Species composition and dynamics in abundance of migrant and sedentary butterflies (Lepidoptera) at Gibraltar during the spring period

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Abstract. In order to understand patterns of abundances of migratory Lepidoptera in southernmost Europe and contrast this with those of sedentary species, we studied butterflies surveyed along transects during three spring migration seasons at the Rock of Gibraltar. Overall, 2508 butterflies belonging to 19 species were recorded. Of these, the four most numerous species accounted for almost 88% of all individuals recorded. These were the migratory Clouded Yellow *Colias croceus*, Red Admiral *Vanessa atalanta* and Painted Lady *Vanessa cardui*, and the sedentary Common Blue *Polyommatus icarus*. There was a significant correlation between abundance of *P. icarus* and *C. croceus*. Furthermore, abundances of *C. croceus* and *V. atalanta* were correlated. The sometimes very high abundance of migratory butterflies at the study site could suggest that Gibraltar is a stopover site for butterflies migrating between Africa and Europe.

INTRODUCTION

The seasonal migration of a range of taxonomic groups within the Lepidoptera is a widespread phenomenon throughout the world (e.g., Williams, 1958; Dingle, 1996; Dingle & Drake, 2007). Among them, butterflies (Rhopalocera) usually migrate closer to the ground than moths (Taylor, 1974; Walker, 1985; Srygley & Oliveira, 2001) because wind speeds are lower here than their own airspeed, making it possible to control their track direction relative to the ground (Dingle & Drake, 2007). This, combined with their diurnal habits, makes them ideal for visual studies on migratory insects.

Although knowledge of migratory insects has increased greatly over recent decades as a result of intensive theoretical and applied research (Drake & Gatehouse, 1995; Dingle, 1996; Dingle & Drake, 2007), gaps remain in our understanding of phenomena surrounding migratory butterflies. Most studies of migratory Lepidoptera (including research with probably the best known Palaearctic migratory species: the Painted Lady *Vanessa cardui*) have generally been conducted in Europe and North America. Further research is required to study African aspects of the African-Eurasian migratory flyway (e.g., Stefanescu et al., 2013) and sites along this flyway as, unlike with Monarch Butterflies *Danaus plexippus* in North America (Davis & Garland, 2004; Meitner et al., 2004; Brower et al., 2006; McCord & Davis, 2010, 2012; Davis et al., 2012), migrant

butterfly stopover has received very little attention in the Old World, even though suitable study sites exist.

The Rock of Gibraltar is a British Overseas Territory of some 6.5 km². It is located on the southern end of the Iberian Peninsula, at the eastern end of the Strait of Gibraltar (36°07'N, 5°21'W) and very close to the African coast (only 21 km). A large proportion of Gibraltar is urbanised and population density of humans is high (4328/km²), but a wide variety of habitats exists and approx. 36% of the land area is protected under local legislation and the EU Habitats Directive. Gibraltar is known as a hotspot for migratory birds due to its proximity to Africa and the bottleneck formed by the Strait of Gibraltar, where migrants can avoid the geographical barrier posed by the Mediterranean Sea (Heath & Evans, 2000). However, the less-well understood phenomenon of insect migration is also observable from Gibraltar (Bensusan et al., 2005), including potentially that of butterflies (Nesbit et al., 2009). Gibraltar thus offers an opportunity to understand patterns in abundance of migratory Lepidoptera in southernmost Europe and contrast this with phenology of abundances of sedentary species.

With this study, we aim to examine composition and relative daily abundance of migrant and sedentary butterflies throughout the spring period at a study site in Gibraltar. We compare the proportions of migratory and sedentary species recorded in order to view the contribution of migratory butterflies to the butterfly fauna and infer possible implications on the site's importance for migrants. We then test

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TABLE 1. Composition of diurnal butterfly species in Gibraltar based on transect surveys (n = 523): total numbers, mean number of individuals from each species calculated per one transect survey and % of transect surveys in which the following species were observed (species known as migratory marked with*).

Species	Total number	Dominance %	$Mean \pm SD$	% of transect surveys
Painted Lady Vanessa cardui*	873	34.81	2.11 ± 7.78	34.54
Clouded Yellow Colias croceus*	692	27.59	1.67 ± 3.10	50.72
Common Blue Polyommatus icarus	450	17.94	1.09 ± 2.36	28.50
Red Admiral Vanessa atalanta*	184	7.34	0.44 ± 1.42	19.08
Small White Pieris rapae	69	2.75	0.17 ± 0.48	12.80
Swallowtail Papilio machaon	66	2.63	0.16 ± 0.52	11.35
Green-striped White Euchloe belemia	50	1.99	0.12 ± 0.53	7.73
Small Copper Lycaena phlaeas	30	1.20	0.07 ± 0.29	6.76
Sage Skipper Muschampia proto	27	1.08	0.07 ± 0.35	4.59
Large White Pieris brassicae	23	0.92	0.06 ± 0.27	4.83
Long-tailed Blue Lampides boeticus	16	0.64	0.04 ± 0.27	2.90
Wall Brown Lasionmata megera	13	0.52	0.03 ± 0.20	2.66
Cleopatra Gonopteryx cleopatra	5	0.20	0.01 ± 0.11	1.21
Spanish Festoon Zerynthia rumina	3	0.12	0.01 ± 0.08	0.72
Speckled Wood Pararge aegeria	3	0.12	0.01 ± 0.08	0.72
False Mallow Skipper Carcharodus tripolinus	1	0.04	0.00 ± 0.05	0.24
Provence Hairstreak Tomares ballus	1	0.04	0.00 ± 0.05	0.24
Morocco Orangetip Anthocharis belia	1	0.04	0.00 ± 0.05	0.24
Portuguese Dappled White Euchloe tagis	1	0.04	0.00 ± 0.05	0.24
Total	2508	100.00	0.31 ± 0.61	10.01 ± 13.95

whether abundances of the most common migratory and sedentary species of butterflies at Gibraltar are associated, as migratory Lepidoptera are often abundant simultaneously (Williams, 1970; Stefanescu et al., 2013). Finally, we tested for differences in abundance of butterflies between years.

MATERIAL AND METHODS

Study area and fieldwork

Data were collected on the Rock of Gibraltar. The study site chosen was Windmill Hill Flats, an area of approx. 12 ha of garigue habitat known for its importance to migratory birds (Cortes et al., 1980; Bensusan et al., 2011) and managed by the UK Ministry of Defence (MOD). The flora at Windmill Hill Flats is diverse, with a wide range of flowering plants during the spring especially (Perez, 2006). 22 species of butterfly have been recorded there regularly in the last decade (C. Perez, pers. obs.), comprising almost 70% of Gibraltar's current butterfly fauna of 32 species (Appendix 1). Windmill Hill Flats is located towards the southern end of Gibraltar.

Data were collected during the spring season $(25^{th} \text{ April} - 5^{th} \text{ June})$ between the years 2006–2008. The butterfly census consisted of 2 × 130 m line transects. All individuals within a distance of 3 m on both sides of the transects were recorded. Butterflies were identified at the species level and counts were recorded for each species. Of the butterflies recorded during the study (Table 1), *Colias croceus, Vanessa atalanta* and *Vanessa cardui* are all known to be migratory (Mikkola, 2003; Sparks et al., 2007). The number of transects was two during 2006–2007 and one in 2008. Surveys along each transect were carried out every day, with several short breaks (year 2006 – 2 one-day and 1 three-days; year 2007 – 7 one-day) and three times a day (around 10 a.m., 1 p.m. and 4 p.m.). Overall, 414 transect surveys were carried out (year 2006 – 152, 2007 – 166, 2008 – 96).

Data processing and analyses

We used all data from all years of the study for general descriptive purposes. Differences in number of species were tested using chi-square test, where we compared the observed and expected numbers of species each year, where the last one was the total number of species recorded during three years of study. Furthermore, 2006 was the only year in which the number of individuals recorded was deemed sufficient to include the data in a further analysis concerning the dynamic in butterflies' occurrence throughout a season. We selected only the four most numerous species in that year, three of which were the migratory species. The number of butterflies recorded during each day of study was expressed as a mean number of individuals calculated per single transect survey.

We used the standard statistical methods to describe and analyse the data (Zar, 1999). All statistical tests were two-tailed. Calculations were performed using STATISTICA for Windows (StatSoft Inc., 2012). Throughout the text, mean values are presented with standard deviation (±SD) and median values with lower (Q_{25}) and upper (Q_{75}) quartiles.

RESULTS

During the 3 spring seasons, 2508 butterflies (year 2006 – 1771 individuals, 2007 – 165, 2008 – 572) belonging to 19 species were recorded. Of these, the four most numerous species accounted for almost 88% of all individuals recorded; three of these, the migratory species *Colias croceus, Vanessa atalanta* and *Vanessa cardui*, accounted for 70% of all observations and *V. cardui* alone comprised 35% of all butterflies observed (Table 1). Mean number of butterflies counted during one survey and % of transect surveys when the species were recorded are also presented (Table 1). Generally, the greater the total number of indi-



Fig. 1. Changes in the mean number of individuals from four analysed species, recorded during transect surveys during spring 2006 at Gibraltar.

viduals of a species recorded during the whole study period, the higher the proportion of transect surveys in which the individual species were recorded (Spearman correlation, $r_s = 0.99$, n = 19, p < 0.001).

Of the 19 species observed during the study, 13 were recorded every year. The other 6 were the least numerous species and were observed irregularly. These were Zerynthia rumina, Tomares ballus, Anthocharis belia, Euchloe tagis, Pararge aegeria and Charcharodus tripolinus (Table 1). Fourteen species were recorded in 2006, 16 in 2007 and 15 in 2008. The differences between years were not significant (chi-square = 2.63, df = 2, p = 0.268). Furthermore the number of butterflies observed during each year of study, expressed as mean number of individuals per single transect survey, differed between years (Kruskal-Wallis ANOVA, $H_2 = 169.08$, n = 414, p < 0.001). Butterflies were most numerous in 2006 ($\bar{x} = 11.65 \pm 15.44$ individuals per transect survey, n = 152). The number was much lower in 2008 ($\bar{x} = 5.96 \pm 4.98$, n = 96) and extremely low in 2007 $(\bar{x} = 0.99 \pm 1.25, n = 166).$

We did not find a significant influence of survey time on the overall number of butterflies along transects (Friedman ANOVA, chi-square = 5.64, df = 2, p = 0.059, 10 am $-\bar{x} =$ 5.05 ± 7.33 , 1 pm $-\bar{x} = 5.97 \pm 7.48$, 4 pm $-\bar{x} = 6.05 \pm 7.46$). Furthermore, no differences were found when analysing only migratory species (Friedman ANOVA, chi-square = 0.52, df = 2, p = 0.771, 10 am $-\overline{x}$ = 3.56 ± 6.71, 1 pm $-\overline{x}$ = 3.54 ± 6.01, 4 pm $-\overline{x}$ = 3.03 ± 4.55).

The four most numerous species in 2006 were: V. cardui: n = 818, C. croceus: n = 460, Polyommatus icarus: n = 166, *V. atalanta*: n = 155. The mean number of individuals observed along transects during that year fluctuated during the season (Fig. 1). Pronounced peaks in numbers of V. cardui, C. croceus and V. atalanta occurred during the second decade of May (i.e., 130-140 Julian day; Fig. 1). In the case of P. icarus, such a peak was not observed: its numbers began to increase halfway through the second decade of May (from around Julian day 135; Fig. 1) and were maintained until the end of the study period. There was a significant correlation between abundance in spring of the sedentary P. icarus and migratory C. croceus (Spearman correlation, $r_{a} = 0.56$, p = 0.002 after Bonferroni correction for multiple comparisons). No such correlations were found between P. icarus and the other migrants, V. cardui $(r_{e} = -0.20, p < 0.26)$ and V. atalanta $(r_{e} = 0.10, p < 0.59)$. Furthermore, abundances of the migratory C. croceus and *V. atalanta* were correlated ($r_s = 0.46$, p = 0.021 after Bonferroni correction for multiple comparisons). No such correlations were found between V. cardui and the other migrants (p > 0.15 in both cases).

The median date of individuals recorded during a season differed between the species analysed (Kruskal-Wallis ANOVA, $H_3 = 342.54$, n = 1599, p < 0.001; *V. cardui*: Me

= 135.0, Q_{25} = 131.0, Q_{75} = 137.0, n = 818; *C. croceus*: Me = 139.0, Q_{25} = 137.0, Q_{75} = 143.0, n = 460; *P. icarus*: Me = 148.0, Q_{25} = 140.0, Q_{75} = 151.0, n = 166; *V. atalanta*: Me = 137.0, Q_{25} = 134.0, Q_{75} = 142.0, n = 155). Differences were found between all species (p value for multiple comparisons of mean ranges after Bonferroni correction < 0.004 in all cases).

DISCUSSION

Nineteen species of butterfly were observed along the transects. Of these, approximately 70% of individuals belonged to the three migrant species and Vanessa cardui alone accounted for 35% of observations. The results confirm Gibraltar as a useful site at which to study migratory butterflies. The sedentary species - seventeen species accounting for approx. 30% of observations - may not be able to attain such high densities as migrants because abundance of sedentary species may be regulated by availability of host plants for larvae (e.g., Krauss et al., 2004, 2005). This contrasts with the non-breeding migratory species, which visit the site in transit to more northerly breeding grounds and rarely oviposit, as evidenced by regular observations of adult butterflies and the lack of larvae present during regular insect surveys (K. Bensusan & C. Perez pers. obs.). Alternatively, competition for nectar-rich flowers may be high due to large influxes of migratory species and this could influence the carrying capacity of sedentary species. Data from the same study site recently showed that abundance of migrant passerine birds affects the behaviour and habitat use of a resident passerine species (Bensusan et al., 2011) and it would be useful to determine whether migrant butterflies have a similar impact on sedentary species. The large differences in abundance recorded between years require explanation, but these could influence dynamics between species.

Abundances of two of the three migratory species were correlated, possibly because their migratory patterns are influenced by similar factors. A similar situation has been observed in migratory Lepidoptera elsewhere. For example, V. cardui, Silver-Y moth Autographa gamma and Rush Veneer Nomophila noctuella are often abundant simultaneously (Williams, 1970; Stefanescu et al., 2013) and this is probably due to shared environmental effects, such as favourable temperatures and other climatic conditions that allow the build-up of a large source population in the overwintering area (Williams, 1970; Sparks et al., 2005; Stefanescu et al., 2013). If the migratory species observed at Gibraltar are making crossings from Africa then this would imply that Lepidopteran population dynamics are influenced by transcontinental climatic patterns (Williams, 1970), but although migratory species of butterfly are sometimes observed arriving from the sea at Gibraltar (C. Perez & K. Bensusan, pers. obs.), this remains to be demonstrated using standardised methods.

The sometimes very high abundance of migratory butterflies at the study site suggests that Windmill Hill Flats could be an important site for the study of migratory butterflies. Although butterflies are capable of making long sea-crossings during their migratory movements (e.g., Gibbs, 1969), Monarchs at least have been shown to favour stopover sites during their migrations (Meitner et al., 2004) and it is sensible to assume that refuelling is important to successful migration. The stopover ecology of butterflies other than Monarchs (Davis & Garland, 2004; Brower et al., 2006; McCord & Davis, 2010, 2012; Davis et al., 2012) has not received much attention so far, but as with birds, we should assume that proper conservation practice should take into account not only wintering and breeding grounds, but also important habitats along the migratory route (Meitner et al., 2004; McCord & Davis, 2012). The relative importance of Windmill Hill Flats to migratory butterflies remains to be assessed at a local and regional scale, but the site is already listed as part of a larger Special Area of Conservation (SAC) under the EU Habitats Directive and is managed as an MOD Conservation Area, with an ecological management plan in place. Such measures are especially important in places like Gibraltar, where responsibilities towards migratory fauna compete with urbanisation and strong land-use pressures.

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APPENDIX 1. List of Butterflies (Lepidoptera: Rhopalocera) occurring regularly in Gibraltar since 2000.

Hesperidae: Carcharodus tripolinus, Muschampia proto.

- Papilionidae: Iphiclides podalirius ssp. feisthamelii, Papilio machaon ssp. hispanicus, Zerynthia rumina ssp. rumina.
- Pieridae: Anthocharis belia ssp. euphenoides, Colias croceus, Colotis evagore ssp. nouna, Euchloe belemia, Euchloe tagis, Gonopteryx cleopatra ssp. cleopatra, Pieris brassicae, Pieris rapae, Pontia daplidice.
- Nymphalidae: Charaxes jasius ssp. septentrionalis, Danaus plexippus, Hipparchia fidia ssp. fidia, Lasiommata megera, Pararge aegeria, Pyronia cecilia ssp. cecilia, Pyronia bathseba, Vanessa atalanta, Vanessa cardui.
- Lycaenidae: Aricia cramera, Cacyreus marshalli, Celastrina argiolus ssp. argiolus, Lampides boeticus, Leptotes pirithous, Lycaena phlaeas ssp. phlaeas, Polyommatus icarus ssp. icarus, Satyrium spini, Tomares ballus.