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Effects of wind and weather on red admiral, *Vanessa atalanta*, migration at a coastal site in southern Sweden

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Each autumn, large numbers of red admirals migrate throughout northern Europe, flying south, to reach areas with conditions suitable for surviving the winter. We observed the visible butterfly migration at Falsterbo peninsula, the southwesternmost point in Sweden, where red admirals are seen most autumns flying towards the Danish coast on their way to more southern parts of Europe. Weather parameters from a local weather station were used to analyse what factors are important for red admiral migration across the sea. Wind direction was among the important weather variables affecting the initiation of the migratory departure; most other studies of butterfly migration reported no large effect of wind direction. This difference is probably because the butterflies in our study were about to cross open sea for more than 20 km, whereas most previous studies were from inland locations where butterflies could avoid wind effects by flying close to the ground or on the lee side of topographical features. Other important weather variables affecting red admiral migration at Falsterbo were low wind speed and clear skies. The flight direction at Falsterbo was towards the west, which is in contrast to the southward direction generally reported during autumn migration in this species. This is probably because the red admirals followed both the local topography and the closest route to land on the other side and therefore deviated from the normally preferred direction to minimize flight over open water.

Keywords: butterfly; migration; orientation; red admiral; sea crossing; topography; *Vanessa atalanta*; visual observation; weather; wind

Many winged animals cover long distances during migration either flying actively or drifting with the wind, sometimes using flight only to stay aloft. Weather conditions, especially temperature and winds, and local topography have a substantial impact on their flight and orientation (e.g. Brown 1970; Alerstam 1981, 1990a; Drake & Farrow 1988; Richardson 1991; Mikkola 2003a; Åkesson & Hedenström 2007) as well as on the decision to initiate migration (Åkesson & Hedenström 2000; Åkesson et al. 2002; Wikelski et al. 2006). The displacement of small flying migrants is more or less determined by the wind, but some large insects and birds can control their track relative to the ground and avoid unwanted wind drift by adjusting their heading. In the latter case, the migrants can save energy and gain speed by choosing the right day and altitude for their migration flight (Åkesson & Hedenström 2007).

Insect migration is a widespread phenomenon all over the world and in different taxonomic groups (e.g. Williams 1958; Dingle 1996; Dingle & Drake 2007). Among lepidopterans there seems to be a large difference in flight altitude between moths and butterflies (Walker 1980). Most moths seem to migrate high above the ground and they are often strongly affected by both wind direction and speed (Drake 1985; Gatehouse 1997; Wood et al. 2006). Butterflies, on the other hand, are mostly found migrating in the flight boundary layer close to the ground (Taylor 1974; Walker 1985; Srygley & Oliveira 2001) where wind speeds are lower than their own airspeed making it possible to control their track direction relative to the ground. They can also adjust their flight path to follow leading lines that protect them from strong side-winds (Nielsen 1961). There are, however, reports of monarchs, *Danaus plexippus* (e.g. Gibo & Pallett 1979; Gibo 1981) and red admirals (Mikkola 2003a) migrating at high altitudes and a recent study suggests that painted ladies,

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Vanessa cardui, on spring migration across the Mediterranean Sea are flying at altitudes around 1500 m (Stefanescu et al. 2007).

There are often concentrations of flying migratory animals at coasts and peninsulas pointing at the migratory direction (e.g. Alerstam 1990b; Bruderer & Liechti 1998; Garland & Davis 2002). This is especially true and well studied in bird species that use thermal soaring, concentrating for instance at Gibraltar and the Bosporus. The passage of bird migration has been studied since the 1940s at Falsterbo, in southernmost Sweden, where birds concentrate in autumn before crossing the sea towards Denmark (Rudebeck 1950; Ulfstrand et al. 1974; Fig. 1). In 1973 the Swedish Environmental Protection Agency started systematic counts of the bird migration passing the Falsterbo peninsula as part of their Bird Monitoring Programme (Kjellen 2006 and earlier references therein). During these studies insects were seen to concentrate to some degree at the Falsterbo peninsula in autumn. This behaviour has been seen in butterflies, dragonflies and hymenopterans. A large migration of red admirals was observed at this location as early as 1946 (Rudebeck 1951), but no systematic counts of any migratory insects had been made at Falsterbo before our study. To shed some light on the migratory behaviour in relation to weather conditions we counted migrating butterflies at Falsterbo during three autumn migration periods: 2004–2006.

The timing of migration, as well as the number of individuals observed, varies between years in studies of butterflies (e.g. Hansen 2001; Walker 2001; Meitner et al. 2004). A large part of this variation is probably caused by the high degree of plasticity that is present in many insects' life histories and may be a response to differences in temperature and other weather-related factors (e.g. Pollard 1988; Roy et al. 2001). Among the butterflies that can be found in Europe, the red admiral stands out among all long-distance migrants by showing perhaps the most regular pattern of migration (Pollard & Yates 1993) and it is therefore suitable as a model species for studies of butterflies. Using the Falsterbo 2004–2006 count data for the red admiral (the most abundant migratory butterfly species at this location) and weather data from the same site, we addressed three questions. First, what factor underlies the difference in the red admirals' migratory period between years? Second, during the migratory period, which factors make certain days suitable for migration but others not? Third, on days with observed migration, which factors influence the numbers seen each day?

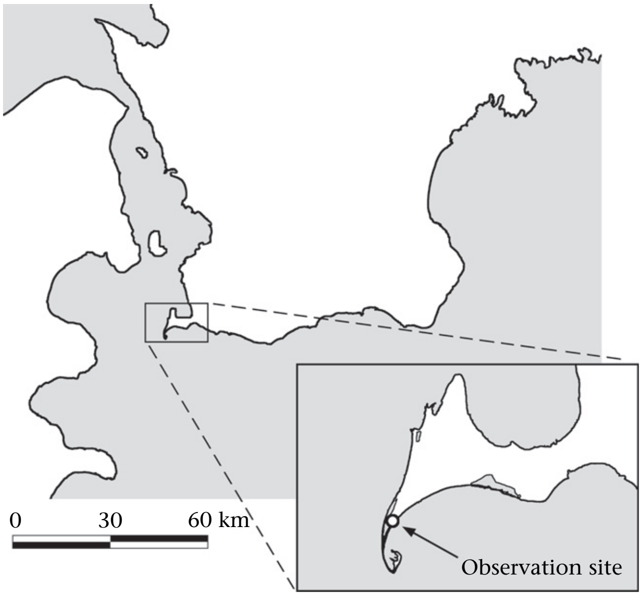

Figure 1. The observation site (marked with a circle) at Falsterbo, at the southwestern point of Sweden. Shortest distance to Denmark from our study location is 24 km towards west–southwest.

METHODS

Study Species

The red admiral is a nymphalid butterfly that can be found in North America, North Africa, most parts of Europe, and in the westernmost parts of Asia (Eliasson et al. 2005). Each spring, the European red admirals initiate large-scale migration towards the north. There are observations of these northward migratory flights from Italy (Benvenuti et al. 1994, 1996), Spain (Stefanescu 2001), Britain (Williams 1951) and Scandinavia (Hansen 2001) from March to June. After reaching suitable breeding regions, the females lay their eggs on nettles, *Urticae dioica*, and later in the summer a new generation hatches. During warm autumns, additional reproduction events might occur and red admirals are regularly observed as late as October in northern Europe (Henriksen & Kreutzer 1982; Eliasson et al. 2005). Each year migration in large numbers towards the south is reported in autumn throughout Europe (Williams 1951; Roer 1991; Imby 1993; Benvenuti et al. 1994, 1996; Hansen 2001; Stefanescu 2001; Mikkola 2003a), but there are also reports of large-scale migrations towards the north at this time of year (Rudebeck 1951; Radford 1975), suggesting a variable migratory pattern in autumn. In addition to all these reports on migration, there are also reports of red admirals in the middle of winter in the northern region (e.g. Steiniger & Eitschberger 1996) and in early spring before any immigrants have had time to reach these areas (e.g. Pollard & Greatorex-Davies 1998). Previously, most literature considered the red admiral to be a true hibernator (e.g. Higgins & Hargreaves 1983) or at least that it remained in reproductive diapause (references in Lempke 1971) during winter in all parts of its distribution. However, observations of breeding during winter in Lebanon (Larsen 1976) and recently from Spain (Stefanescu 2001) and Italy (Brattström 2006) suggest that hibernation is not a general strategy (Pollard & Greatorex-Davies 1998; Mikkola 2003b). Experimental studies trying to induce hibernation in captured red admirals in Germany failed to keep any specimens alive over the winter (Roer 1961; references in Lempke 1971). The general trend over time has been to upgrade the red admiral to a migrant species. In the early 1900s it was considered to be a resident species and then a short-distance migrant 50 years later (Williams 1958; Roer 1961). The present literature (e.g. Mikkola 2003b;

Eliasson et al. 2005) suggests that the red admiral is a long-distance migrant that does not regularly hibernate.

Migration Counts

We counted red admirals at the Falsterbo peninsula (55°23′N, 12°49′E; Fig. 1) when they left Sweden flying out over the sea, and noted their flight behaviour. The observation site is situated at the eastern coastline of the point of the Falsterbo peninsula, approximately 100 m east of the western coastline, running in a north−south direction. The environment consists of low, sparsely vegetated sand dunes and a golf course. It is not particularly rich in flowers and thus does not attract large numbers of butterflies for foraging. Typical resident butterfly species are queen of Spain fritillary, *Issoria lathonia*, rock grayling, *Hipparchia semele*, and small copper, *Lycaena phlaeas*.

Two observers recorded butterflies migrating out over the water between 1 August and 25 October from dawn until 1400 hours during the three autumns of 2004−2006. Butterflies passing the observation site were followed to determine a departure direction. If they stopped to feed or followed the coastline they were not observed further. Individuals venturing out over the sea were followed for roughly 50 m and if they continued in a straight direction they were regarded as migrants. An approximate migratory direction for each individual was obtained based on the vanishing bearing estimated to the nearest 45 degrees. In general most of the individuals observed on a single day had the same migratory direction, and on days when flight was observed in more than one sector it was always in two adjacent sectors. On such days we used the mean direction of both of these sectors. The observers were positioned in such a way that they could detect butterflies flying out across open water in any direction except a small sector towards land in the northeastern quadrant.

Weather Data

We obtained data for weather variables from the Swedish Meteorological and Hydrological Institute (SMHI) for the weather station located around 5 m above sea level at Falsterbo, close to the observation site. Among the variables recorded at the station we used wind direction and speed, air pressure, temperature, precipitation and cloud cover. Data for all of these variables except precipitation are recorded every 3 h. Precipitation is recorded in 12 h intervals from 0600 to 1800 hours and 1800 to 0600 hours. Since counts of migrating red admirals are given as one value per single day, we calculated a daily mean value for all our weather variables. For variables believed to influence the flight of the red admirals directly (wind direction and speed as well as cloud cover) we used the mean value recorded between 0600 and 1500 hours, the time of day when they are actively flying. Variables such as air pressure and temperature are more likely to influence the decision to migrate, making it necessary to include data from the evening and night before the actual observation day. For air pressure measurement we used the mean from the evening before each observation day (1800 hours) up until the end of the flight period the actual day (1500 hours) and for temperature measurement we selected minimum temperature during the preceding night (1800−0600 hours) as well as daily mean temperature. For both air pressure and temperature, we also calculated the change from the preceding day. To make the wind direction more suitable for linear analysis, we calculated the sine and cosine values from the circular variable obtained from the weather station (corresponding to the east/west and north/south components, respectively, of the wind direction). All wind directions are given as the direction from which the wind is blowing.

Statistical Analysis

We excluded the data from 2004 from our analysis since that year had very low numbers of butterflies compared to the other 2 years. We focused only on red admirals since it is an abundant species, easy to identify in the field, and well known for its migratory behaviour. Before analysing the data with respect to factors important for migration, we excluded days before and after the main migration period, as it would not make sense to study factors influencing migration outside the normal migratory window. For this analysis, we therefore excluded all days up until a week before the main migration period began (when higher densities of butterflies were observed), and all days after the last observation. In 2006 we had a few outlying observations with a total of 20 red admirals observed before the start of the main migration. These individuals occurred up to a month before the main migration started and were not considered representative for the migration as a whole and therefore excluded from further analyses. The remaining days for each year were 9 August−18 October 2005 and 5 September−20 October 2006.

We tested whether there was any significant difference in mean date of passage of red admirals between the 2 years by conducting a Mann−Whitney *U* test on the date of passage. To take differences in migratory intensity between days into account, each observed individual was represented by one value. To analyse whether temperatures were different between the 2 years, we used an ANCOVA, examining the relation between daily mean temperatures recorded during the 2 study years.

We used the Rayleigh test (Batschelet 1981) to analyse whether there was a mean population direction in observed migratory directions and the Watson−Williams *F* test (Batschelet 1981) to analyse whether there was any difference in orientation between the 2 years. To analyse whether wind drift was present on days with side-winds, we compared the mean orientation (also calculated with the Rayleigh test) on days with northerly or southerly winds, again with the Watson−Williams *F* test.

To avoid autocorrelation between weather variables, we computed a bivariate correlation matrix between all the calculated variables. Mean air pressure and precipitation were both strongly correlated with most of the other variables and therefore removed from the analysis. Mean and minimum temperatures were naturally correlated with each other so only one temperature measurement was used at the same time in each analysis.

We used a logistic regression analysis with observed migration/no migration as the dependent variable. Year was included as a factor and we used wind direction (sine and cosine), wind speed, air pressure change, cloud cover and change in minimum temperature as covariates. Using temperature change instead of a mean daily value was important since mean temperature naturally decreases over the migratory period, as do numbers of red admirals seen since fewer individuals are prepared to migrate. This would lead to a correlation without a biological significance. Change in minimum temperature is also an important cue for initiating migration in dragonflies (Wikelski et al. 2006). The statistical significance of independent variables in the logistic regression was assessed by the change in deviance, *G*, which is approximated by a chi-square distribution (Sokal & Rohlf 1995). We removed variables stepwise in a backward procedure until no variable could be removed without changing the model in a significant way ($P < 0.1$).

To analyse what factors influence the numbers of observed red admirals on days with migration, we removed all days with no observation of red admirals from the data set. Multiple regression was then carried out using the logarithm of the observed admirals as the dependent value (to make data more normally distributed and suited for the analysis). Year was included as a factor and wind direction (sine and cosine), wind speed, air pressure change, cloud cover, change in minimum temperature and the number of days since the beginning of the migratory period were included as covariates.

All tests are two tailed.

RESULTS

Migratory Behaviour as Observed During Counting

Red admiral migration rarely took place under cloudy conditions or in wind speeds exceeding 5 m/s. Most red admirals were migrating within 2 m of the ground. Upon reaching the waterline the majority gained height and continued 3–10 m above the sea. On a few occasions butterflies were discovered flying in a western direction at greater height (up to roughly 20 m). Although this was rare, individuals travelling high obviously stand a much smaller chance of being spotted. Generally, red admirals hesitated less than most other butterfly species when reaching the coastline. Most other butterflies ventured out only a few metres over the water, before quickly returning to the shore.

Annual Migration Period

We observed 222 and 311 red admirals in 2005 and 2006, respectively, whereas only 35 individuals were observed in 2004. The timing of migration differed between 2005 and 2006 (Fig. 2) with a difference of 24 days in median date of passage (31 August in 2005 compared to 24 September in 2006). The difference in mean passage date of all the individual migrants was significantly different between 2005 and 2006 (Mann–Whitney *U* test: $U = 16\,996.0$, $N_{2005} = 222$, $N_{2006} = 311$, $P < 0.001$).

The ANCOVA using mean temperature as the dependent variable and the day from the start of the counting period as a covariate and year as a factor showed

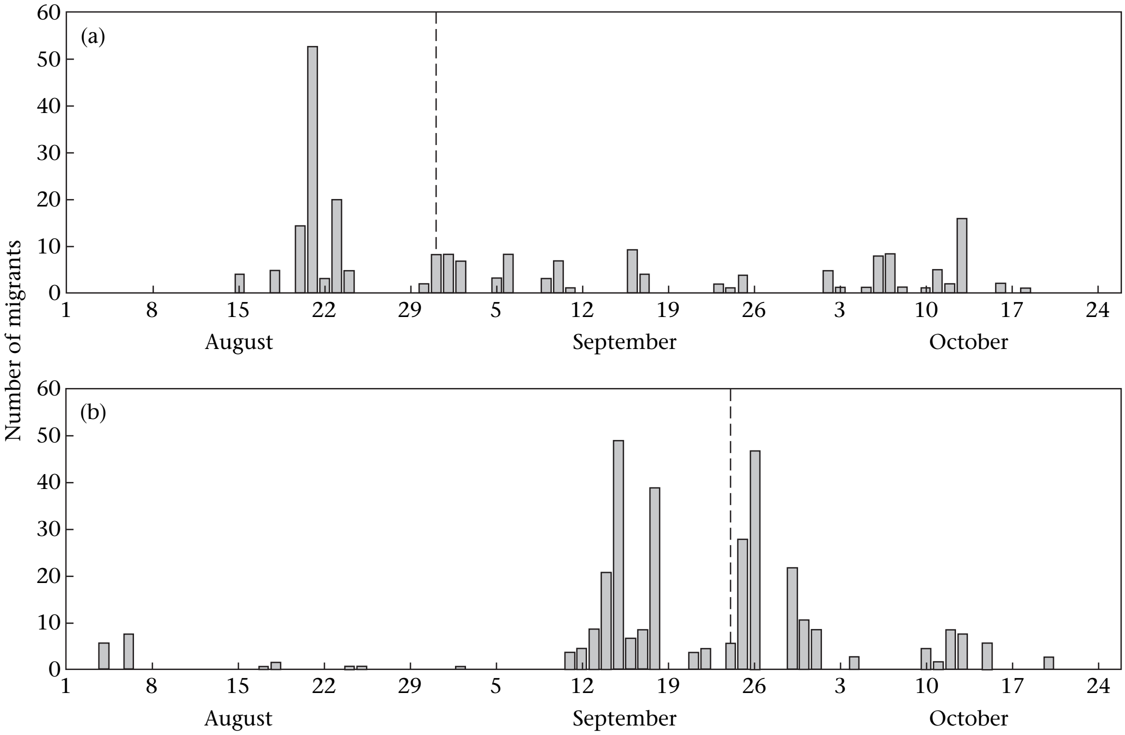

Figure 2. Numbers of red admirals migrating out over the sea at Falsterbo each day during autumn (a) 2005 and (b) 2006. The broken line indicates the median date of passage for each year.

a significant effect of both year and date, but no interaction between the two. The difference in the intercept of the regression line between the years is 1.52 °C with 2006 as the warmer year and the slope of temperature change per day is −0.074 °C (Fig. 3). This translates to the mean temperature for a day being reached about 21 days later during 2006.

Yearly Flight Directions and Side-wind Effects

The mean daily flight direction was clearly nonrandom in both years with limited variation (Fig. 4a). In 2005 the mean flight direction was 265 ± 5.9° (95% confidence interval, CI), $N = 33$ (Rayleigh test: $r = 0.96$, $P < 0.001$) and in 2006 it was 255 ± 6.5° (95% CI), $N = 22$ ($r = 0.96$, $P < 0.001$). There was no significant difference in flight direction between the 2 years (Watson−Williams F test: $F_{1,53} = 3.56$, $P = 0.065$). One day in 2006 was removed from these analyses since there was no recorded flight direction from that day.

The mean daily flight directions observed when prevailing winds had a southerly component was 261 ± 5.5° (95% CI), $N = 42$ (Rayleigh test: $r = 0.95$, $P < 0.001$; Fig. 4b) and for days with a northerly component the direction was 258 ± 11.0° (95% CI), $N = 10$ ($r = 0.97$, $P < 0.001$; Fig. 4b). These directions were not significantly different from each other (Watson−Williams F test: $F_{1,50} = 0.17$, $P = 0.68$). Three more days were excluded from these analyses since the wind direction was directly from the east or west.

We have reported all individuals from the same day in general as having the same estimated flight direction, but these values might be somewhat unrealistic, and scatter would probably have been more pronounced if we had known individual directions; there is still no doubt, however, that the directions were highly similar between both days and years. Of 55 days with migration with recorded flight directions, these were reported from only one 45-degree sector on 44 (80%) of these days. On the remaining 11 days with more scattered flight directions, flight was always observed in two adjacent 45-degree sectors.

Weather Factors Affecting Migration

The logistic regression found four parameters to be significant as predictors for days with or without migration. The final model predicted the correct outcome in 79.5% of the cases. The variables left in the model in order of explanatory power are: sine of wind direction (east/west component), cloud cover, wind speed and cosine of wind direction (north/south component). Probability of migration was highest when a northeasterly wind of low speed was combined with a clear sky (Table 1, Fig. 5).

The multiple regression found no significant factors, except days since beginning of the migratory period, explaining the difference in numbers seen migrating on days with at least one migrating individual (Table 2). Thus, the daily variation in numbers seen on migration could not be explained by the weather variables included in our analysis.

DISCUSSION

Timing of Migration

Our results show that there is considerable variation in the timing of migration of red admirals at Falsterbo

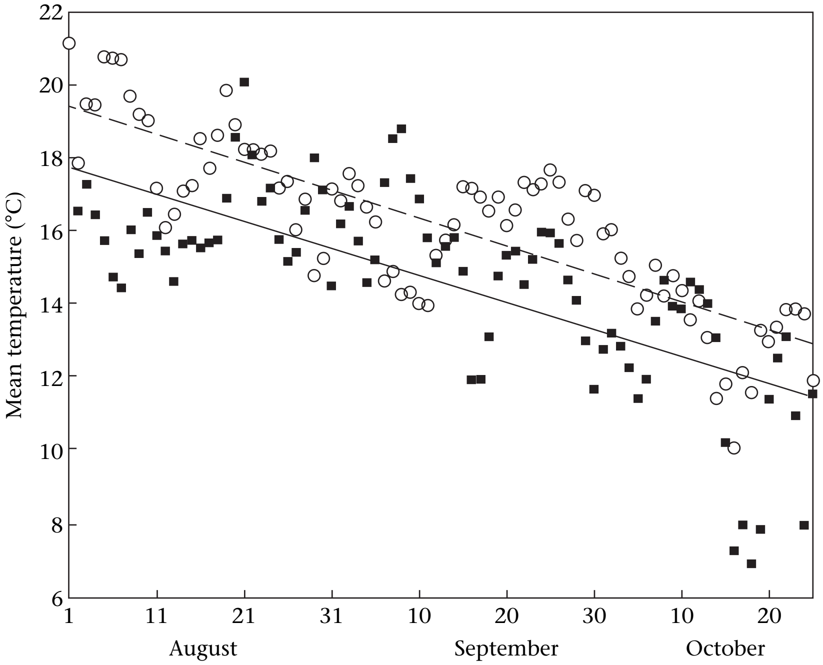

Figure 3. Daily mean temperature recorded at Falsterbo during autumn 2005 (■, —) and 2006 (○, - - -).

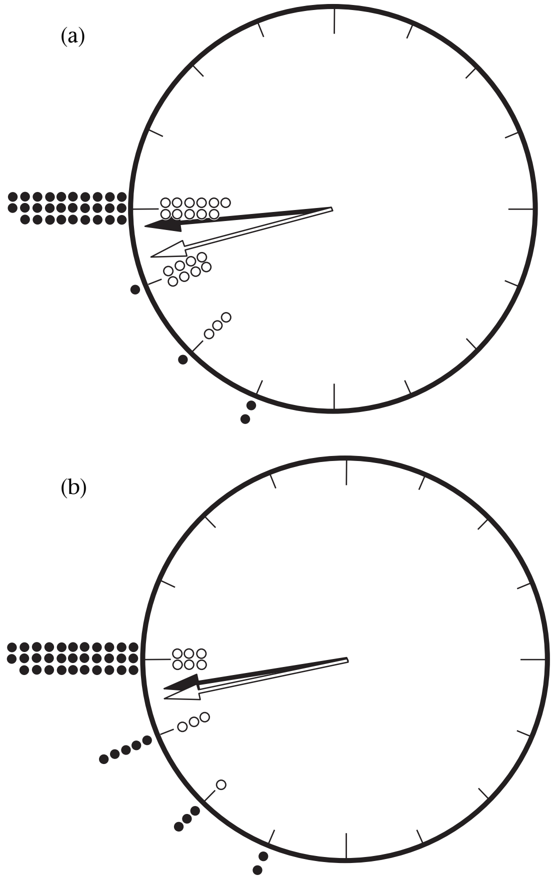

Figure 4. Circular diagrams showing the mean directions of migrating red admirals recorded at Falsterbo in autumn. (a) The mean orientation of the 2 study years (●: 2005; ○: 2006). (b) The mean directions depending on direction of side-winds (●: northerly winds; ○: southerly winds). Each dot represents a daily mean flight direction for all individuals observed on 1 observation day. The arrows show the mean direction for each group and the length of the line is related to the scatter of the distribution (*r*).

between years. Considering that temperature is one of the few variables that can give a reasonably good indication of how far the autumn season is progressing and that we found a temperature difference that matches the difference in median date of passage at Falsterbo (Fig. 3), temperature must be considered as a likely factor triggering the start of migration in red admirals. Since we have data for large red admiral migrations from only 2 years, it was not possible to analyse this effect statistically. A study of red admirals in Denmark also reported differences between years in peak dates of autumn migration ranging from 25 August to 8 October (1995–2000; Hansen 2001). The same has been reported for the monarch in North America (Meitner et al. 2004), considered to be the most regular migrant of all butterflies. Thus, in general, butterflies and other insects are more variable in their migration phenology than many other animals, and especially relative to birds (e.g. Edelstam 1972; Ulfstrand et al. 1974; Enquist & Pettersson 1986). Many migratory birds have reasonably fixed locations of breeding and wintering, whereas insects in general migrate until suitable areas are reached and the location of these areas changes between years because of prevailing weather and climatic conditions. The insects' migratory programme is thought to consist of a set of simple rules with external cues initiating and terminating migration (Wikelski et al. 2006), so differences between years in wind and temperature can have large effects on the distribution of migratory species of insects each year. The number of red admirals seen during monitoring programmes in Great Britain fluctuates on average two-fold between years and even more irregular migrants, such as the painted lady, show on average six-fold fluctuations between years (Pollard & Yates 1993). This again indicates a migration programme where both direction and length of migratory flights are presumably highly variable. In addition, part of this variation between years is likely to be caused by differences in breeding success affecting the size of the annual northerly immigration.

Table 1. Probability of migration of red admirals at Falsterbo in relation to daily local weather variables and year of study estimated by logistic regression

Final logistic regression model*	Estimate	*df*	*G*	*P*†
Final model		112		
Constant	4.03	1		
Sine of wind direction	1.68	1	26.44	<0.001
Cloud cover	−0.50	1	19.50	<0.001
Wind speed	−0.39	1	8.97	0.003
Cosine of wind direction	1.02	1	4.70	0.030
(Air pressure change)	−0.10	1	2.16	NS
(Observation year)	−0.37	1	0.46	NS
(Difference in minimum temperature)	−0.02	1	0.01	NS

Nonsignificant variables were removed stepwise in a backward procedure and reported values for the removed variables are from the last step in which they were still included in the model.
*Variables within parentheses are excluded in the final model.
†NS indicates $P > 0.1$.

Flight Behaviour and Effects of Wind

At Falsterbo, days with red admiral migration were characterized by light northeasterly winds and clear skies. Since the absolute numbers seen migrating were not related to the weather as long as it was good enough to allow migration (Table 2), it seems that most butterflies present in the area on a suitable day for migration will cross the sea. The decreasing trend over the migratory period is probably caused by a continuous depletion of individuals that still have to leave the region.

Most studies of butterfly migration have not found a large effect of wind direction since the butterflies generally stay close to the ground and fly on the lee side of topographical features to avoid strong cross-winds. The positive correlation between migration and following winds in our study is probably caused by the red admirals flying out over water where they cannot avoid the effect of winds and they will not be able to land if conditions turn for the worse. The low-altitude flight we observed was also reported for red admirals migrating in northwestern Italy

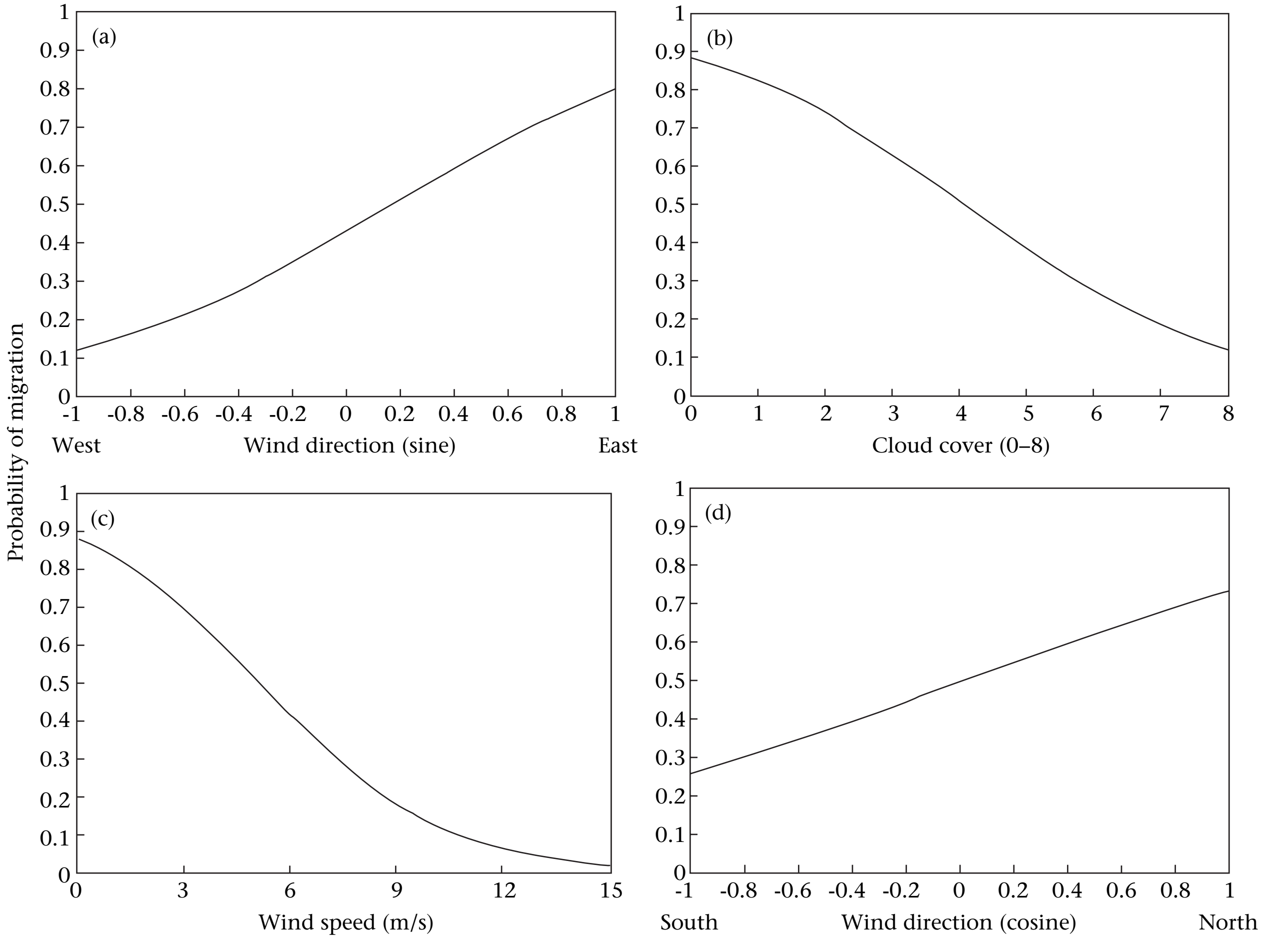

Figure 5. Relation between predicted probability of migration and recorded weather variables. (a) Sine component of wind direction, west (−1)—east (+1), (b) cloud cover, (c) wind speed and (d) cosine component of wind direction, south (−1)—north (+1).

where the butterflies stayed close to the ground and, just like at Falsterbo, they often gained height if they flew out over water (Benvenuti et al. 1994). Presumably the butterflies make this small ascent to leave a safety margin above the sea's surface. They do not need the safety of being close to the ground for predator avoidance (Walker 1980) over the sea since they cannot land anyway. Higher flight altitudes also increase the range of vision, so that the closest land could be detected more easily.

Although most observations of butterfly migrants match ours, reporting a low flight level with no sightings more than a few metres above ground (e.g. Williams 1976; Walker 1985; Benvenuti et al. 1994; Srygley et al. 1996; Srygley 2001), we cannot be sure that red admirals at Falsterbo do not migrate higher up, out of view of the observers. The only migrating butterfly regularly reported to fly at high altitudes (Gibo 1981), and also use thermal soaring during migration (Gibo & Pallett 1979), is the monarch in North America. There exist, however, some reports on high-altitude flights in other butterfly species (Schaefer 1976; Giuliani & Shields 1997) and it is possible that the importance of this flight strategy is underestimated because it is hard to detect. One study that traced insects with radar, carried out at the southern coast of Finland, suggested a large migration of red admirals, observed as high as 1000 m or more (Mikkola 2003a). Mikkola (2003a) also reported sightings of red admirals gaining altitude by thermal soaring and disappearing out of view at high altitudes. This was in an area where the butterflies were about to cross an area of open water for at least

Table 2. Results of the multiple regression on migration intensity of red admirals at Falsterbo (log-transformed values from days with observed migration only) in relation to daily local weather variables, days since start of migration and study year

Variable	Sum of squares	*df*	*F*	*P*
Days since beginning of migratory season	0.83	1	7.66	<0.01
Year	0.23	1	2.15	0.15
Difference in minimum temperature	0.11	1	0.98	0.33
Sine of wind direction	0.05	1	0.47	0.49
Wind speed	0.05	1	0.45	0.50
Air pressure change	0.03	1	0.27	0.60
Cosine of wind direction	0.03	1	0.26	0.62
Cloud cover	<0.01	1	0.04	0.84
Error	5.11	47		
Total	47.44	56		

60 km. However, the red admirals at Falsterbo have only 24 km of flight over open water before reaching the coast of Denmark.

If the red admirals were mainly relying on soaring flight during the sea crossing at Falsterbo, we would probably have seen lower numbers at the observation site on the most favourable days for thermal flight. In studies of monarchs, well known for their soaring behaviour during migration, most individuals are observed on partly overcast days. When the skies are perfectly clear the numbers drop (Meitner et al. 2004), presumably because they are flying well out of sight of the ground-based observers. Even though our observations are applicable only for migrants flying low enough for us to see, the above facts support the hypothesis that the main migration at Falsterbo occurs at lower levels.

Flight Directions and Orientation

The direction of the red admiral migrants observed at several different locations in Denmark (Hansen 2001) was towards the south, so the westward migratory direction reported at Falsterbo might have been selected to cross the sea at the shortest distance or, alternatively, follow the local topographical features. Since red admirals have fluctuating migration patterns without locally adapted subpopulations (O. Brattström, S. Åkesson & S. Bensch, unpublished data), it is unlikely that they have evolved a preference for a specific migratory direction connected to a geographical location of the route used to cross water efficiently. It is more likely that they can somehow detect the presence of the Danish coast and minimize the distance of the sea crossing or react to local topography. The coast is visible from Falsterbo on reasonably clear days for a human observer, but we cannot tell for sure whether the red admiral butterflies have visual capacities enabling them to see the coast directly at the same distance as humans. Light reflected against water surfaces becomes linearly polarized (Wehner 2001; Horváth & Varjú 2003) and this can be detected over longer distances through an optical phenomenon, caused by fog, called 'water-sky' (Hegedüs et al. 2007). Linearly polarized light can be used by insects to detect water surfaces (Schwind 1991; Shashar et al. 2005), but such behaviour has not been studied in butterflies, and we do not know whether they can use this information to see how wide a water body is or to detect the closest land. The fact that our red admirals selected a westerly migratory direction coinciding with the shortest sea-crossing route to Denmark suggests that they can detect the coastline on the other side and orient towards it. However, this orientation also coincides with the local topography suggesting that the red admirals observed at Falsterbo react to the nearby coastline as both diurnal (Alerstam & Ulfstrand 1974) and nocturnal (Åkesson 1993) bird migrants do. Many birds seem to follow the eastern coastline of the Falsterbo peninsula and continue their flight across open water towards the west to southwest (Alerstam & Ulfstrand 1974; Åkesson 1993; Åkesson et al. 1996).

We found no difference in flight direction on days with northerly winds compared to days with southerly winds, which suggests that the red admirals compensate for wind drift. However, since the flight directions were measured using a fairly rough scale, small amounts of drift might have passed undetected. Benvenuti et al. (1994) reported the flight speed of migrating red admirals in calm weather to be around 4 m/s and the mean wind speed in our study was 4.7 m/s. A direct cross-wind situation without compensation would result in a wind drift of more than 45 degrees, a deviation large enough to be detected easily with our method of recording flight directions, suggesting that the butterflies (at least to some degree) compensated for wind drift while flying past the observation site. Other studies looking explicitly at drift compensation in single individuals of migratory butterflies found some compensation in several species when flying over water (Srygley et al. 1996), even when there were no visible landmarks available to the butterflies (Srygley 2001). When butterfly migration has been studied at inland locations, a direct effect of wind direction seems to be of less importance since the migrants fly close to the ground (e.g. Srygley & Oliveira 2001) where wind speeds are lower and they can find protection from cross-winds behind topographical features (Nielsen 1961). However, even under these conditions some wind compensation can still be present (Walker 1985). Nocturnal passerine migrants, flying at low altitudes, have been shown to follow the coastline of the Falsterbo peninsula and to compensate completely for wind drift (Site 2 in Åkesson 1993). By doing so, their orientation might deviate slightly from the mean orientation recorded for high-altitude migration passage at Falsterbo (Zehnder et al. 2001), suggesting that low-flying birds react to and fly along local topography more than the majority of the birds flying at higher altitude on migration flights. Recoveries reported shortly after ringing at the Falsterbo peninsula (Falsterbo Bird Observatory) further suggest that, at least for diurnal migrants such as the blue tit, *Cyanistes caeruleus*, a west to southwest course, very similar to what we observed for our red admirals, is kept all the way across the sea to Denmark (Åkesson et al. 1996). Blue tits also select very similar weather conditions for their migration at Falsterbo (Nilsson et al. 2006) as red admirals do.

Our observations were conducted on a narrow coastal peninsula and, thus, we cannot tell how representative our observations at Falsterbo are for the migration of red admirals across the whole southern part of Sweden. Migrating butterflies generally avoid crossing large bodies of water and follow the coastline as long as this does not lead them too far from their preferred migratory direction (Reichholf 1978). If this is true at our study site, the coastline of southern Sweden would act as a leading line to Falsterbo (Fig. 1). Even though red admiral migration has only rarely been observed at high altitudes (Mikkola 2003a), it is of course still possible that important migration from southern Sweden also takes place at high altitudes, beyond the range of visible observations. Our study, however, shows that the red admirals that are passing Falsterbo at low altitudes in autumn migrate on clear, sunny days with favourable easterly winds of low speed, and that they seem to select an adaptive migratory direction, to minimize the sea crossing. This shows that there are important adaptive similarities in the effects of wind and weather on the migratory activity and flight courses between red admirals and some species of passerine birds at Falsterbo.

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References

Åkesson, S. 1993. Coastal migration and wind compensation in nocturnal passerine migrants. *Ornis Scandinavica*, **24**, 87–94.

Åkesson, S. & Hedenström, A. 2000. Selective flight departure in passerine nocturnal migrants. *Behavioral Ecology and Sociobiology*, **47**, 140–144.

Åkesson, S. & Hedenström, A. 2007. How migrants get there: migratory performance and orientation. *Bioscience*, **57**, 123–133.

Åkesson, S., Karlsson, L., Walinder, G. & Alerstam, T. 1996. Bimodal orientation and the occurrence of temporary reverse bird migration during autumn in south Scandinavia. *Behavioral Ecology and Sociobiology*, **38**, 293–302.

Åkesson, S., Walinder, G., Karlsson, L. & Ehnbom, S. 2002. Nocturnal migratory flight initiation in reed warblers: effect of wind on orientation and timing of migration. *Journal of Avian Biology*, **33**, 349–357.

Alerstam, T. 1981. The course and timing of bird migration. In: *Animal Migration* (Ed. by D. J. Aidley), pp. 9–54. Cambridge: Cambridge University Press.

Alerstam, T. 1990a. *Bird Migration.* Cambridge: Cambridge University Press.

Alerstam, T. 1990b. Ecological causes and consequences of bird orientation. *Experientia*, **46**, 405–415.

Alerstam, T. & Ulfstrand, S. 1974. A radar study of the autumn migration of wood pigeons *Columba palumbus* in southern Sweden. *Ibis*, **116**, 522–542.

Batschelet, E. 1981. *Circular Statistics in Biology.* London: Academic Press.

Benvenuti, S., Dall'Antonia, P. & Ioalè, P. 1994. Migration pattern of the red admiral, *Vanessa atalanta* L. (Lepidoptera, Nymphalidae), in Italy. *Bollettino di Zoologia*, **61**, 343–351.

Benvenuti, S., Dall'Antonia, P. & Ioalè, P. 1996. Directional preferences in the autumn migration of the red admiral (*Vanessa atalanta*). *Ethology*, **102**, 177–186.

Brattström, O. 2006. Is there seasonal variation in size and mass of red admirals *Vanessa atalanta* on Capri, Italy. *Ornis Svecica*, **16**, 69–73.

Brown, E. S. 1970. Nocturnal insect flight direction in relation to the wind. *Proceedings of the Royal Entomological Society of London, Series A*, **45**, 39–43.

Bruderer, B. & Liechti, F. 1998. Flight behaviour of nocturnally migrating birds in coastal areas: crossing or coasting. *Journal of Avian Biology*, **29**, 499–507.

Dingle, H. 1996. *Migration: The Biology of Life on the Move.* New York: Oxford University Press.

Dingle, H. & Drake, V. A. 2007. What is migration? *BioScience*, **57**, 113–121.

Drake, V. A. 1985. Radar observations of moths migrating in a nocturnal low-level jet. *Ecological Entomology*, **10**, 259–265.

Drake, V. A. & Farrow, R. A. 1988. The influence of atmospheric structure and motions on insect migration. *Annual Review of Entomology*, **33**, 183–210.

Edelstam, C. 1972. *The Visible Migration of Birds at Ottenby, Sweden.* Stockholm: Swedish Ornithological Society.

Eliasson, C. U., Ryrholm, N., Holmer, M., Jilg, K. & Gärdenfors, U. 2005. *Encyclopedia of the Swedish Flora and Fauna. Butterflies: Hesperiidae–Nymphalidae.* Uppsala: ArtDatabanken, Swedish University of Agricultural Sciences.

Enquist, M. & Pettersson, J. 1986. *The Timing of Migration in 104 Bird Species at Ottenby: an Analysis Based on 39 years Trapping Data.* Degerhamn: Ottenby Bird Observatory.

Garland, M. S. & Davis, A. K. 2002. An examination of monarch butterfly (*Danaus plexippus*) autumn migration in coastal Virginia. *American Midland Naturalist*, **147**, 170–174.

Gatehouse, A. G. 1997. Behavior and ecological genetics of windborne migration by insects. *Annual Review of Entomology*, **42**, 475–502.

Gibo, D. L. 1981. Altitudes attained by migrating monarch butterflies, *Danaus p. plexippus* (Lepidoptera: Danaidae), as reported by glider pilots. *Canadian Journal of Zoology*, **59**, 571–572.

Gibo, D. L. & Pallett, M. J. 1979. Soaring flight of monarch butterflies, *Danaus plexippus* (Lepidoptera: Danaidae), during the late summer migration in southern Ontario. *Canadian Journal of Zoology*, **57**, 1393–1401.

Giuliani, D. & Shields, O. 1997. Migratory activity in *Vanessa cardui* (Nymphalidae) during 1992 in western North America, with special reference to eastern California. *Journal of the Lepidopterists' Society*, **51**, 256–263.

Hansen, M. D. D. 2001. Observations on migrating red admirals (*Vanessa atalanta* L.) in Denmark 1995–2000. *Flora og Fauna*, **107**, 1–5.

Hegedüs, R., Åkesson, S. & Horváth, G. 2007. Polarization of 'water-skies' above arctic open waters: how polynyas in the ice-cover can be visually detected from a distance. *Journal of the Optical Society of America A*, **24**, 132–138.

Henriksen, H. J. & Kreutzer, I. 1982. *The Butterflies of Scandinavia in Nature.* Odense: Skandinavisk Bogforlag A/S.

Higgins, L. E. & Hargreaves, B. 1983. *The Butterflies of Britain and Europe.* London: Collins.

Horváth, G. & Varjú, D. 2003. *Polarized Light in Animal Vision: Polarization Patterns in Nature.* Berlin: Springer-Verlag.

Imby, L. 1993. South migrating red admirals (*Vanessa atalanta* L.) on southern Öland. *Entomologisk Tidskrift*, **114**, 115–116.

Kjellen, N. 2006. Migration counts at Falsterbo in the autumn of 2005. In: *Fåglar i Skåne* (Ed. by M. Svensson, D. Erterius, H.-Å. Gustavsson & O. Jönsson), pp. 7–44. Lund: Skånes Ornitologiska Förening.

Larsen, T. B. 1976. The importance of migration to the butterfly faunas of Lebanon, East Jordan, and Egypt (Lepidoptera, Rhopalocera). *Notulae Entomologicae*, **56**, 73–83.

Lempke, B. J. 1971. Problems around *Vanessa atalanta* Linnaeus. *Entomologist's Record and Journal of Variation*, **83**, 199–204.

Meitner, C. J., Brower, L. P. & Davis, A. K. 2004. Migration patterns and environmental effects on stopover of monarch butterflies (Lepidoptera, Nymphalidae) at Peninsula Point, Michigan. *Environmental Entomology*, **33**, 249–256.

Mikkola, K. 2003a. Red admirals *Vanessa atalanta* (Lepidoptera: Nymphalidae) select northern winds on southward migration. *Entomologica Fennica*, **14**, 15–24.

Mikkola, K. 2003b. The red admiral butterfly (*Vanessa atalanta*, Lepidoptera: Nymphalidae) is a true seasonal migrant: an evolutionary puzzle resolved? *European Journal of Entomology*, **100**, 625–626.

Nielsen, E. T. 1961. On the habits of the migratory butterfly *Ascia monuste* L. *Biologiske Meddelelser*, **23**, 1–81.

Nilsson, A. L. K., Alerstam, T. & Nilsson, J.-Å. 2006. Do partial and regular migrants differ in their response to weather? *Auk*, **123**, 537–547.

Pollard, E. 1988. Temperature, rainfall and butterfly numbers. *Journal of Applied Ecology*, **25**, 819–828.

Pollard, E. & Greatorex-Davies, J. N. 1998. Increased abundance of the red admiral butterfly *Vanessa atalanta* in Britain: the roles of immigration, overwintering and breeding within the country. *Ecology Letters*, **1**, 77–81.

Pollard, E. & Yates, T. J. 1993. *Monitoring Butterflies for Ecology and Conservation*. London: Chapman & Hall.

Radford, J. T. 1975. Migration of *Vanessa atalanta* (Linnaeus) (Lep., Nymphalidae) and *Pieris rapae* (Linnaeus) (Lep., Pieridae) in Sussex in 1973. *Entomologist's Gazette*, **26**, 151–152.

Reichholf, J. 1978. Migration patterns of great white (*Pieris brassicae*) and red admiral (*Vanessa atalanta*) in Adriatic. *Deutsche Entomologische Zeitschrift*, **25**, 191–194.

Richardson, W. J. 1991. Wind and orientation of migrating birds: a review. In: *Orientation in Birds* (Ed. by P. Berthold), pp. 226–249. Basel: Birkhäuser-Verlag.

Roer, H. 1961. Zur Kenntnis der Populationsdynamik und des Migrationsverhaltens von *Vanessa atalanta* L. im paläarktischen Raum. *Beiträge zur Entomologie*, **11**, 594–613.

Roer, H. 1991. On the direction of migration and flight capacity of the nymphalids *Inachis io, Aglais urticae* and *Vanessa atalanta* in the central European area after recapturing marked butterflies. *Entomologische Berichten*, **51**, 179–182.

Roy, D. B., Rothery, P., Moss, D., Pollard, E. & Thomas, J. A. 2001. Butterfly numbers and weather: predicting historical trends in abundance and the future effects of climate change. *Journal of Animal Ecology*, **70**, 201–217.

Rudebeck, G. 1950. *Studies of Bird Migration*. Stockholm: Swedish Ornithological Society.

Rudebeck, G. 1951. Some observations concerning migratory movements in *Pyrameis atalanta* L. together with some general considerations. *Opuscula Entomologica*, **16**, 49–54.

Schaefer, G. W. 1976. Radar observations of insect flight. In: *Insect Flight* (Ed. by R. C. Rainey), pp. 157–197. Oxford: Blackwell Scientific.

Schwind, R. 1991. Polarization vision in water insects and insects living on a moist substrate. *Journal of Comparative Physiology A*, **169**, 531–540.

Shashar, N., Sabbah, S. & Aharoni, N. 2005. Migrating locusts can detect polarized reflections to avoid flying over the sea. *Biology Letters*, **1**, 472–475.

Sokal, R. R. & Rohlf, F. J. 1995. *Biometry: the Principles and Practice of Statistics in Biological Research*. New York: W. H. Freeman.

Srygley, R. B. 2001. Compensation for fluctuations in crosswind drift without stationary landmarks in butterflies migrating over seas. *Animal Behaviour*, **61**, 191–203.

Srygley, R. B. & Oliveira, E. G. 2001. Orientation mechanisms and migration strategies within the flight boundary layer. In: *Insect Movement: Mechanisms and Consequences* (Ed. by I. P. Woiwod, D. R. Reynolds & C. D. Thomas), pp. 183–206. Oxford: CAB International.

Srygley, R. B., Oliveira, E. G. & Dudley, R. 1996. Wind drift compensation, flyways, and conservation of diurnal, migrant Neotropical Lepidoptera. *Proceedings of the Royal Society of London, Series B*, **263**, 1351–1357.

Stefanescu, C. 2001. The nature of migration in the red admiral butterfly *Vanessa atalanta*: evidence from the population ecology in its southern range. *Ecological Entomology*, **26**, 525–536.

Stefanescu, C., Alarcón, M. & 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.

Steiniger, H. & Eitschberger, U. 1996. *Cynthia cardui* and *Vanessa atalanta* 1994. *Atalanta*, **27**, 29–32.

Taylor, L. R. 1974. Insect migration, flight periodicity and the boundary layer. *Journal of Animal Ecology*, **43**, 238.

Ulfstrand, S., Roos, G., Alerstam, T. & Österdahl, L. 1974. *Visible Bird Migration at Falsterbo, Sweden*. Stockholm: Swedish Ornithological Society.

Walker, T. J. 1980. Migrating lepidoptera: are butterflies better than moths? *Florida Entomologist*, **63**, 79–98.

Walker, T. J. 1985. Butterfly migration in the boundary layer. In: *Migration: Mechanisms and Adaptive Significance* (Ed. by M. A. Rankin), pp. 704–722. Austin: University of Texas Press.

Walker, T. J. 2001. Butterfly migrations in Florida: seasonal patterns and long-term changes. *Environmental Entomology*, **30**, 1052–1060.

Wehner, R. 2001. Polarization vision: a uniform sensory capacity? *Journal of Experimental Biology*, **204**, 2589–2596.

Wikelski, M., Moskowitz, D., Adelman, J. S., Cochran, J., Wilcove, D. S. & May, M. L. 2006. Simple rules guide dragonfly migration. *Biology Letters*, **2**, 325–329.

Williams, C. B. 1951. Seasonal changes in flight direction of migrant butterflies in the British Isles. *Journal of Animal Ecology*, **20**, 180–190.

Williams, C. B. 1958. *Insect Migration*. London: Collins.

Williams, C. B. 1976. The migrations of the hesperid butterfly, *Andronymous neander* Plötz, in Africa. *Ecological Entomology*, **1**, 213–220.

Wood, C. R., Chapman, J. W., Reynolds, D. R., Barlow, J. F., Smith, A. D. & Woiwod, I. P. 2006. The influence of the atmospheric boundary layer on nocturnal layers of noctuids and other moths over southern Britain. *International Journal of Biometeorology*, **50**, 193–204.

Zehnder, S., Åkesson, S., Liechti, F. & Bruderer, B. 2001. Seasonal and diurnal patterns of nocturnal bird migration at Falsterbo, south Sweden. *Journal of Avian Biology*, **32**, 239–248.