

Feeding on migratory butterflies: opportunistic observations of birds preying on the Painted Lady *Vanessa cardui*

Constantí Stefanescu¹

Many butterfly species are often seen with severe wing damage, which is regarded as evidence of unsuccessful predation, most likely by insectivorous birds. However, observations of bird predation are rare for the vast majority of butterflies. During a long-term study of the ecology of the Painted Lady *Vanessa cardui*, a common migratory butterfly, a high frequency of wing damage was noted, especially in North African populations. Attacks by several bird species were confirmed during fieldwork which, along with a number of published and unpublished records from ornithological colleagues, are reported in this note. Twenty-four bird species have been recorded preying on the Painted Lady in the Palaearctic-Afrotropical region. Records from eight additional species from the Nearctic region were obtained from photographs and from the literature. With 16 families (13 passerines and three non-passerines), this bird community embraces a notable diversity of morphologies and prey-capture techniques. The most represented families were the Tyrannidae, the Sylviidae and the Turdidae while the species most frequently recorded as predators were European Bee-eater *Merops apiaster*, Blue-checked Bee-eater *Merops persicus*, White-crowned Wheater *Oenanthe leucopyga*, and Cattle Egret *Bubulcus ibis*. Most observations occurred in March–April and October when the Painted Lady migrates in large numbers, suggesting that a sudden increase in abundance may lead to a regular use of this resource by predators. Moreover, unsuccessful attacks are common, which suggests that butterflies may quite often escape with some form of wing damage. The consequences these interactions have on butterfly populations are speculative but deserve further study.

Key words: bird predation, migratory butterfly, temporal specialization, Morocco, Spain

¹ Natural Sciences Museum of Granollers, c/ Francesc Macià, 51, 08402 Granollers, Spain.
E-mail: cstefanescu@mcng.cat

Received: 09.12.23; Accepted: 29.12.23 / Edited by S. Mañosa

Many species of butterflies are often seen with what appear to be the impressions of beak marks on their wings, which many authors regard as evidence of unsuccessful bird attacks (e.g. Carpenter 1941, Shapiro 1974, Wourms & Wasserman 1985, Molleman *et al.* 2020). However, although the butterflies that manage to survive by birds do present this type of marks (Burger & Gochfeld 2001), direct observations of bird predation are rare for the vast majority of butterfly species, especially in the temperate region (Carpenter 1935, Bengtson 1981). The paucity of such observations has puzzled some authors, even though occasional episodes of intensive predation by birds apparently specialising on butterflies do exist (e.g. Blue Tits *Parus caeruleus*

preying on the Small Tortoiseshell *Aglais urticae* in an English garden, Warren 2021). In the Neotropics, on the other hand, bird predation on butterflies is a well-known phenomenon that has been the subject of much research (e.g. Chai 1986, Srygley & Dudley 1993, Langham 2004). Indeed, jacamars (family Galbulidae) specialise in hunting butterflies and have even been suggested to act as a strong selective agent for mimicry in Neotropical butterflies (Mallet & Barton 1989). Albeit more generalists, flycatchers (family Tyrannidae) also regularly feed on Neotropical butterflies (Pinheiro 1996) and could also play a crucial role in the evolution of aposematism and mimicry in these insects (Pinheiro 2011).

A recent survey of wing damage the Painted Lady butterfly *Vanessa cardui* along a latitudinal gradient from Spain to Senegal showed that about 50% of over 2,200 collected butterflies had lost more than 1% of their wing surface (Stefanescu *et al.* in prep.). Wing marks strongly suggested that this migratory insect was frequently targeted by birds (Fig. 1), especially in Africa, where wing damage was significantly higher than in Spain. This possibility was confirmed by field observations of successful and unsuccessful bird attacks in Morocco, where we are currently conducting long-term research into the ecology of this butterfly (e.g. Stefanescu *et al.* 2011, 2017).

To expand the range of documented interactions between birds and the Painted Lady we searched the literature and contacted ornithologists for further observations. This note collates all this information and shows that bird predation on the Painted Lady is probably a common phenomenon, which can result in butterfly wing damage when unsuccessful. The importance of common migratory butterflies as a temporally abundant resource on which birds may specialise is also discussed.

Material and methods

The Painted Lady is a multi-generational migratory insect that regularly performs long-range movements throughout its almost cosmopolitan distribution range (Stefanescu *et al.* 2013). In the Western Palaearctic-Afrotropical system,

Painted Lady populations move from tropical regions south of the Sahara in winter to European Nordic countries in the peak of summer (Stefanescu *et al.* 2013, Talavera *et al.* 2023). The Maghreb region of North Africa and the northern Mediterranean region are critical breeding areas both in spring and autumn. Moreover, recent surveys indicate that the Maghreb also regularly harbours a Painted Lady population in winter (C. Stefanescu, pers. obs.).

Between 2009 and 2023, systematic fieldwork studying the migratory ecology of the Painted Lady was conducted in Morocco. A large number of transects and timed counts covered a high diversity of habitats and periods (each month from September to May) across the whole country and gave rise to opportunistic observations of bird predation on this butterfly. Additional records were provided by ornithologists working in Catalonia and the Balearic Islands (N Spain).

To gather more data, in summer 2023 ornithologists working primarily on bird migration in both the eastern and western Mediterranean were contacted and asked for observations and pictures of birds preying on Painted Ladies. In this way, new records were made available, mainly by Nir Sapir (University of Haifa) and his network of collaborators in Israel. Further records were obtained by checking photos on the website <https://spain.inaturalist.org/projects/mariposas-y-aves-butterflies-and-birds>, which includes pictures from North America, where the Painted Lady is also present.



Figure 1. Wing damage in two Painted Ladies collected in Morocco in October 2019 and 2017, respectively. In both cases, the symmetrical wing damage is indicative of attacks on resting butterflies with closed wings, presumably by a bird. Photos: Marta Torrent.

Danys a les ales de dues migradores dels cards recollides al Marroc l'octubre de 2019 i 2017, respectivament. En ambdós casos, els danys simètrics de les ales són indicatius d'atacs a papallones en repòs amb les ales tancades, presumiblement per part d'un ocell. Fotos: Marta Torrent.



Figure 2. Successful predation of Painted Ladies by (a) *Merops cyanophrys*, Israel, March 2023; (b) *Onychognathus tristramii*, Israel, April 2019; (c) *Curruca nana*, Israel, March 2013; and (d) *Ammomanes deserti*, Israel, March 2019. Pictures: E. Golan (a), M.J. Pearson (b), Y. Perlman (c), F. Trabalon (d).
Predació amb èxit de migradores dels cards per (a) Merops cyanophrys, Israel, març de 2023, (b) Onychognathus tristramii, Israel, abril de 2019, (c) Curruca nana, Israel, març de 2013, i (d) Ammomanes deserti, Israel, març de 2019 Imatges: E. Golan (a), M.J. Pearson (b), Y. Perlman (c), F. Trabalon (d).

Results

Twenty-four bird species were recorded preying (successfully or unsuccessfully) on the Painted Lady in the Palaearctic-Afrotropical region (Table 1; Fig. 2). Data from 23 species came from our own and other ornithologists' field work, while a further species, the Red-backed Shrike, *Lanius collurio*, was added based on a picture found on the *inaturalist* website of a bird holding a Painted Lady in its beak in Russia. Records from eight additional species from the Nearctic region were obtained from pictures and from the literature (Table 1).

The diversity of the bird community preying on the Painted Lady was notably high (species from 16 families, 13 passerines and three non-passerines). The Tyrannidae, with five species, and the Sylviidae and the Turdidae with four species each, were the families with most species preying on Painted Ladies, followed by

the Meropidae and the Hirundinidae, with three species each. At species level, the birds most frequently recorded as predators were European Bee-eater *Merops apiaster* (five observations), Blue-cheeked Bee-eater *Merops persicus* (three observations), White-crowned Wheatear *Oenanthe leucopyga* (three observations) and Cattle Egret *Bubulcus ibis* (three observations).

Records from the Palaearctic were concentrated primarily in March (43% of records), and then in October (26%). Only 11% of records were obtained in summer and none in winter.

Discussion

Up to 32 species of birds were recorded preying on Painted Ladies in the Palaearctic and Nearctic regions. This number is undoubtedly an important underestimation of the actual number of predators given the intrinsic difficulty of

Table 1. Confirmed observations of attacks on Painted Ladies by birds. See text for more details. *Observacions confirmades d'atacs d'ocells a la migradora dels cards. Per a més detalls, vegeu el text.*

Species	Family	Region	Date	Source	Observations
<i>Acrocephalus arundinaceus</i>	Sylviidae	The Netherlands	June 2019	Y. Verkuil	From DNA metabarcoding of faecal sample.
<i>Acrocephalus arundinaceus</i>	Sylviidae	Israel	March 2023	S. Blitzblau	
<i>Alaemon alaudipes</i>	Alaudidae	Morocco	March 2016	C. Oliver	
<i>Ammomanes deserti</i>	Alaudidae	Israel	March 2019	F. Trabalon	Photograph available (Fig. 2).
<i>Bubulcus ibis</i>	Ardeidae	Morocco	October 2019	CS pers. obs.	Successful and unsuccessful attacks on nectaring butterflies.
<i>Bubulcus ibis</i>	Ardeidae	N Spain	May 2009	ICO	Wing remains in pellets.
<i>Bubulcus ibis</i>	Ardeidae	Israel	March 2023	I. Darob	Photograph available.
<i>Eriothacus rubecula</i>	Turdidae	N Spain	October 2012	CS pers. obs.	On a damaged adult.
<i>Cecropis daurica</i>	Hirundinidae	Morocco	March 2009	Stefanescu <i>et al.</i> (2011)	Predation at an emergence site.
<i>Hirundo rustica</i>	Hirundinidae	Morocco	March 2009	Stefanescu <i>et al.</i> (2011)	Predation at an emergence site.
<i>Lanius collurio</i>	Laniidae	Unknown	June 2019	internet photograph	
<i>Lanius nubicus</i>	Laniidae	Israel	March 2023	A. Goldstein	Photograph available.
<i>Merops apiaster</i>	Meropidae	N Spain	May 1995	J. Martí	Frequent attacks by birds in a breeding colony.
<i>Merops apiaster</i>	Meropidae	N Spain	July 1996	R. Aymí	Frequent attacks by birds in a breeding colony.
<i>Merops apiaster</i>	Meropidae	Italy	May 2021	internet photograph	
<i>Merops apiaster</i>	Meropidae	Russia	July 2020	internet photograph	
<i>Merops apiaster</i>	Meropidae	N Spain	April 1988	Larsen (1989)	Several attacks by a bird on butterflies landing on a ship.
<i>Merops cyanophrys</i>	Meropidae	Israel	March 2023	E. Golan	Photograph available (Fig. 2).
<i>Merops persicus</i>	Meropidae	Morocco	October 2019	CS pers. obs.	Attacks from a perch on an electric wire.
<i>Merops persicus</i>	Meropidae	Morocco	March 2022	M. Illa	
<i>Merops persicus</i>	Meropidae	Turkey	Unknown	Fry & Kirwan (2020)	Temporal specialisation by birds in a breeding colony.
<i>Motacilla alba</i>	Motacillidae	Morocco	March 2009	CS pers. obs.	Preying on butterflies killed by cars.
<i>Muscicapa striata</i>	Muscicapidae	N Spain	April 2002	Stefanescu & Julià (2002)	Successful and unsuccessful attacks on Illa de l'Aire.
<i>Muscicapa striata</i>	Muscicapidae	N Spain	April 2022	R. Matesanz	
<i>Cercomela melanura</i>	Turdidae	Israel	March 2019	F. Trabalon	
<i>Oenanthe hispanica</i>	Turdidae	Israel	March 2023	Y. Shamir	Photograph available.
<i>Oenanthe leucopyga</i>	Turdidae	Morocco	October 2009	CS pers. obs.	Predation of a flying butterfly.
<i>Oenanthe leucopyga</i>	Turdidae	Morocco	October 2015	CS pers. obs.	Predation of a flying butterfly.
<i>Oenanthe leucopyga</i>	Turdidae	Morocco	October 2019	CS pers. obs.	Predation of a flying butterfly.
<i>Onychognathus tristramii</i>	Sturnidae	Israel	April 2019	M.J. Pearson	Photograph available (Fig. 2).
<i>Passer domesticus</i>	Passeridae	Morocco	March 2009	CS pers. obs.	Preying on butterflies killed by cars.
<i>Ptyonoprogne obsoleta</i>	Hirundinidae	Morocco	October 2019	J. Mauri	Unsuccessful attacks of hill-topping males.
<i>Pycnonotus barbatus</i>	Pycnonotidae	Morocco	October 2019	CS pers. obs.	Successful attack on a nectaring butterfly.
<i>Sylvia atricapilla</i>	Sylviidae	Israel	March 2023	E. Amir	Video available.
<i>Curruca melanocephala</i>	Sylviidae	S Spain	October 2022	M Cuadrado	Several unsuccessful attacks.
<i>Curruca nana</i>	Sylviidae	Israel	March 2013	Y. Perlman	Photograph available (Fig. 2).
<i>Aphelocoma californica</i>	Corviidae	USA		internet photograph	
<i>Contopus sordidulus</i>	Tyrannidae	USA		internet photograph	
<i>Melospiza melodia</i>	Emberizidae	USA		Knowlton (1953)	
<i>Myiarchus crinitus</i>	Tyrannidae	Canada		internet photograph	
<i>Sayornis phoebe</i>	Tyrannidae	USA		internet photograph	
<i>Sayornis saya</i>	Tyrannidae	USA		internet photograph	
<i>Sayornis nigricans</i>	Tyrannidae	USA		internet photograph	
<i>Trogon mexicanus</i>	Trogonidae	Mexico		internet photograph	

making this kind of observation and the lack of intensive field work matching that carried out in Morocco and Spain performed in the other regions of the world where this butterfly occurs.

The species in Table 1 exemplify the diversity of morphologies and prey-capture techniques. Amongst the most frequent predators are species belonging to unrelated families that specialise in catching insects in flight (e.g. New World and Old World flycatchers, bee-eaters, swallows and martins). Flycatchers typically use the search-and-sally technique, which involves sitting on a perch from where the prey are located and then attacking by aerial hawking. In a classical spring migration stopover site on the small Illa de l'Aire, off Menorca, for example, three Spotted Flycatchers *Muscicapa striata* were seen preying on Painted Ladies from perches on low *Tamarix* trees (Stefanescu & Julià 2002). Bee-eaters have also been seen frequently capturing Painted Ladies on the wing. A remarkable example of an interaction between co-migrants was reported by Larsen (1989), who saw a single European Bee-eater repeatedly preying on a large group of Painted Ladies that had landed on a ship off Cape Finisterre during spring migration. But more often, records come from breeding colonies, where birds temporally use this resource when the butterfly is common (e.g. Stefanescu & Julià 2002, Fry & Kirwan 2020). The same occurred with Barn Swallows *Hirundo rustica* in a patch in southern Morocco where butterflies were emerging in large numbers in March 2009 (Stefanescu *et al.* 2011). In that occasion, birds from a nearby breeding colony were attracted by the butterfly swarm and were seen capturing the insects on the wing but also picking them off the vegetation. Another bird that captures Painted Ladies by aerial hawking is the White-crowned Wheater *Oenanthe leucopyga* (Table 1). Together with other wheatears co-occurring in the arid landscapes of S Morocco (e.g. Black Wheater *Oenanthe leucura*, Mourning Wheater *O. lugens* and Desert Wheater *O. deserti*), they represent a community of regular predators on the Painted Lady, especially in autumn, when the butterfly can be exceedingly common (Stefanescu *et al.* 2017).

More unusual sightings of Painted Lady predation involve birds grabbing butterflies while they are perched on the ground or feeding on flowers. A Common Bulbul *Pycnonotus barbatus*,

for instance, was seen catching a butterfly in a field of orange trees in the Souss valley, Morocco, where Painted Ladies had concentrated on the flowers of *Verbesina encelioides*, a favourite nectar resource. On another occasion, a Common Bulbul was seen stalking insects, including Painted Ladies, on a blooming carob tree in southern Morocco. Although no attack was ultimately recorded that time, the behaviour displayed by this bird strongly suggested that Painted Ladies could have been among its potential prey.

Also remarkable is the observation of a Cattle Egret catching Painted Ladies nectaring on a yellow Brassicaceae in a humid meadow in central Morocco. The bird slowly walked among the flower patch, darting to catch butterflies when they were close enough. One successful and several failed attacks were recorded on that occasion. Two other records indicate that this bird consumes Painted Ladies relatively frequently. Especially interesting was the finding of wing remains of this butterfly in pellets in the heronry in the Zoo of Barcelona (ICO, com. pers.) in May 2009. This was the year that Painted Ladies migrated in vast numbers into the Mediterranean region (Stefanescu *et al.* 2011). Similarly, in October 2022, when Painted Ladies were very common in a coastal area of southern Spain, Sardinian Warblers *Currucula melanocephala* were seen attacking Painted Ladies repeatedly but unsuccessfully (M. Cuadrado, com. pers.).

Another hunting technique used by House Sparrows *Passer domesticus* and White Wagtails *Motacilla alba* is to patrol along busy roads where migrating Painted Ladies are frequently hit by cars. Then the birds (mainly seen foraging in pairs) easily capture the dead or injured butterflies.

Many of the examples described above suggest that Painted Ladies are an important temporary resource for birds when this butterfly is abundant, for instance during migratory periods in March–April and October (80% of the records in Table 1). The importance of insect migrations (including butterflies and moths) as resource pulses leading to their use by a variety of predators has been previously noted by several authors (Larsen 1992, Dudley *et al.* 2002, Satterfield *et al.* 2020, Hawkes *et al.* 2022) and is probably well exemplified by the Painted Lady, as our current and previous data suggest (see Stefanescu & Páramo (2010) for an example

of temporary specialisation by the Saharan frog *Pelophylax saharicus* on Painted Ladies in the Moroccan Anti-Atlas).

When migrants become very common, it is thus to be expected that birds other than those in Table 1 will prey on Painted Ladies. Amongst other likely predators are two common migratory species, the Hobby *Falco subbuteo* and the Common Swift *Apus apus*, that have been recorded preying on two closely related butterflies, the Red Admiral *Vanessa atalanta* and the Small Tortoiseshell *Aglais urticae*. A Hobby was observed during an hour by M. Friberg (com. pers.) catching over 60 Red Admirals in Klagshamn south of Malmö, Sweden, in October 2017. Butterflies were migrating southwards at canopy height, which allowed the falcon to attack and catch them; it would then eat the thorax and abdomen but let the wings and head go. Then, the falcon would ascend a few meters to regain its bearings and single out another butterfly to attack. Common Swifts could also be regular predators in the airspace (N. Sapir, com. pers.), when they coincide in migration with the butterflies or when they concentrate for hunting near mountain ridges where butterflies are also common. For example, Common Swifts were seen successfully preying on Small Tortoiseshells on the summit of Mulhacen in the Sierra Nevada, Spain, in June 2017 (C. Stefanescu, pers. obs.).

Overall, our observations show that a wide variety of birds prey on the Painted Lady, especially when this butterfly migrates in large numbers and thus becomes a temporarily abundant resource. They also suggest that unsuccessful attacks are common, from which butterflies may escape but possibly quite often with some form of wing damage. The consequences these interactions may have on butterfly populations is speculative but deserve further study. We hope that this note will serve to increase interest in this phenomenon and, at the same time, encourage ornithologists to make similar observations known in the literature.

Acknowledgements

We are very grateful to the following colleagues for providing their observations on bird predation: Raül Aymí, Mariano Cuadrado, Magne Friberg, Marc Illa, Jordi Martí, Rosa Matesanz, Juli Mauri, Ferran Páramo, Carles Oliver and Fran Trabalón. Nir Sapir pro-

vided very valuable information through his contacts with ornithologists in Israel. Crinan Jarrett provided interesting bibliographical and unpublished information, and made insightful comments on the manuscript. José Luis Copete kindly confirmed the identification of Nearctic birds and provided valuable information on butterfly predation by birds. Andreu Ubach shared with me much of the field work in Morocco and always enthusiastically supports my work. Marta Torrent kindly took the pictures of Figure 1. This work was partially funded by Fundació Barcelona Zoo.

Resum

Alimentant-se de papallones migradores: observacions oportunistes d'ocells depredant la migradora dels cards *Vanessa cardui*

Moltes espècies de papallones mostren freqüentment les ales trencades, la qual cosa suggereix que han estat objecte d'atacs fallits, molt probablement per part d'ocells insectívors. Tanmateix, les observacions de depredació d'ocells són rares per a la gran majoria de papallones. Com a part d'un estudi a llarg termini sobre l'ecologia de la migradora dels cards *Vanessa cardui*, una papallona migratòria comuna, es va observar una alta freqüència d'exemplars amb trencadures a les ales, especialment a les poblacions nord-africanes. El treball de camp va permetre confirmar atacs de diverses espècies d'ocells que, juntament amb alguns registres publicats i inèdits de col·legues ornitòlegs, es detallen en aquesta nota. Es van registrar 24 espècies d'ocells depredant la migradora dels cards a la regió paleàrtica-afrotropical. Es van obtenir registres de vuit espècies addicionals de la regió neàrtica a partir de fotografies i de la literatura. Amb 16 famílies (13 pertanyents als passeriformes i 3 als no passeriformes), aquesta comunitat d'ocells inclou una notable diversitat de morfologies i tècniques de captura de preses. Les famílies més representades van ser els Tyrannidae, els Sylviidae i els Turdidae i les espècies registrades amb més freqüència com a depredadors van ser l'abellerol *Merops apiaster*, l'abellerol de Pèrsia *Merops persicus*, el còlit tuareg *Oenanthe leucopyga*, i l'esplugabous *Bubulcus ibis*. La majoria de les observacions es van produir al març-abril i octubre, coincidint amb les migracions de la migradora dels cards a les regions mostrejades, la qual cosa suggereix que un augment sobtat de l'abundància d'aquest insecte pot provocar un fenomen d'especialització temporal per part dels depredadors. A més, una freqüència relativament alta d'atacs sense èxit també suggereix que la papallona pot escapar sovint amb algun tipus de dany a les ales. Les conseqüències que aquestes interaccions poden tenir sobre les poblacions de la papallona segueixen sent especulatives i haurien de ser objecte de futurs estudis.

Resumen

Alimentándose de mariposas migradoras: observaciones oportunistas de aves depredando a la cardera *Vanessa cardui*

Muchas especies de mariposas muestran frecuentemente las alas dañadas, lo que sugiere que han sido objeto de ataques fallidos, muy probablemente por parte de aves insectívoras. Sin embargo, las observaciones de depredación de aves son raras para la gran mayoría de mariposas. Como parte de un estudio a largo plazo sobre la ecología de la cardera *Vanessa cardui*, una mariposa migratoria común, se observó una alta frecuencia de ejemplares con las alas dañadas, especialmente en las poblaciones norteafricanas. El trabajo de campo permitió confirmar ataques de diversas especies de aves que, junto a algunos registros publicados e inéditos de colegas ornitólogos, se detallan en esta nota. Se registraron 24 especies de aves depredando a la cardera en la región paleártico-afrotropical. Se obtuvieron registros de ocho especies adicionales de la región neártica a partir de fotografías y literatura. Con 16 familias (13 pertenecientes a los passeriformes y 3 a los no passeriformes), esta comunidad de aves incluye una notable diversidad de morfologías y técnicas de captura de presas. Las familias más representadas fueron los Tyrannidae, Sylviidae y Turdidae, y las especies registradas con mayor frecuencia como depredadores fueron el abejaruco *Merops apiaster*, el abejaruco de Persia *Merops persicus*, la collalba negra de Brehm *Oenanthe leucopyga*, y la garcilla bueyera *Bubulcus ibis*. La mayoría de las observaciones se produjeron en marzo-abril y octubre, coincidiendo con las migraciones de la cardera en las regiones muestreadas, lo que sugiere que un aumento repentino de la abundancia de este insecto puede provocar un fenómeno de especialización temporal por parte de los depredadores. Además, una frecuencia relativamente alta de ataques sin éxito también sugiere que la mariposa puede escapar a menudo con algún tipo de daño en las alas. Las consecuencias que estas interacciones pueden tener sobre las poblaciones de la mariposa siguen siendo especulativas y deberían ser objeto de estudios futuros.

References

Bengtson, S.-A. 1981. Does bird predation influence the spot-number variation in *Maniola jurtina* (Lepidoptera)? *Biol. J. Linn. Soc.* 15: 23–27.

Burger, J. & Gochfeld, M. 2001. Smooth-billed ani (*Crotophaga ani*) predation on butterflies in Mato Grosso, Brazil: risk decreases with increased group size. *Behav. Ecol. Sociobiol.* 49: 482–492.

Chai, P. 1986. Field observation and feeding experiments on the responses of rufous-tailed jacamars

(*Galbula ruficauda*) to free-flying butterflies in a tropical rainforest. *Biol. J. Linn. Soc.* 29: 161–189.

Carpenter, G.D.H. 1935. Attacks of birds upon butterflies. *Nature* 135: 194–195.

Carpenter, G.D.H. 1941. The relative frequency of beak marks on butterflies of different edibility to birds. *Proc. Zool. Soc. Lond. (A)* 111: 223–231.

Dudley, R., Srygley, R.B., Oliveira, E.G. & de Vries, P.J. 2002. Flight speeds, lipid reserves, and predation of the migratory neotropical moth *Urania fulgens* (Uraniidae). *Biotropica* 34: 452–458.

Fry, H. & Kirwan, G.M. 2020. Blue-cheeked Bee-eater (*Merops persicus*), version 1.0. In del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A. & de Juana, E. (eds): *Birds of the World*. Cornell Lab of Ornithology, Ithaca, NY, USA. <https://doi.org/10.2173/bow.bcbat1.01>

Hawkes, W.L.S., Walliker, E., Gao, B., Forster, O., Lacey, K., Doyle, T., Massy, R., Roberts, N.W., Reynolds, D.R., Özden, Ö., Chapman, J.W. & Wotton, K.R. 2022. Huge spring migrations of insects from the Middle East to Europe: quantifying the migratory assemblage and ecosystem services. *Ecography* 10: e06288.

Knowlton, G.F. 1953. Predators of *Vanessa cardui*. *Lepid. News* 7: 55.

Langham, G.M. 2004. Specialized avian predators repeatedly attack novel colour morphs of *Heliconius* butterflies. *Evolution* 58: 2783–2787.

Larsen, T.B. 1989. Painted Ladies (*Cynthia cardui*) eaten by a bee-eater aboard ship at sea. *Entomol. Rec. J. Var.* 101: 87.

Larsen, T.B. 1992. Temporary prey-specialization on migrant butterflies by bluecheeked bee-eaters. *Entomol. Rec. J. Var.* 104: 253–255.

Mallet, J. & Barton, N.H. 1989. Strong natural selection in a warning-color hybrid zone. *Evolution* 43: 421–431.

Molleman, F., Javois, J., Davis, R.B., Whitaker, M.R.L., Tammaru, T., Prinzing, A., Ounap, E., Wahlberg, N., Kodandaramiah, U., Aduse-Poku, K., Kaasik, A. & Carey, J.R. 2020. Quantifying the effects of species traits on predation risk in nature: A comparative study of butterfly wing damage. *J. Anim. Ecol.* 89: 716–729.

Pinheiro, C.E.G. 1996. Palatability and escaping ability in Neotropical butterflies: tests with wild kingbirds (*Tyrannus melancholicus*, Tyrannidae). *Biol. J. Linn. Soc.* 59: 351–365.

Pinheiro, C.E.G. 2011. On the evolution of warning coloration, Batesian and Müllerian mimicry in Neotropical butterflies: the role of jacamars (Galbulidae) and tyrant-flycatchers (Tyrannidae). *J. Avian Biol.* 42: 277–281.

Satterfield, D.A., Scott Sillett, T., Chapman, J.W., Altizer, S. & Marra, P.P. 2020. Seasonal insect migrations: massive, influential, and overlooked. *Front. Ecol. Environ.* DOI:10.1002/fee.2217

Shapiro, A.M. 1974. Beak-mark frequency as an index of seasonal predation intensity on common butterflies. *Amer. Nat.* 108: 229–232.

Srygley, R.B. & Dudley, R. 1993. Correlations of the position of center of body mass with butterfly escape tactics. *J. Exp. Biol.* 174: 155–166.

Stefanescu, C., Alarcón, M., Izquierdo, R., Páramo, F. & Ávila, A. 2011. Moroccan source areas of the Painted Lady butterfly *Vanessa cardui* (Nymph-

- halidae: Nymphalinae) migrating into Europe in spring. *J. Lepid. Soc.* 65: 15–26.
- Stefanescu, C. & Julià, L.** 2002. Adults de *Cynthia cardui* atacats per ocells insectívors, amb comentaris sobre la migració primaveral de ropalòcers a l'illa de l'Aire. *Butll. Soc. Cat. Lepid.* 87: 45–50.
- Stefanescu, C. & Páramo, F.** 2010. Frogs eat butterflies: temporary prey-specialization on the Painted Lady butterfly, *Vanessa cardui*, by Sahara frog, *Pelophylax saharicus*, in the Moroccan Anti Atlas. *Nota Lepid.* 33: 127–131.
- Stefanescu, C., Páramo, F., Åkesson, S., Alarcón, M., Ávila, A., Brereton, T., Carnicer, J., Cassar, L., Fox, R., Heliölä, J., Hill, J.K., Hirneisen, N. et al.** 2013. Multi-generational long-distance migration in insects: studying the painted lady butterfly in the Western Palaearctic. *Ecography* 36: 474–486.
- Stefanescu, C., Puig-Montserrat, X., Samraoui, B., Izquierdo, R., Ubach, A. & Arrizabalaga, A.** 2017. Back to Africa: autumn migration of the painted lady butterfly *Vanessa cardui* is timed to coincide with an increase in resource availability. *Ecol. Entom.* 42: 737–747.
- Talavera, G., García-Berro, A., Talla, V.N.K., Ng'iru, I., Bahleman, F., Kébé, K., Nzala, K.M., Plasencia, D., Marafi, M.A.J., Kassie, A. et al.** 2023. The Afrotropical breeding grounds of the Palearctic-African migratory painted lady butterflies (*Vanessa cardui*). *Proc. Nat. Acad. Sci., USA*, 120, e2218280120
- Warren, M.S.** 2021. *Butterflies. A Natural History.* British Wildlife Collection. London: Bloomsbury.
- Wourms, M. K. & Wasserman, F.E.** 1985. Bird predation on Lepidoptera and the reliability of beak-marks in determining predation pressure. *J. Lepid. Soc.* 39: 239–261.