advantage of this feeding resource. This occurred in mid–July when the first adult generation had emerged several days earlier. Thus, we estimated a longer life expectancy of 2–3 weeks, which is shorter than that estimated in the laboratory (around one month: Wiklund et al., 2003), where predation and environmental variability are absent.

Differences between survival in males and females commonly indicates higher survival for females. This

was not the case of the comma butterfly in our study (table 3). Although anecdotal, we observed a cricket of the species *Tettigonia cantans* preying on an older comma female that was feeding on a thistle during our field season. This predation occurred two days after the female had been caught and marked in the same habitat patch. The difference in local survival between males and females may be caused by a real difference in survival related perhaps to breeding investment and by a greater chance of permanent dispersal out of the study area for females. However, we cannot discard the possibility that differences were caused by our small sample size. Other studies found that females disperse less but at longer distances than males (Bergman and Landin, 2002; Fred and Brommer, 2009).

The sex–ratio tends to be male–biased in all studies (table 3). The main difference between our study and others appears to be related to recapture probability:

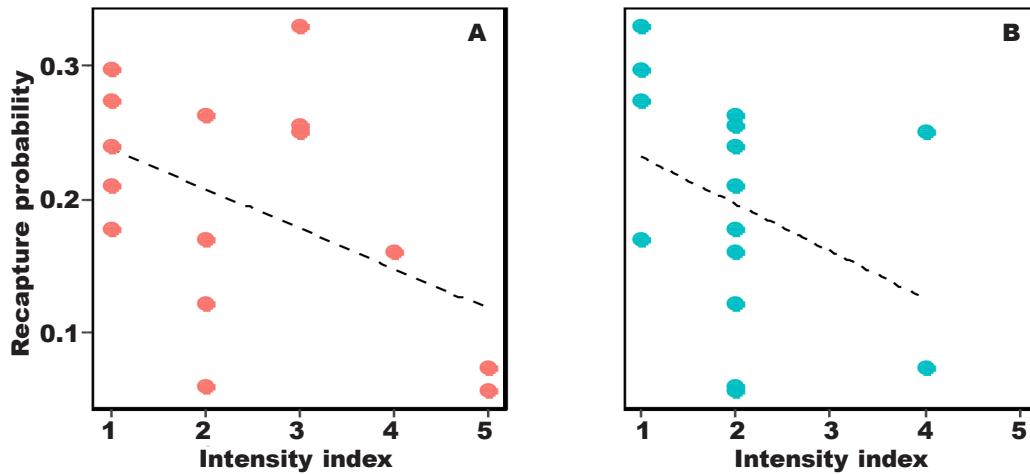


Fig. 4. Recapture probabilities of comma butterflies in the study area for each occasion (only mean values estimated from model 3, see table 1) decrease with cloudiness (A) and wind speed (B) in the study area. Dashed lines show the regression lines for each panel.

Fig. 4. La probabilidad de recaptura de las mariposas c–blanca en la zona de estudio para cada ocasión (solo se calcularon los valores medios del modelo 3, véase la tabla 1) disminuye con la presencia de nubes (A) y la velocidad del viento (B) en la zona de estudio. Las líneas discontinuas representan las líneas de regresión de cada panel.

although this tends to be higher for males in all other studies, we found a higher estimate for females. Because sex differences in recapture probabilities are commonly linked to differences in behaviour, we suggest that in the highly mobile comma butterfly,

females may stay for longer periods than males in patches that offer good conditions for oviposition. During our fieldwork, we recorded several instances of females laying eggs on nettles. One female was observed ovipositing alternatively in the two studied

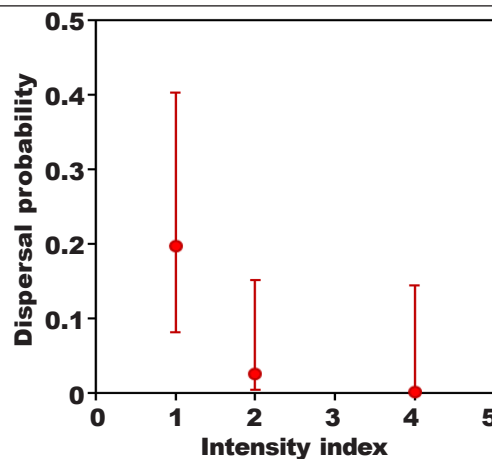


Fig. 5. Mean dispersal probabilities (and 95% CI) of comma butterflies in the study area of El Catllar between the two study patches as a function of wind intensity from the best model (model 1, table 1). Due to the small sample size, dispersal was considered symmetric between the two patches in all models.

Fig. 5. Promedio de la probabilidad de dispersión (IC 95%) de las mariposas c–blanca entre los dos sitios de la zona de estudio de El Catllar como función de la intensidad del viento a partir del mejor modelo (modelo 1, tabla 1). Debido al pequeño tamaño de la muestra, la dispersión se consideró simétrica entre los dos sitios en todos los modelos.

Table 3. Demographic parameters (survival, sex-ratio and recaptures p) of several butterfly species and estimates for the comma butterfly in our study for comparison: * statistically significant differences; ** averaged values for three years; No, similar values between sexes; NA, no data available.

Tabla 3. Parámetros demográficos (supervivencia, proporción de sexos y probabilidad de recaptura) de varias especies de mariposa y estimaciones para la mariposa c–blanca en nuestro estudio a efectos de comparación: * diferencias estadísticamente significativas; ** valores medios de tres años; No, valores similares entre sexos; NA, sin datos disponibles.

Species	Survival	Sex ratio	p	Reference
<i>Euryades corethrus</i>	0.863	♂*	No	Mega et al. (2020)
<i>Parnassius clodius</i>	0.743**	♂	♂	Auckland et al. (2004)
<i>Maniola jurtina</i>	0.825 ♀ – 0.870 ♂	NA	NA	Brakefield (1982)
<i>Polyommatus coridon</i>	0.914 ♀ – 0.886 ♂	♂*	♂*	Casula (2006)
<i>Melitaea diamina</i>	0.89	NA	NA	Hanski et al. (2000)
<i>Anartia fatima</i>	0.803 ♀ – 0.878 ♂	NA	NA	Srygley and Kingsolver (2000)
<i>Euphydryas maturna</i>	0.85 ♀ – 0.74 ♂	No	No	Konvicka et al. (2005)
<i>Aphantopus hyperantus</i>	0.885	NA	NA	Öckinger and Smith (2007)
<i>Coenonympha pamphilus</i>	0.884	NA	NA	Öckinger and Smith (2007)
<i>Maniola jurtina</i>	0.835	NA	NA	Öckinger and Smith (2007)
<i>Parnassius mnemosyne</i>	0.82 ♀ – 0.77 ♂	♂*	♂*	Vlasanek et al. (2009)
<i>Maculinea teleius</i>	0.574	♀	NA	Nowicki et al. (2005)
<i>Maculinea nausithous</i>	0.669	♀	NA	Nowicki et al. (2005)
<i>Pseudophilotes sinaicus</i>	0.73	No	No	James (2006)
<i>Erebia nivalis</i>	NA	♂*	♂*	Ehl et al. (2018)
<i>Pyrgus sidae</i>	0.90	♂*	♂*	Hernandez–Roldan et al. (2009)
<i>Proclissiana eunomia</i>	0.90 ♀ – 0.82 ♂	♂*	♂*	Schtickzelle et al. (2006)
<i>Polygonia c–album</i>	0.87 ♀ – 0.92 ♂	♂*	♀*	Our study

habitat patches for more than two weeks. In contrast, males engage each afternoon in territorial behaviour, defending sunny forest edges, which may lead to a more nomadic behaviour in search of unoccupied good spots. This is supported by the observation that males rarely recorded feeding on thistles on our second daily marking session. Differences in recapture probability are also likely related to the greater attachment of females to sap exudates where butterflies were captured (see also Sielezniew and Nowicki, 2017).

Dispersal at several spatial scales and ranges has been found in most studies of butterflies occupying very different habitats and ecosystems (Ehrlich, 1961; Casula, 2006; Öckinger and Smith, 2007; Junker et al., 2010). Drivers of dispersal are related to changes in habitat selection for finding better trophic and mating resources (Pe'er et al., 2004; Fred and Brommer, 2009), density-dependent processes linked to source–sink dynamics and social attraction (Casula, 2006; Öckinger and Smith, 2007), and the spatial habitat structure and heterogeneity (e.g. patch fragmentation) (Hill et al., 1996; Schtickzelle et al., 2006). We also

found that dispersal between patches separated ca. 200 m from each other is a common phenomenon in the comma butterfly, although we could not assess the mechanisms involved. Nevertheless, we found that comma butterflies dispersed only when the wind was absent or very light. Wind is crucial in mountainous regions for thermoregulation and thus for butterfly activity. In these regions, windy conditions would not allow comma butterflies to attain a sufficient temperature to be active. Besides, calm conditions may favour choice about where to disperse for mating and feeding. This hypothesis is supported by the fact that the probability of recapture also decreased when cloudiness and wind intensity were higher, likely due to the lower activity of individuals under environmental conditions that become unsuitable.

In addition to climate, future studies could assess the role of resource availability on dispersal parameters, and how this is influenced by pastoral practices in the Pyrenees. Although alpine and subalpine meadows have been maintained for centuries through extensive grazing mainly by sheep and cattle, rural

exodus and the cessation of traditional activities in the past decades are leading to rapid dramatic land-use changes, especially an increase in the forest cover and vegetation encroachment at the expense of pastures (Gracia et al., 2011). Paradoxically, in some areas, there is also a growing tendency for meadows to be overgrazed, as the remaining local shepherds tend to buy and unify livestock in larger herds. This will likely lead to a decrease in resource availability for comma butterflies, as both nettles and thistles are highly nitrophilous plants that benefit from cattle activity. On the other hand, the latter second situation will certainly produce local concentrations of resources for this butterfly. It would be interesting to compare dispersal parameters at sites with these contrasting land uses and assess to what extent dispersal in this highly mobile butterfly relates to resource availability.

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