

ORIGINAL ARTICLE

The frequency of wing damage in a migrating butterfly

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Abstract The ability to fly is crucial for migratory insects. Consequently, the accumulation of damage on the wings over time can affect survival, especially for species that travel long distances. We examined the frequency of irreversible wing damage in the migratory butterfly *Vanessa cardui* to explore the effect of wing structure on wing damage frequency, as well as the mechanisms that might mitigate wing damage. An exceptionally high migration rate driven by high precipitation levels in their larval habitats in the winter of 2018–2019 provided us with an excellent opportunity to collect data on the frequency of naturally occurring wing damage associated with long-distance flights. Digital images of 135 individuals of *V. cardui* were collected and analyzed in Germany. The results show that the hindwings experienced a greater frequency of damage than the forewings. Moreover, forewings experienced more severe damage on the lateral margin, whereas hindwings experienced more damage on the trailing margin. The frequency of wing margin damage was higher in the painted lady butterfly than in the migrating monarch butterfly and in the butterfly *Pontia occidentalis* following artificially induced wing collisions. The results of this study could be used in future comparative studies of patterns of wing damage in butterflies and other insects. Additional studies are needed to clarify whether the strategies for coping with wing damage differ between migratory and nonmigratory species.

Key words biomechanics; cost of migration; flight; Lepidoptera; *Vanessa cardui*; wing structure

Introduction

The evolution of powered flight has potentially driven the diversification of insects (Wilson, 1969) and provided them with many advantages, including mobility in threatening situations and for intra- and intersexual interactions, protection against predators and mechanical damage, and thermoregulatory benefits (Rudolf *et al.*, 2019). Insect wings are subject to continuous wear (Cartar, 1992; Rajabi *et al.*, 2020). Aside from collisions, another cause of wing damage in Lepidoptera is the

continuous friction against the wings' leading and trailing edges during downward movement (Wootton, 1992). *Vanessa cardui* (Linnaeus, 1758) is a migratory butterfly that is vulnerable to both collisions and friction between the leading and trailing edges of the wings, especially the latter. Further investigation is needed to characterize the relative importance of different sources of damage, their effect on flight performance, and strategies used to mitigate such damage during long-term migrations.

Nearly 600 species of butterflies are estimated to migrate (Chowdhury *et al.*, 2021). Butterfly migration varies greatly by continental region, geographic distribution, and family. Migratory species from the Papilionidae mainly occur in the Palearctic (23%), whereas members of the Nymphalidae, containing the painted lady, are most abundant in the Nearctic (15%). Migratory butterflies occur in all continents except Antarctica: 12%

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in both the Nearctic and Palearctic (corresponding to 24% in the Holarctic), approximately 5% in the Neotropics and Afrotropics combined, 7% in Australia, and approximately 8% in the Oriental region (Chowdhury *et al.*, 2021).

The seasonal trans-Saharan migration of animals between the Palearctic and tropical Africa across the 1500–2000 km wide Saharan Desert is a phenomenon predominantly associated with birds (Biebach, 1990). Traveling between temperate and tropical regions allows long-distance migrants to take advantage of seasonal peaks in resources in different geographical regions and avoid unfavorable climatic conditions. These migrations are not only carried out by birds but also by several insects, such as butterflies (Brower, 1961), some dragonflies (Wikelski *et al.*, 2006; Hobson *et al.*, 2021), and the painted lady butterfly *V. cardui* (Talavera *et al.*, 2018). *Vanessa cardui* makes perennial migrations in successive generations, predominantly in the northern hemisphere. They have a worldwide distribution, with the exception of parts of South America and Australia. *Vanessa cardui* thus has one of the most extensive ranges of any terrestrial animal known to make long-distance migrations (Talavera & Vila, 2017).

The environmental conditions in the Sahel zone are only temporarily suitable for *V. cardui* to engage in reproductive activities. The rate of reproduction of *V. cardui* is high shortly after periods of increased precipitation. However, subsequent generations of the painted lady can experience drought and unfavorable environmental conditions in the Sahel zone. As a result, subsequent generations migrate northward to locate sites with more favorable conditions (Stefanescu *et al.*, 2012, 2016). This migration continues northward until they reach northern Europe (Fig. 1) (Talavera & Vila, 2017). During autumn, they migrate southward from Europe back to tropical Africa (Talavera *et al.*, 2018). In autumn and winter, the painted lady is found in North Africa (Stefanescu *et al.*, 2007, 2016). The cycle starts again in the spring. The migration cycle of this species includes six generations and involves a latitudinal shift of thousands of kilometers (up to 60 degrees of latitude; Stefanescu *et al.*, 2013). This shift covers a distance of at least 4 000 km (Stefanescu *et al.*, 2016) up to 12 000 km (Dobronosov, 2019). According to Pollard *et al.* (1998), Stefanescu *et al.* (2013), and Talavera *et al.* (2018), *V. cardui* migrates up to approximately 15 000 km throughout its entire route, which occurs over at least 6–7 generations in six regions. During the migrations, the painted lady butterflies fly at a speed of 15–22 km/h (Williams, 1930; Abbott, 1951) and can travel up to 500 km per day (Nesbit *et al.*, 2009). Such travel distances are most likely reached in high-



Fig. 1 The spring migration routes of painted lady butterflies. *Vanessa cardui* migrates northward from the Sahara to the Maghreb up to northern Europe, where conditions are more favorable during the summer months. The migration cycle of the painted lady includes six generations and spans a distance of at least 4000 km. Wing damage accumulates during their migratory flights. An undamaged individual from North Africa is shown. An individual with wing damage from Kiel, Germany is also shown.

altitude flights with the help of air currents (Stefanescu *et al.*, 2016). During high-altitude gliding, relatively little wing damage is expected (Ford, 1945), but wing damage can have a major effect on gliding flight (Le Roy *et al.*, 2019b) in that reduced gliding capability results in more energetically costly flight (Dudley, 2002). High precipitation levels during the winter of 2018–2019 increased the abundance of resources in Saudi Arabia. This was an unusual event given that climate change has generally resulted in reductions in precipitation levels in Saudi Arabia (Eitze, 2017). Because of the high availability of resources, populations of caterpillars of the painted lady butterfly increased, and this resulted in a large migration of butterflies (Dobronosov, 2019). This unique

opportunity allowed us to characterize naturally accumulating wing damage in a long-distance migrating species.

Studies on insect wing damage have focused on both bee and dragonfly wing wear. For example, the rear distal area of the wings and the posterior proximal area of the hind wings are most susceptible to wear in the dragonfly *Sympetrum vulgatum* (Linnaeus, 1758) (Rajabi *et al.*, 2017a). Moreover, Rudolf *et al.* (2019) described four mechanisms for mitigating damage in dragonfly wings that might apply to other venous wings: crack deflection, termination, bifurcation, and bridging. In bees, wing area is typically lost at the wing's trailing edge, and this has also been observed in dragonflies (Higginson & Barnard, 2004; Buchwald & Dudley, 2010). Behavioral responses to wing area loss include increased flapping frequency and/or extended stroke amplitude (Roberts & Cartar, 2015). The responses to wing damage depend on several factors, including species identity, environmental conditions, season, and sex (Burkhard *et al.*, 2002).

Only a few studies have characterized butterfly wing damage (e.g., Leong *et al.*, 1993; Kingsolver, 1999; Fernández *et al.*, 2012; Le Roy *et al.*, 2019a,b). These studies have mainly been carried out in the laboratory or in the Nearctic Region. In the Nearctic region, samples of monarch butterflies have been collected at two Californian wintering sites, Pismo Beach State Park and Natural Bridges State Park, from October to March 1990–1991 (Leong *et al.*, 1993). A loss of wing area of approximately 2% was observed in monarch butterflies that migrate over long distances. Although the hind wings were damaged more frequently than the forewings, the extent of the missing wing area did not differ significantly (Roberts & Cartar, 2015). In the laboratory, previous studies have focused on behavioral response mechanisms to wing damage, such as increased wingbeat frequency (Kingsolver, 1999) and changes in flight behavior (Haas, 2005) rather than wing wear frequency. Unlike dragonflies and bees, butterflies have fewer cross-veins and different vein patterns (Combes & Daniel, 2003).

Few studies have examined the role of veins on wing wear in butterflies during long-term migration. Although energy efficiency and damage prevention are critically important for long-migrating insects, these factors, which affect wing shape evolution, have been scarcely investigated (Arnold, 1983; Le Roy *et al.*, 2019a,b). Given that thermal gliding is probably one of the main flight strategies employed during the long-distance migration of *V. cardui*, wing area loss is likely detrimental to the survival of these butterflies. Gliding flight is progressively replaced by flapping flight in damaged individuals of *Morpho* butterflies (Le Roy *et al.*, 2019b) because the

energetic costs of flight increase as wings become more damaged. Analyses of the location and frequency of wing damage provide insights into the selective pressures and evolution of wings in *V. cardui* and butterflies more generally. Because of their important roles as pollinators in ecosystems, especially for plant species with tube-like flowers, we characterized the frequency, location, shape, and size of the damaged areas on the wings of *V. cardui* using various imaging techniques. Specifically, we aimed to document the location and extent of wing damage on *V. cardui* individuals during the first arrival wave to Germany during their spring migration. Moreover, we compared the extent of damage between the fore- and hindwings and between the right and left wings. All wing damage recorded in our study was assumed to occur during their migration.

These data are crucial for understanding the effects of wing damage on flight performance during migration, the potential causes of wing damage, and the mechanisms by which the effects of wing damage are mitigated.

It is estimated that half of all lepidopteran species are declining worldwide (Chowdhury *et al.*, 2021), and hundreds of such declines might go undetected. The success of conservation efforts for migratory butterflies depends on a robust understanding of the biology of migratory species, including whether and why populations are declining. Studies of wing damage and its causes are thus critically important for the conservation of migratory butterfly species. For example, in North America, monarch butterfly populations are decreasing (80% over the last decade, Wagner *et al.*, 2021). The causes of the declines in migratory butterflies can be difficult to determine given that several factors likely contribute to observed declines. In the case of the monarch butterfly, the threats to its wintering grounds in Mexico have received much attention, but threats to its breeding range and migration have received less attention by comparison (Malcolm, 2018; Chowdhury *et al.*, 2021, 2022). The presence or absence of food plants controls butterfly diversity and abundance, and landscape-scale declines in host plants can have tremendous impacts on migrants, including the loss of larval food plants, such as *Asclepias* spp. (Reppert & de Roode, 2018) and nectar resources (Stenoien *et al.*, 2018; Freedman *et al.*, 2020; Zylstra *et al.*, 2021). Nectar plant availability also depends on rainfall; consequently, drought affects nectar availability for migratory butterflies, such as monarch butterflies (Wagner *et al.*, 2021). Butterflies are sensitive to environmental factors, and even small changes in the environment can lead to rapid population declines. Climate change is likely to lead to changes in moisture and

temperature and thus disrupt migration patterns (Chowdhury *et al.*, 2021; Zylstra *et al.*, 2021). In addition, habitat loss due to urbanization and agricultural expansion reduces the availability of resting sites (Chowdhury *et al.*, 2017). Unlike monarchs, however, the painted lady is not declining in Europe (Fox *et al.*, 2015).

Materials and methods

To characterize patterns of wing damage in *V. cardui*, digital images of *V. cardui* were obtained. Photos of butterflies were taken *in situ* all over Germany during the beginning of the migration season in 2019 when the butterflies recently arrived in Northern Germany. The animals were recorded only at the beginning of the arrival period when large numbers of *V. cardui* butterflies were observed reaching Northern Germany. We thus sampled one distinct migratory wave, which would minimize the likelihood of sampling individuals that had experienced various migration conditions, such as damage during foraging or the sampling of individuals from subsequent generations in Germany. The images were accumulated by various volunteers from all over Germany via the “Helmholtz Centre for Environmental Research” from the German Butterfly Monitoring project (see Acknowledgments). We recorded an additional 43 individuals in Kiel, Botanical Garden (54°20′49.4″N, 10°07′03.5″E) and in Kronshagen, Domänental (54°19′47.7″N 10°04′02.5″E), when the first individuals arrived. A total of 484 wing samples from 135 individuals were gathered, and each wing was analyzed separately. A wing was only selected and considered for the analysis if the wing area was visible and if the orientation of the wing permitted measurements of wing damage. Wings that were oriented in a way that did not allow a proper estimation of wing area loss were not analyzed. The butterflies were recorded during their migration from south to north shortly after their arrival to ensure that they had traveled a considerable distance before measurements were taken. Hence, the samples were not newly pupated or hatched nor did they originate from Scandinavia; the wing damage that we document thus stems from the migratory event that had just occurred. If any part of a wing was covered, it was considered undamaged. If there were cracks and only part of the wing membrane was still attached to the whole wing, the whole section of the wing was considered missing.

After selecting a reference image, it was then scaled and traced with the vector drawing program Inkscape v. 0.92 (Inkscape Community, <https://inkscape.org>) (length

of the front wing, 9.974 mm; width of the front wing, 13.315 mm; length of the hind wing, 44.191 mm; width of the hind wing, 76.935 mm). This was done separately for the forewing and hindwing. All instances of wing damage were then manually drawn into the reference image either by overlaying an intact wing image on the damaged samples or, if this was not possible, by estimating the extent of damage (see Fig. S1). Lastly, the frequency of damage in different wing regions was calculated using MATLAB (R2012a, Mathworks, Natick, MA, USA). Using the image processing software ImageJ v.1.5i (National Institutes of Health, Bethesda, MD), the area of the damaged wing parts was marked and measured as a fraction of the total wing area. A custom Matlab script employing the boundary extraction method from Eshghi *et al.* (2020) and the method for failure calculation in Rajabi *et al.* (2017a,b) was used to measure the frequency of wing failure in this study. All marked images were imported into the Matlab code, and the frequency and location of failure in each wing were automatically extracted. Mapping the extracted information generated a matrix corresponding to the amount of loss in specific wing areas. All four wings were analyzed separately. The measured values were graphically summarized by plotting the data (Fig. 3), and the damaged areas of the right and left wings and the fore and hind wings were compared. The statistical significance of differences in the extent of wing damage on the different wings was determined using the software SigmaPlot v. 14.0 (Systat Software, Inc., San Jose California USA). Because the data were not paired nor normally distributed, a Mann–Whitney *U* test was conducted.

Results and discussion

Based on our examination of the wings of *V. cardui*, 81% of the observed forewings and 88% of the observed hindwings had some damage; damage was observed on 73% and 77% of the left fore- and hindwings and on 76% and 81% of the right fore- and hindwings, respectively. The extent of damage observed was drastic in some cases (Fig. 1). However, butterflies with such damaged wings were still capable of flight.

Types of wing damage

Figure 2 illustrates the different types of wing damage observed. Holes (Fig. 2B), cracks (Fig. 2C), a mix of cracks and area loss (Fig. 2E), loss of area (Fig. 2F, D), and damaged setal structures on the wing margins

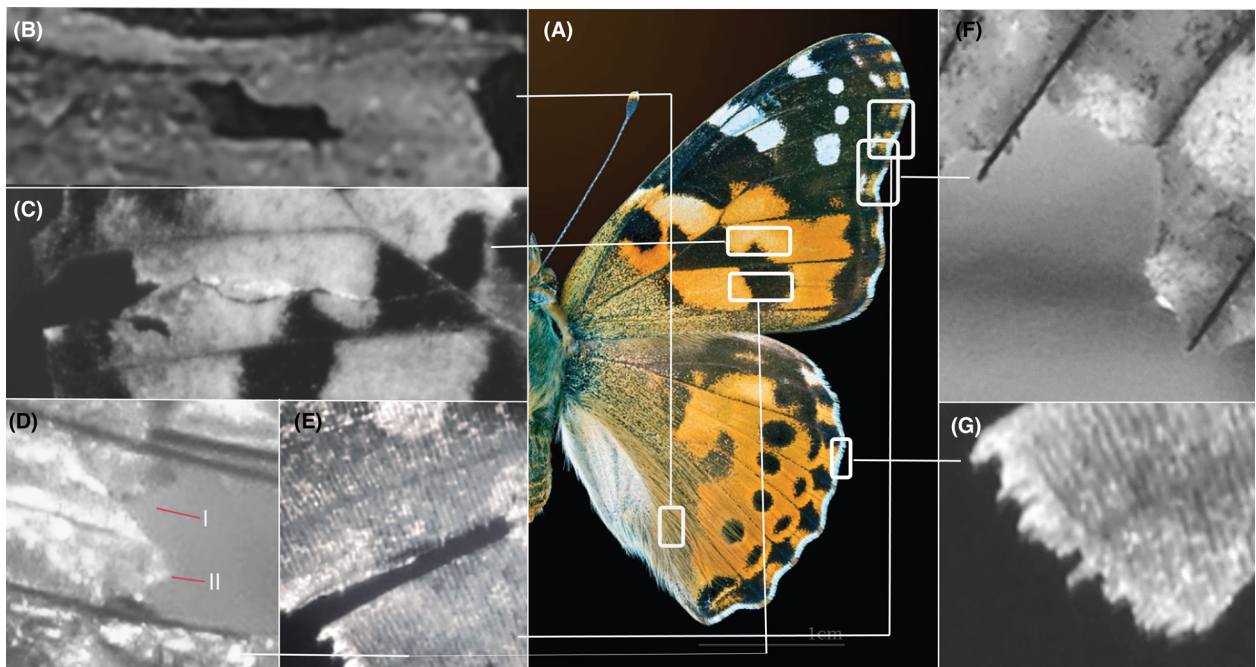


Fig. 2 Different wing damage types. (A) Reference and site map (Descouens, 2015, subject to CC BY license); (B) hole; (C) crack; (D) (I) concave area loss and (II) convex area loss; (E) cracks and area loss; (F) area loss; (G) damaged hairs of the trailing edge.

(Fig. 2G) were all observed. Some of these types of damage have also been documented in other insects. For example, area loss has been observed in dragonflies, bees, and yellow dung flies (Burkhard *et al.*, 2002). Bees also show flaps, valleys, and holes (Roberts & Cartar, 2015). In our *V. cardui*, we expected to see cracks such as those in dragonflies (Rudolf *et al.*, 2019). However, we did not observe tears and notches in the painted lady butterflies as has been observed in yellow dung flies (Burkhard *et al.*, 2002).

Butterfly wings have almost no transverse veins and many longitudinal veins, which confers more flexibility and results in reduced energy requirements because of reduced stiffness (Wootton, 1992). Missing transverse veins in the butterfly wings potentially increase the risk of damage at the edges (Fig. 3).

Frequency of damage at the wing margins

Depending on the location of the damage, the frequency of area loss was highest at the lateral wing edge, with approximately 35%–40% loss (Fig. 3). In addition, for all wings, the margin is followed by a damaged band running along the margin, and this type of damage was observed at a frequency of 15%–25%. The frequency of

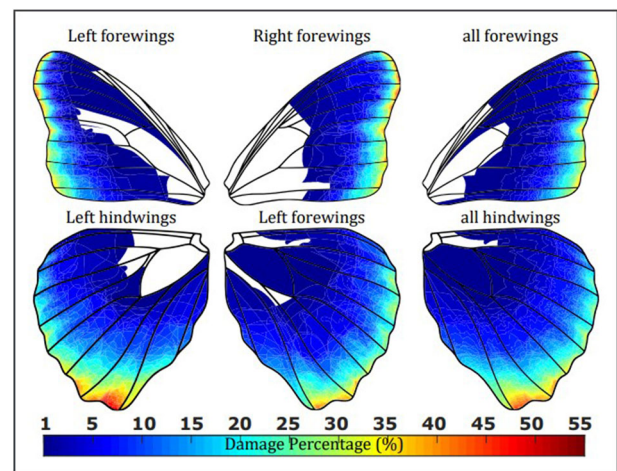


Fig. 3 Frequency of damage in the forewing and hindwing of the butterfly *V. cardui*. The base is the only area that was never damaged in the forewings and hindwings. The frequency of damage increases toward the periphery. Damage is most prominent on the distal trailing margin of the hindwings and the lateral margin of the forewings. No significant difference was observed between the right and left wings. The color code indicates the percentage of observations in which the particular area was lost. Warmer colors indicate a higher frequency of area loss. White colors indicate regions that were not lost in any individuals.

area loss decreases proximally. The wing margin of butterflies lacks transverse veining, which makes the wings flexible toward the margins, but this also makes them more vulnerable to damage. By contrast, because of the simultaneous movement of the fore- and hindwings during flapping (Ma *et al.*, 2021), the trailing margin of the forewings and the upper margin of the hindwings are not vulnerable to collisions with obstacles (Le Roy *et al.*, 2019b).

Damage at the wing base

The white areas in Figure 3 are the most proximal cells of the wings, which were not affected by wing failure. Interestingly, these areas are isolated from the remaining wing areas through transverse veins. Such transverse veins were found to impede crack propagation in locusts (Dirks & Taylor, 2012; Rajabi *et al.*, 2015, 2017b) and dragonfly wings (Rudolf *et al.*, 2019; Rajabi *et al.*, 2020), and they potentially protect crucial parts of the wing. Less than 5% of the wing bases connected to the axillary sclerites were damaged, and these structures play a key role in insect flapping (Wootton, 1992). However, insects with area loss at the wing base might have a reduced chance of survival and hence were not observed. Studies of naturally occurring wing damage are potentially biased, given that individuals with substantial wing damage do not survive and are hence removed from the pool of surviving individuals. Nevertheless, the observed individuals of *V. cardui* with major damage might indicate the minimum intact wing area necessary for survival (see Fig. 3), given that butterflies with such substantial damage were still able to continue their migration. According to Wald (1943), who examined the distribution of damage on planes that survived enemy fire in war, observations of damage-free areas can be informative for identifying the areas most critically affected by damage. That is, the areas showing no damage in our observations are likely essential areas that, if lost, have the largest effect on the survival of butterflies. In the painted lady, damage was more frequent on the margins of the wings, and the frequency of damage on the center of the wing base was low (Fig. 3). This suggests that individuals with damage on the base of the wing do not survive and were consequently not observed. In a study of artificially induced wing damage in captive *Morpho* butterflies (Le Roy *et al.*, 2019b), damage to these vital parts was less frequent than that observed in painted lady butterflies in our study. The frequency of damage derived from artificial environments is not as high as that observed in the field; consequently, such studies do not provide useful insights into the fre-

quency of major wing damage in butterflies. Wing area loss has been shown to increase the energetic cost of migration, because gliding efficiency is reduced as a result of changes in flight behavior (Le Roy *et al.*, 2019b). Subsequent observations of flight performance of artificially induced wing damage in *V. cardui* would help evaluate the effects of wing damage on their migration.

Wing damage comparisons

There was no significant difference in wing loss between the right and left forewings (Mann–Whitney *U* test, $U = 8319.500$, $n_1 = 91$, $n_2 = 92$, $P = 0.883$) nor between the right and left hindwings (Mann–Whitney *U* test, $U = 9201$, $n_1 = 92$, $n_2 = 97$, $P = 0.219$). However, there was a significant difference in wing loss between hindwings and forewing (Mann–Whitney *U* test, $U = 10226.5$, $n_1 = 110$, $n_2 = 115$, $P < 0.001$). Hindwings show greater wing damage than forewings. The forewings cover the hindwings to some extent; therefore, the hindwings are protected by the forewings. Butterflies are capable of flying without hindwings. However, hindwings are essential for evasive flight (Jantzen & Eisner, 2008). Because of their high visibility, evasive flight is important for the survival of butterflies. During flight, the hindwings point downward; they are therefore highly vulnerable during collisions. This might explain the higher frequency of damage on hindwings compared with that on forewings.

Causes of wing damage

Most damage is likely associated with low-altitude flights or periods of rest rather than long-range gliding because the wings are more vulnerable to colliding with vegetation at roosting or feeding sites or experiencing damage from predators when engaging in such activities. According to Ford (1945), the extent of wing damage is not necessarily correlated with travel distance, given that no damage occurs during gliding. Similar observations have been made in bumblebees, where wing damage is not always correlated with wing use (Foster & Cartar, 2011). Therefore, the damage observed on the wings of painted lady butterflies in our study most likely reflects the accumulation of damage while roosting and nectaring during migration. During such periods, the risk of damage from both predation and intraspecific interactions is likely increased. If males establish temporary territories (Cuadrado, 2021), they might experience increased damage associated with territorial encounters. This could lead to increases in hindwing damage, which, in yellow

dung flies, is related to temporal variation in territorial behavior (Burkhard *et al.*, 2002). Females might also experience increased hindwing damage because of collisions associated with oviposition. Additional studies are needed to characterize differences in wing damage between male and female painted lady butterflies. There is also a need to assess the extent of symmetry in wing damage; symmetrical wing damage is often observed in butterflies that use distastefulness as an antipredator strategy (Shapiro, 1974). The effects of weather conditions on the frequency of damage during migration in painted lady butterflies also merit investigation. Steady southerly winds might aid butterflies on their northward spring migration because such winds would increase their gliding range (Dobronosov, 2019); by contrast, variable weather conditions can increase the time that butterflies spend at low altitudes and thus increase the risk of wing damage.

Comparisons with other butterflies

Similar to painted lady butterflies, monarch butterflies are migratory. In winter, they migrate south to Mexico and then return to the north of North America in spring. Overwintering occurs in groves along the California coast from Mendocino County to the Ensenada region of Baja California and Mexico. The insects spend 5–6 months there and are exposed to winter storms, avian predation, and other factors that can potentially induce wing damage. Leong *et al.* (1993) collected monarch butterflies at two Californian overwintering sites in October–March 1990–1991 and found that butterflies showed an average loss of wing area of approximately 2% (Leong *et al.*, 1993). This loss is lower than that observed in our study of the painted lady (6.69%). This difference might be explained by the toxicity of monarch butterflies, which would increase their unpalatability to birds (Agrawal, 2017). Naturally occurring wing damage is also lower in *Morpho* butterflies than in painted lady butterflies in our study (Le Roy *et al.*, 2019b). However, artificial wing damage in captive butterflies is increased by collisions with walls in their enclosures (Le Roy *et al.*, 2019b). This artificial damage is higher than the observed natural wing damage of painted lady butterflies. The distribution of wing damage differs between *Morpho* butterflies (Le Roy *et al.*, 2019b) and painted lady butterflies, even when accounting for the increased wing damage associated with wall collisions in captivity in *Morpho* butterflies. This likely stems from differences in wing shape. The higher frequency of damage on the forewings of cage-reared *Morpho* butterflies might stem from the effects of being held captive in an artificial enclosure, given

that such damage is not frequently observed in *Morpho* butterflies *in situ*; this likely is associated with collisions with the ceiling and walls of their enclosures. Nevertheless, the forewings of *Morpho* butterflies are larger than their hind wings, and the frequency of damage on the forewings is greater than that on the hindwings. The opposite pattern was observed in *V. cardui*: the hindwings are larger and show more damage than the forewings. The wings of migrating monarch butterflies are larger and more elongated than the wings of nonmigrating populations. The elongation of wings has been hypothesized to reduce the flight costs of long migrations (Dockx, 2007; Altizer & Davis, 2010). However, large wings appear to be more prone to damage than small wings. To evaluate the effects of wing damage on migration costs, as well as the sources of wing damage, isotope data to determine the actual flight distances of particular individuals should be collected as in Stefanescu *et al.* (2016); such data would provide a link between individual flight distance and observed wing damage. Isotope data can also help to provide insights into the relative contributions of long-range gliding at high altitudes and low-altitude flights to wing damage risk, as well as the vulnerability of wings to damage along different stretches of their migratory routes.

Comparison of patterns of wing damage in various insects

Patterns of wing damage in *V. cardui* were similar to those in dragonflies, which have elongated wings. The frequency of wing damage in the dragonfly *Sympetrum vulgatum* (Linnaeus, 1758), which can also make migratory flights, was <10% according to field observations in a previous study (Rajabi *et al.*, 2017a). This is noticeably higher than the frequency of damage observed in *V. cardui* wings (forewings: 3.31%; hind wings: 10.06%; overall: 6.69%). The lower number of transverse veins, the absence of marginal veins, and the larger wing area in painted lady butterflies suggest that their wings can withstand long-distance migratory flights. Adult dragonflies are aerial predators that make use of a direct flight mechanism to catch prey in mid-air (Corbet, 1999), whereas butterflies use an indirect flight mechanism (Dudley, 2002). In general, this pattern of flight behavior suggests that dragonflies are more at risk of experiencing wing damage than butterflies. However, dragonflies also possess a high damping capacity (Lietz *et al.*, 2021), which can mitigate wing damage.

The longitudinal veins of butterflies sometimes protrude following the loss of wing area. Butterflies

have almost no transverse veins but have more stable longitudinal veins, which do not easily break off. The low number of transverse veins reduces their weight. The distal lateral edge is exposed to the environment and thus to collisions, but the decreased diameter of veins increases the flexibility of the wing tip and allows butterflies to avoid unpredictable impacts (Wootton, 1992). In both dragonfly and butterfly wings, the outermost edge is followed by a region with a slightly lower frequency of damage, which is approximately 8% in dragonflies (Rajabi *et al.*, 2017a) and approximately 20% in butterflies, and the frequency of damage decreases toward the base. Although butterflies exhibit a decrease in the frequency of damage from the distal to the proximal ends of their wings, the damage frequency decreases vertically from the bottom to the top of dragonfly wings. Despite their substantial morphological differences, the frequency of damage to the proximal trailing edge of the hindwing and the wing tip was high in both dragonflies (18%, Rajabi *et al.*, 2017a) and butterflies in our study (35%–50%, Fig. 3).

Damage-accompanying phenomena

Additional damage-related phenomena were also observed in our study. For example, we observed a damaged membrane folded back but still attached to the wing (Fig. S2). This might be caused by plastic deformation; a phenomenon that has also been observed in dragonfly wings (Rudolf *et al.*, 2019). We also found that the color of the wings tended to be faded when the extent of damage was higher. In extreme cases, some wings appeared to be almost transparent. This likely stems from the fact that the scales, which provide most of the wings' coloration, were removed by wear (Schiffman & Schauer, 2009). Fading colors associated with scale loss might have deleterious effects on the butterflies. For example, if wing coloration is involved in courtship or mate selection, fading coloration might affect intraspecific communication between the sexes. The abundances of painted lady butterflies depend on eclosion conditions and influence the ratios of the sexes; given that the painted lady is polygynous, male coloration can have a major effect on reproductive success (Rutowski, 1991). Furthermore, coloration can affect predator–prey interactions, such as the efficiency of camouflage or warning coloration (Thery & Gomez, 2010). The painted lady butterfly possesses several small eyespots in the periphery of the wing (Fig. 2). These small eyespots might encourage predatory attacks on nonvital body regions (Stevens, 2005). Consequently, wing area loss, including the loss of these

eyesspots, might reduce the efficiency of individual butterflies to escape from predators. Additional studies that examine the effects of different types of wing damage on intra- and interspecific interactions of painted lady butterflies are needed. Another potential negative effect of area loss is associated with the role of wings in thermoregulation (Clench, 1966). The loss of wing area can negatively affect the thermoregulatory function of the wings.

Acknowledgments

We thank the team of the butterfly monitoring of the Helmholtz Centre for Environmental Research for butterfly monitoring, particularly R. Feldmann and E. Kühn, for supporting the image acquisition and the coordination with contributors. All contributors of images are thanked for their submissions, especially A. Alzner, J. Burkei, G. Czerwinski, J. Fenske, T. Frankenhauser, J. Frederiksen, M. Harder, R. Hoppe, B. Klofat, J. Neumann, B. Schmälter, K. Steindorf, H. Wallner, R. Winkler, and further anonymous contributors. Braxton R. Jones (University of Sydney, Australia) is thanked for proofreading the manuscript.

Open access funding enabled and organized by Projekt DEAL.

Data availability statement

The images of the damaged wings are available as electronic supplementary material (Fig. S1), as well as supporting images of damage accompanying phenomena (Fig. S2).

The MATLAB script is available on request.

Disclosure

The authors declare no competing or financial interests.

References

- Abbott, C.H. (1951) A quantitative study of the migration of the painted lady butterfly, *Vanessa cardui*. *Ecology*, 32, 155–171.
- Agrawal, A. (2017) *Monarchs and Milkweed: A Migrating Butterfly, A Poisonous Plant, and their remarkable story of co-evolution*. Princeton University Press, New Jersey, p. 31.
- Altizer, S. and Davis, A.K. (2010) Populations of monarch butterflies with different migratory behaviors show divergence in wing morphology. *Evolution; International Journal of Organic Evolution*, 64, 1018–1028.
- Arnold, S.J. (1983) Morphology, performance, and fitness. *American Zoologist*, 23, 347–361.

- Biebach, H. (1990) Strategies of trans-Saharan migrants. In *Bird-Migration* (eds. Gwinner, E.), pp. 352–367. Springer, Berlin, Heidelberg.
- Brower, L.P. (1961) Studies on the migration of the monarch butterfly I. Breeding populations of *Danaus plexippus* and *D. gilippus berenice* in south-central Florida. *Ecology*, 42, 76–83.
- Buchwald, R. and Dudley, R. (2010) Limits to vertical force and power production in bumblebees (Hymenoptera: *Bombus impatiens*). *Journal of Experimental Biology*, 213, 426–432.
- Burkhard, D.U., Ward, P.I. and Blanckenhorn, W.U. (2002) Using age grading by wing injuries to estimate size-dependent adult survivorship in the field: a case study of the yellow dung fly *Scathophaga stercoraria*. *Ecological Entomology*, 27, 514–520.
- Cartar, R.V. (1992) Morphological senescence and longevity: an experiment relating wing wear and life span in foraging wild bumble bees. *Journal of Animal Ecology*, 61, 225–231.
- Chowdhury, S., Hesselberg, T., Böhm, M., Islam, M.R. and Aich, U. (2017) Butterfly diversity in a tropical urban habitat (Lepidoptera: Papilionoidea). *Oriental Insects*, 51, 417–430.
- Chowdhury, S., Fuller, R.A., Dingle, H., Chapman, J.W. and Zalucki, M.P. (2021) Migration in butterflies: a global overview. *Biological Reviews*, 96, 1462–1483.
- Chowdhury, S., Jennions, M.D., Zalucki, M.P., Maron, M., Wat-son, J.E. and Fuller, R.A. (2022) Protected areas and the future of insect conservation. *Trends in Ecology & Evolution*, in press. <https://doi.org/10.1016/j.tree.2022.09.004>
- Clench, H.K. (1966) Behavioral thermoregulation in butterflies. *Ecology*, 47(6), 1021–1034.
- Corbet, P.S. (1999) *Dragonflies: behavior and ecology of Odonata*. Harley Books, Colchester.
- Cuadrado, M. (2021) Assessing year-round phenology and reproduction of the migratory painted lady butterfly, *Vanessa cardui* (Lepidoptera: Nymphalidae), in a Mediterranean area in southern Spain. *European Journal of Entomology*, 118, 288–296.
- Dockx, C. (2007) Directional and stabilizing selection on wing size and shape in migrant and resident monarch butterflies, *Danaus plexippus* (L.), in Cuba. *Biological Journal of the Linnean Society*, 92, 605–616.
- Combes, S.A. and Daniel, T.L. (2003) Flexural stiffness in insect wings I. Scaling and the influence of wing venation. *Journal of Experimental Biology*, 206, 2979–2987.
- Descouens, D. (2015) *Painted Lady—Dorsal Side*. Wikimedia Commons.
- Dirks, J.H. and Taylor, D. (2012) Veins improve the fracture toughness of insect wings. *PLoS ONE*, 7, e43411.
- Dobronosov, V. (2019) About mass migration of Painted Lady Butterfly (*Vanessa cardui* L.) to Eurasia in 2019. *Concepts of Dairy & Veterinary Sciences*, 2, 244–248.
- Dudley, R. (2002) *The Biomechanics of Insect Flight: Form, Function, Evolution*. Princeton University Press, Princeton.
- Eitze, J. (2017) *Klimareport 2017 / Saudi-Arabien*. Konrad-Adenauer-Stiftung e.V., Europäische und internationale Zusammenarbeit, Berlin, p. 5 pp.
- Eshghi, S., Nooraefar, V., Darvizeh, A., Gorb, S.N. and Rajabi, H. (2020) WingMesh: a Matlab-based application for finite element modeling of insect wings. *Insects*, 11, 546.
- Fernández, M.J., Springthorpe, D. and Hedrick, T.L. (2012) Neuromuscular and biomechanical compensation for wing asymmetry in insect hovering flight. *Journal of Experimental Biology*, 215, 3631–3638.
- Ford, E.B. (1945) Butterflies. New Naturalist No. 30. Collins, London.
- Foster, D.J. and Cartar, R.V. (2011) What causes wing wear in foraging bumble bees? *Journal of Experimental Biology*, 214, 1896–1901.
- Freedman, M.G., Dingle, H., Strauss, S.Y. and Ramírez, S.R. (2020) Two centuries of monarch butterfly collections reveal contrasting effects of range expansion and migration loss on wing traits. *Proceedings of the National Academy of Sciences USA*, 117, 28887–28893.
- Fox, R., Brereton, T.M., Asher, J., August, T.A., Botham, M.S., Bourn, N.A.D. et al. (2015) *The State of the UK's Butterflies 2015*. Butterfly Conservation and the Centre for Ecology and Hydrology, Wareham, Dorset, p. 28 pp.
- Haas, C.A. (2005) *Flight performance of bumble bees with wing wear*. Doctoral dissertation, University of Lethbridge, Lethbridge, p. 64 pp.
- Higginson, A.D. and Barnard, C.J. (2004) Accumulating wing damage affects foraging decisions in honeybees (*Apis mellifera* L.). *Ecological Entomology*, 29, 52–59.
- Hobson, K.A., Jinguji, H., Ichikawa, Y., Kusack, J.W. and Anderson, R.C. (2021) Long-distance migration of the Globe Skimmer Dragonfly to Japan revealed using stable hydrogen (δ 2H) isotopes. *Environmental Entomology*, 50, 247–255.
- Jantzen, B. and Eisner, T. (2008) Hindwings are unnecessary for flight but essential for execution of normal evasive flight in Lepidoptera. *Proceedings of the National Academy of Sciences USA*, 105, 16636–16640.
- Kingsolver, J.G. (1999) Experimental analyses of wing size, flight, and survival in the western white butterfly. *Evolution; International Journal of Organic Evolution*, 53, 1479–1490.
- Le Roy, C., Debat, V. and Llaurens, V. (2019a) Adaptive evolution of butterfly wing shape: from morphology to behaviour. *Biological Reviews*, 94, 1261–1281.
- Le Roy, C., Cornette, R., Llaurens, V. and Debat, V. (2019b) Effects of natural wing damage on flight performance in Morpho butterflies: what can it tell us about wing shape evolution? *Journal of Experimental Biology*, 222, jeb204057.
- Leong, K.L.H., Frey, D., Hamaoka, D. and Honma, K. (1993) Wing damage in overwintering populations of monarch

- butterfly at two California sites. *Annals of the Entomological Society of America*, 86, 728–733.
- Lietz, C., Schaber, C.F., Gorb, S.N. and Rajabi, H. (2021) The damping and structural properties of dragonfly and damselfly wings during dynamic movement. *Communications Biology*, 4, 737.
- Ma, Y., Zhao, H., Ma, T., Ning, J. and Gorb, S.N. (2021) Wing coupling mechanism in the butterfly *Pieris rapae* (Lepidoptera, Pieridae) and its role in taking off. *Journal of Insect Physiology*, 131, 104212.
- Malcolm, S.B. (2018) Anthropogenic impacts on mortality and population viability of the monarch butterfly. *Annual Review of Entomology*, 63, 277–302.
- Nesbit, R.L., Hill, J.K., Woiwod, I.P., Sivell, D., Bensusan, K.J. and Chapman, J.W. (2009) Seasonally adaptive migratory headings mediated by a sun compass in the painted lady butterfly, *Vanessa cardui*. *Animal Behaviour*, 78, 1119–1125.
- Pollard, E., Van Swaay, C.A.M., Stefanescu, C., Lundsten, K.E., Maes, D. and Greatorex-Davies, J.N. (1998) Migration of the painted lady butterfly *Cynthia cardui* in Europe: evidence from monitoring. *Diversity and Distributions*, 4, 243–253.
- Rajabi, H., Darvizeh, A., Shafiei, A., Taylor, D. and Dirks, J.H. (2015) Numerical investigation of insect wing fracture behaviour. *Journal of Biomechanics*, 48, 89–94.
- Rajabi, H., Schroeter, V., Eshghi, S. and Gorb, S.N. (2017a) The probability of wing damage in the dragonfly *Sympetrum vulgatum* (Anisoptera: Libellulidae): a field study. *Biology Open*, 6, 1290–1293.
- Rajabi, H., Bazargan, P., Pourbabaei, A., Eshghi, S., Darvizeh, A., Gorb, S.N. et al. (2017b) Wing cross veins: an efficient biomechanical strategy to mitigate fatigue failure of insect cuticle. *Biomechanics and Modeling in Mechanobiology*, 16, 1947–1955.
- Rajabi, H., Dirks, J.H. and Gorb, S.N. (2020) Insect wing damage: causes, consequences and compensatory mechanisms. *Journal of Experimental Biology*, 223, jeb215194.
- Reppert, S.M. and de Roode, J.C. (2018) Demystifying monarch butterfly migration. *Current Biology*, 28, R1009–R1022.
- Roberts, J.C. and Cartar, R.V. (2015) Shape of wing wear fails to affect load lifting in common eastern bumble bees (*Bombus impatiens*) with experimental wing wear. *Canadian Journal of Zoology*, 93, 531–537.
- Rudolf, J., Wang, L.Y., Gorb, S.N. and Rajabi, H. (2019) On the fracture resistance of dragonfly wings. *Journal of the Mechanical Behavior of Biomedical Materials*, 99, 127–133.
- Rutowski, R.L. (1991) The Evolution of male mate-locating behavior in butterflies. *The American Naturalist*, 138, 1121–1139.
- Schiffman, J.D. and Schauer, C.L. (2009) Solid state characterization of α -chitin from *Vanessa cardui* Linnaeus wings. *Materials Science and Engineering: C*, 29, 1370–1374.
- Shapiro, A.M. (1974) Beak-mark frequency as an index of seasonal predation intensity on common butterflies. *American Naturalist*, 108, 229–232.
- Stefanescu, C., Alarcón, M. and Àvila, A. (2007) Migration of the painted lady butterfly, *Vanessa cardui*, to north-eastern Spain is aided by African wind currents. *Journal of Animal Ecology*, 76, 888–898.
- Stefanescu, C., Páramo, F., Åkesson, S., Alarcón, M., Ávila, A., Brereton, T. et al. (2013) Multi-generational long-distance migration of insects: studying the painted lady butterfly in the Western Palaearctic. *Ecography*, 36, 474–486.
- Stefanescu, C., Soto, D.X., Talavera, G., Vila, R. and Hobson, K.A. (2016) Long-distance autumn migration across the Sahara by painted lady butterflies: exploiting resource pulses in the tropical savannah. *Biology Letters*, 12, 20160561.
- Stenoien, C., Nail, K.R., Zalucki, J.M., Parry, H., Oberhauser, K.S. and Zalucki, M.P. (2018) Monarchs in decline: a collateral landscape-level effect of modern agriculture. *Insect Science*, 25, 528–541.
- Stevens, M. (2005) The role of eyespots as anti-predator mechanisms, principally demonstrated in the Lepidoptera. *Biological Reviews*, 80, 573–588.
- Talavera, G. and Vila, R. (2017) Discovery of mass migration and breeding of the painted lady butterfly *Vanessa cardui* in the Sub-Sahara: the Europe–Africa migration revisited. *Biological Journal of the Linnean Society*, 120, 274–285.
- Stefanescu, C., Askew, R.R., Corbera, J., and Shaw, M.R. (2012). Parasitism and migration in southern Palaearctic populations of the painted lady butterfly, *Vanessa cardui* (Lepidoptera: Nymphalidae). *European Journal of Entomology*, 109(1), 85–94.
- Talavera, G., Bataille, C., Benyamini, D., Gascoigne-Pees, M. and Vila, R. (2018) Round-trip across the Sahara: Afrotropical Painted Lady butterflies recolonize the Mediterranean in early spring. *Biology Letters*, 14, 20180274.
- Thery, M. and Gomez, D. (2010) Insect colours and visual appearance in the eyes of their predators. *Advances in Insect Physiology*, 38, 267–353.
- Wagner, D.L., Grames, E.M., Forister, M.L., Berenbaum, M.R. and Stopak, D. (2021) Insect decline in the Anthropocene: death by a thousand cuts. *Proceedings of the National Academy of Sciences USA*, 118, e2023989118.
- Wald, A. (1943) *A Method of Estimating Plane Vulnerability Based on Damage of Survivors*. Statistical Research Group, Columbia.
- Wikelski, M., Moskowicz, D., Adelman, J.S., Cochran, J., Wilcove, D.S. and May, M.L. (2006) Simple rules guide dragonfly migration. *Biology Letters*, 2, 325–329.
- Williams, C.B. (1930) *The Migration of Butterflies*. Oliver & Boyd, London.

- Wilson, E.O. (1969) Mechanisms of insect dispersal: Migration and dispersal of insects by flight. *Science*, 166, 592.
- Wootton, R.J. (1992) Functional morphology of insect wings. *Annual Review of Entomology*, 37, 113–140.
- Zylstra, E.R., Ries, L., Neupane, N., Saunders, S.P., Ramírez, M.I., Rendón-Salinas, E. *et al.* (2021) Changes in climate drive recent monarch butterfly dynamics. *Nature Ecology & Evolution*, 5, 1441–1452.

Manuscript received July 23, 2022

Final version received November 9, 2022

Accepted November 13, 2022

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Vector drawings of the samples of *V. cardui*.

Fig. S2 Damage accompanying phenomena.