Butterfly survival on an isolated island by improved grip

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Evolutionary biology

On small isolated islands, natural selection is expected to reduce the dispersal capacity of organisms, as short distances do not require a high rate of dispersal, which might lead to accidental emigration from the population. In addition, individuals foregoing the high cost of maintaining flight capacity may instead allocate resources to other functions. However, in butterflies and many other insects, flight is necessary not only for dispersal but also for most other activities. A weakly flying individual would probably do worse and have an elevated rather than reduced probability of accidental emigration. Here, we report results consistent with the hypothesis that a butterfly population on an isolated island, instead of having lost its flight capacity, has evolved better grip to resist the force of wind and to avoid being blown off the island. Our study suggests that local adaptation has occurred in this population in spite of its very small size ($N_e \approx 100$), complete isolation, low genetic variation and high genetic load.

1. Introduction

Reduced or completely lost flight capacity in island populations is a classic example of evolution [1]. On small islands, dispersal by flight is not necessary because of short distances, and individuals may gain fitness by foregoing the high cost of maintaining flight capacity. However, in many insect species, flight is necessary not only for dispersal but also for foraging, competition for mates and searching for oviposition host plants [2], hence losing flight capacity would be detrimental. Furthermore, a weakly flying individual on a small isolated island would have an elevated rather than reduced probability of being blown out to the sea. Although selection is expected to minimize emigration from an isolated population, reduced or lost flight capacity is not always the likely mechanism.

The population of the Glanville fritillary butterfly (*Melitaea cinxia*) on the small Russian island of Pikku-Tyta¨rsaari (PT) in the Baltic Sea has been completely isolated on 10 ha of suitable habitat for more than 70 generations [3]. The population is small ($N_e \approx 100$) and has low genetic diversity and high genetic load, with lifetime larval production of only 30 per cent of that in a large reference population in the Åland Islands (AL). There are no differences in flight morphology between the two populations [3]. The flight metabolic rate of PT butterflies is significantly lower than in AL butterflies, but this is likely to reflect high genetic load rather than adaptation to reduced flight, as there is immediate recovery of the metabolic rate in PT/C2 AL crosses. Furthermore, there was no evidence of local adaptation in tens of morphological, physiological, behavioural and life-history traits previously studied [3].

The coastal meadow on PT is exposed to strong westerly winds (figures 1a and 2), which most probably increase the risk of accidental emigration. In the laboratory, we observed that PT butterflies were reluctant to fly off when disturbed, and in an outdoor population cage PT males flew with half the probability of AL males [3]. These observations could reflect general reluctance to initiate flight, but given the windy conditions on the island, some local adaptation could be involved. Here, we test the hypothesis that PT butterflies are...
especially good at holding onto their substrate and thereby making it less likely that they would be blown out to the sea.

2. Material and methods

(a) Study populations
PT is a 1 × 2 km island located about 30 km north of the Estonian coast in the Gulf of Finland (figure 2). The Glanville fritillary butterfly (M. cinxia) was first recorded on the island in 1936. The population was accidentally introduced by humans at the larval stage roughly 100 years (and generations) ago [3]. It has persisted on a single 10 ha shoreline meadow exposed to strong winds from the west (figures 1a and 2). The metapopulation in the ÅL, in the Gulf of Finland, includes thousands of meadows distributed across an area of 50 × 70 km [4]. ÅL was used as a large mainland-type population (N, of the order of 10 000) for comparison. See Mattila et al. [3] for rearing of larvae.

Table 1. ANOVA for the traits measured. Landscape type is isolated island (PT) versus mainland (three populations). Population is nested within landscape type. For sample sizes, see figure 1.

<table>
<thead>
<tr>
<th>capacity to hold on to the substrate</th>
<th>sex</th>
<th>landscape</th>
<th>population</th>
<th>age class</th>
<th>pupal weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>distance to airflow</td>
<td></td>
<td>n.s.</td>
<td>—</td>
<td>p = 0.0029</td>
<td>n.s.</td>
</tr>
<tr>
<td>leg features</td>
<td></td>
<td>n.s.</td>
<td>—</td>
<td>n.s.</td>
<td>n.s.</td>
</tr>
<tr>
<td>claw surface area</td>
<td>n.s.</td>
<td>n.s.</td>
<td>—</td>
<td>p = 1.3 × 10⁻¹¹</td>
<td></td>
</tr>
<tr>
<td>claw chord</td>
<td>n.s.</td>
<td>n.s.</td>
<td>—</td>
<td>p = 8.98 × 10⁻⁴</td>
<td></td>
</tr>
<tr>
<td>claw width</td>
<td>n.s.</td>
<td>n.s.</td>
<td>—</td>
<td>p = 2.65 × 10⁻⁶</td>
<td></td>
</tr>
<tr>
<td>claw curvature</td>
<td>n.s.</td>
<td>p = 0.00094</td>
<td>—</td>
<td>n.s.</td>
<td>—</td>
</tr>
<tr>
<td>metatarsus length</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
<td>—</td>
<td>p = 1.88 × 10⁻⁶</td>
</tr>
</tbody>
</table>

Figure 1. (a) Ten-year average wind speed (m s⁻¹) in June, on small islands (blue) and mainland-like sites on the Åland Islands (red) in the Baltic Sea. (b) Butterfly grip: distance (cm) to the air source, and the calculated relative airflow force, when the butterfly lost its grip, for young (less than 3 days) and old butterflies from AL (grey boxes) and PT (empty boxes) (effect of population, p = 0.0029). (c) Tarsal claw with the angle of curvature. (d) The angle of curvature of the claw in three mainland populations from Finland (ÅL), Estonia (SA) and Sweden (UP; grey boxes) and in PT butterflies (empty box; effect of landscape type, p = 0.0009; table 1). Heavy horizontal lines represent median values and numbers on top of the boxes give sample size (♂/♀) for each category plotted.
had no effect on the measurement, butterflies were similarly placed facing the airflow, and their weight. Drag and mass density of the air ($p$) are taken as constants. The force of the airflow is thus directly proportional to the coefficient of drag ($c_D$) and the surface of the object, hit by the airflow. As all butterflies’ grip was recorded. The butterfly from the hair dryer at the point when it lost its grip was recorded. The force of the airflow is thus directly proportional to the coefficient of drag ($c_D$) and the surface of the object, hit by the airflow. As all butterflies’ grip was recorded.

The Finnish Meteorological Institute provided June daily average wind speeds for a 10-year period from five meteorological stations: (i) Jomala Jomalaby (60.18’ N, 23.50’ E), (ii) Kumlinge (60.23’ N, 20.75’ E), (iii) Lemland Nyhamn (59.96’ N, 19.95’ E), (iv) Loviisa Orrengrund (60.27’ N, 26.44’ E) and (v) Kotka Haapasaari (60.29’ N, 27.19’ E). The first two stations are located within mainland ÅL, whereas the last three are small islands in the Baltic Sea, exposed to similar wind conditions as PT.

To examine the ability of butterflies to hold on to a flat and smooth wooden surface, we exposed butterflies of two different age classes (aged less than 3 days, or 3 or more days old) from PT and ÅL populations (sample sizes in figure 1b) to a cold air current from a hair dryer (Remington CW 2130, UK). The experiment took place at 20°C, at the end of the day, in a small laboratory room with low light intensity, thus minimizing the risk of the butterfly flying before the start of or during the experiment. Each butterfly was placed, without the experimenter knowing its origin, on a flat wooden surface, 140 cm away from the air source. The hair dryer was turned on and held at 140 cm for 5 s, allowing the butterfly to secure its grip under low airflow. If the butterfly was blown out or flew away at that moment, the air source was turned off and the butterfly was later reexposed to the treatment. After 5 s, the force of the airflow was increased by gradually bringing the hair dryer closer to the butterfly, at the constant speed of 25 cm s$^{-1}$. The distance of the butterfly from the hair dryer at the point when it lost its grip was recorded.

We used a ventilation meter (VelociCalc TSI incorporated, USA) to measure the velocity ($V$) of the airflow when placed 140, 110, 80, 50 and 20 cm away from the sensor. Four measurements were recorded for each distance. The force ($F$) of the air current is given by the formula $F = (1/2) p V^2 c_A$, where $p$ is the mass density of the air ($p = 1.204$ at 20°C), $c$ the coefficient of drag and $A$ the surface of the object, hit by the airflow. As all butterflies were similarly placed facing the airflow, and their weight had no effect on the measurement, $c$ and $A$ are taken as constants. The force of the airflow is thus directly proportional to the square of velocity. The mean velocity (s.d.) of the airflow at 140, 110, 80, 50 and 20 cm was 3.1 (0.39), 4.4 (0.09), 5.2 (0.42), 6.8 (0.60) and 18.9 (1.45) m s$^{-1}$.

### Meteorological data

The Finnish Meteorological Institute provided June daily average wind speeds for a 10-year period from five meteorological stations: (i) Jomala Jomalaby (60.18’ N, 23.50’ E), (ii) Kumlinge (60.23’ N, 20.75’ E), (iii) Lemland Nyhamn (59.96’ N, 19.95’ E), (iv) Loviisa Orrengrund (60.27’ N, 26.44’ E) and (v) Kotka Haapasaari (60.29’ N, 27.19’ E). The first two stations are located within mainland ÅL, whereas the last three are small islands in the Baltic Sea, exposed to similar wind conditions as PT.

The 10-year average wind speed in June at the mainland weather stations (Jomala Jomalaby and Kumlinge) was 3.92 m s$^{-1}$, while it reached 5.61 m s$^{-1}$ at the isolated island stations (Lemland Nyhamn, Loviisa Orrengrund and Kotka Haapasaari) (figure 1a).

PT butterflies were blown away when the air source was on average 35.9 cm away, while ÅL butterflies lost their grip when the air source was on average 50.9 cm away (figure 1b), corresponding to relative air forces of 111 and 45.5, respectively. Thus, the PT butterflies were able to resist two and a half times stronger force than ÅL butterflies ($p = 0.0029$, figure 1b) with no difference between the sexes or age classes (table 1).

There was no difference in the length of the metatarsus, and the tarsal claws showed similar chord, width and surface area in all populations (table 1). By contrast, tarsal claws of...
PT butterflies were significantly more curved than the claws of butterflies from the three mainland populations (97.7° versus 102.3°, P = 0.0009; figure 1d).

4. Discussion

Other things being equal, small isolated populations have lower genetic diversity and less heritable variation than large ones and may suffer from inbreeding depression and accumulation of deleterious mutations, all of which may reduce the potential for local adaptation [5,6]. Nonetheless, if the strength of selection is strong enough, even small populations may adapt to their environment [7–9], as exemplified by Darwin’s finches on the Galapagos Islands [7].

Legs and tarsal claws (figure 1c) are the most likely morphological structures influencing the grip of insects. They allow the insect to hold onto various surfaces while foraging for food resources and oviposition sites [10,11] and while copulating [12]. The setae and claws have evolved various morphologies in apparent response to the needs of insects. For instance, the Colorado potato beetle (Leptinotarsa decemlineata) shows sexual dimorphism in the structure of the tarsal setae, improving males’ grip of the smooth surface of their mate’s elytra [12]. We suggest that the more curved claws of the PT butterflies contribute to their superior grip, and potentially to the persistence of this isolated population. At mainland sites, more curved claws may impose a cost in the form of slower take-off, e.g. in response to predator attack and would therefore not be selected for.

The Glanville fritillary on PT island may represent another example of selection reducing emigration losses from isolated populations [13,14], although the mechanism is not reduced flight capacity but rather enhanced capacity to avoid being dislodged by strong wind. It is noteworthy that such local adaptation appears to have occurred in this population in spite of its small size, low genetic variation and high genetic load [3].

Windy conditions may pose other challenges apart from the risk of accidental emigration. In windy conditions, the handling of flowers by pollinators becomes more difficult. Previous studies have demonstrated that pollinators preferred moving flowers with conical epidermal cells in petals, which are easier for the insects to hold on after landing and thereby facilitate pollination [15,16]. It is possible that the improved grip of the Glanville fritillary on PT island has evolved in relation to nectar feeding in windy conditions. If so, one could expect similar adaptations in other pollinating insects and perhaps related adaptations in plants.

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References