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ORIGINAL PAPER

Radio telemetry helps record the dispersal patterns of birdwing butterflies in mountainous habitats: Golden Birdwing (*Troides aeacus*) as an example

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Abstract

Birdwing butterflies are a monophyletic group of swallowtail butterflies (Papilionidae) protected by national and international laws and often serve as flagships of insect conservation. Selecting the Golden Birdwing (*Troides aeacus*) as an example, we demonstrate an effective way to simultaneously record the activity of multiple birdwing butterflies using radio telemetry in hard-to-access mountainous terrain. During the summer flight period of *T. aeacus* (June and July), a single researcher was able to obtain 30-min records of movement patterns for ten individuals for an average of 4 days by fastening 0.22 g transmitters onto the butterflies, in the mountainous valleys of Mt. Gongga, China. The maximum distance the butterflies traveled over the 4 day period was 4314 m away from the starting location. During this time, the average dispersal rate was 38.07 m/h ($n=9$, $sd=85.11$); average movement speed was 293.48 m/h ($n=9$, $sd=121.45$). Flight patterns of butterflies collected from low and high elevation habitats showed no significant differences. Activity levels of individuals from both low and high elevation habitats track diurnal fluctuation in temperature. Flight activity is positively correlated with temperature and negatively correlated with humidity. Our data provide basic parameters of real-time flight activity and dispersal ability for a species of conservation importance. The methodology is highly suitable for monitoring endangered lepidopteran species in otherwise difficult-to-access terrain.

Keywords Birdwing butterfly · Conservation · Insects · Mt. Gongga · Radio telemetry · Radio tracking · *Troides aeacus*

Introduction

Understanding animal movement is fundamental to developing conservation management plans. This is often accomplished through GPS tracking in relatively large animals such as birds and mammals (e.g. Kays et al. 2015; Tucker et al. 2018). For smaller invertebrates such as insects, studies of movement have relied upon mark-recapture techniques (e.g. Roland et al. 2000), sometimes combined with modeling (e.g. Turchin and Thoeny 1993; Brown and Crone 2016), and passive tagging techniques such as harmonic radar (e.g. Drake and Reynolds 2012) and radio frequency identification (RFID) (e.g. Schneider et al. 2012). To actively track insect movements, recording theodolites have been employed to track butterflies in three dimensions over short distances (ca 25 m) (e.g. Zalucki et al. 1980). At two dimensions, very high frequency (VHF) radio transmitters are also used to understand the exact movement patterns of insects (e.g. Kissling et al. 2014). Transmitters as light as 0.2 g have been successfully used in studies of bumblebees (Hagen et al. 2011), beetles (Svensson et al. 2011), dragonflies (Levett and Walls 2011), crickets (Fornoff et al. 2012) and moths (Liégeois et al. 2016). Tracking using quick response (QR) codes (e.g. Mersch et al. 2013; Crall et al. 2018) or automated scan or artificial intelligence (AI) techniques (e.g. Ulrich et al. 2018) can provide full information for movement patterns at short ranges (such as within the

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nest), but are not suitable for following flying insects in the field over unpredictable terrain.

Active radio tracking with VHF radio transmitters is not without drawbacks. Unlike GPS data, where individuals can be localized in real time; radio tracking requires triangulation (taking bearings at multiple localities) to estimate the position of the transmitter. Ideally, a search team would simultaneously take bearings of the same target at multiple localities, or employ aerial surveys to cover large landscapes. A costly but automated process was developed by Kays et al. (2011) by setting up multiple receiver stations across a known area. In conservation projects with limited budget or personnel, however, triangulation is often done by the same researcher moving throughout the terrain to obtain multiple bearings. This approach is problematic if (1) the terrain is difficult for the researcher to move across or (2) the target carrying the transmitter is expected to move long distances between measurements.

The birdwings, a monophyletic group of Papilionidae comprising the genera *Trogonoptera*, *Troides*, and *Ornithoptera*, are a group of large swallowtail butterflies known for their spectacular wing coloration and for including species of extreme rarity (Wallace 1869; Parsons 1998; Matsuka 2001; Wilts et al. 2015; Condamine et al. 2018). Specimens of birdwings are avidly traded and collected worldwide, and all species are listed in the appendices of Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). They are also important flagship species in conservation (Sands 2008; Sands and New 2013). Among the Lepidoptera with the largest forewing lengths and heaviest body weight, the birdwing butterflies are ideally suited to be studied using active radio telemetry, and the results can help conservation practitioners develop effective conservation policies.

Difficulties of using radio telemetry to study these species include (1) They are restricted to the tropics and subtropics of the Indo-Australian region (Condamine et al. 2015, 2018) in countries where biologists often have limited resources and costly triangulation methods are not sustainable (Da Fonseca 2003; Yale Center for Environmental Law & Policy [YCELP] 2018); (2) Birdwing habitats are often mountainous forests (D'Abrera 1975; Matsuka 2001), making the movement of the researcher required for triangulation challenging (Vlasanek et al. 2013); (3) Birdwing butterflies, as their name suggests, are known for robust flight—their positions can shift rapidly between the two consecutive bearing measurements (although this is the first study to estimate their dispersal ability).

In this study, we report the results of applying radio telemetry techniques to the Golden Birdwing (*Troides aeacus*) in the mountainous valleys of Mt. Gongga, western China. Instead of using multipoint triangulation of the signal bearing, all samples were monitored with a single researcher at a fixed point. By noting the signal strength from multiple directions at a fixed position, a single researcher was able to track movements every 30 min over an average of 4 days for each of ten individual butterflies across relatively inaccessible mountainous terrain (only ten freshly-eclosed *T. aeacus* were obtained because the valley terrain tremendously reduced the researchers' mobility). From this dataset, we examined three questions: (1) what are the differences in flight patterns between individuals of *T. aeacus* collected from relatively high (2128 m) and low (1937 m) elevations? (2) Does *T. aeacus* activity correlate with specific environmental variables? (3) Do adults of *T. aeacus* show particular habitat preferences? We hypothesized that butterfly activity levels, measured as distance traveled per unit time, should be greatest at solar noon when the sun has reached its azimuth but temperatures have not yet peaked, as observed by Niitepõld et al. (2009).

Apart from elucidating the detailed flight behaviour of an endangered lepidopteran species, we hope our methodology will be useful to conservation practitioners working in hard-to-access terrain with low-budget programs to monitor species of interest and thereby make informed conservation decisions.

Materials and methods

A schematic representation of our experimental procedure is shown in Fig. 2.

Study area

Studies were conducted at Yanzigou valley, Mt. Gongga (Fig. 1). Mt. Gongga is the highest peak of the Hengduan mountain region. The area is known as a "region of extreme relief" mountain topology (Irving and Hebda 1993) and has high biodiversity (Boufford and Van Dyck 1999; Boufford 2004). Yanzigou Valley is one of the four major glacier valleys on the eastern side of Mt. Gongga, formed during the peak of the last glacial maximum (Wang et al. 2013). The river flowing through this valley extends more than 20 km from west to east, from the terminus of the Yanzigou Glacier (3680 m) until it merges with the Moxi River at the eastern side of Mt. Gongga around 1900 m. Vegetation in this location ranges from alpine grassland to temperate forest. The upper region of the valley is mostly undisturbed alpine grassland. The middle region of the Yangzigou Valley (2000–3000 m) remains mostly undisturbed, except for a 'bottled-water' plant at 2200 m and some sparse land clearings made for livestock grazing. The lower part of the valley is inhabited by 200 villagers, and land has been partly converted into maize and cabbage crop fields. A road connecting the villages at

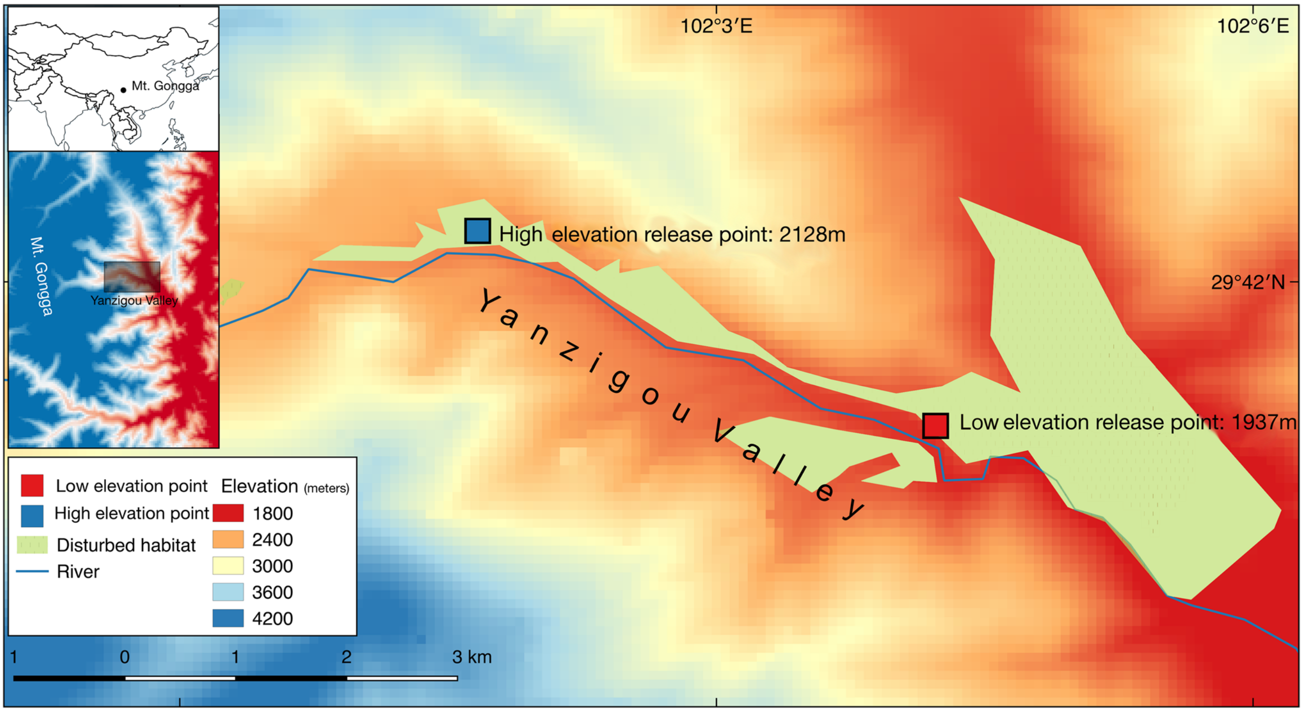


Fig. 1 Our study site, Yanzigou Valley, along the eastern slope of Mt. Gongga. The red square indicates the location of low elevation telemetry measurements (June 13th to June 18th); the blue square indicates indicates the location of high elevation telemetry measurements (July 9th to 14th). Disturbed habitat is indicated in green. The river originates from the Yanzigou Glacier at the foothill of Mt. Gongga and flows west to east out of the valley. The inset maps show the location of Mt. Gongga in China and several parallel glacial valleys on the eastern side of Mt. Gongga. (Color figure online)

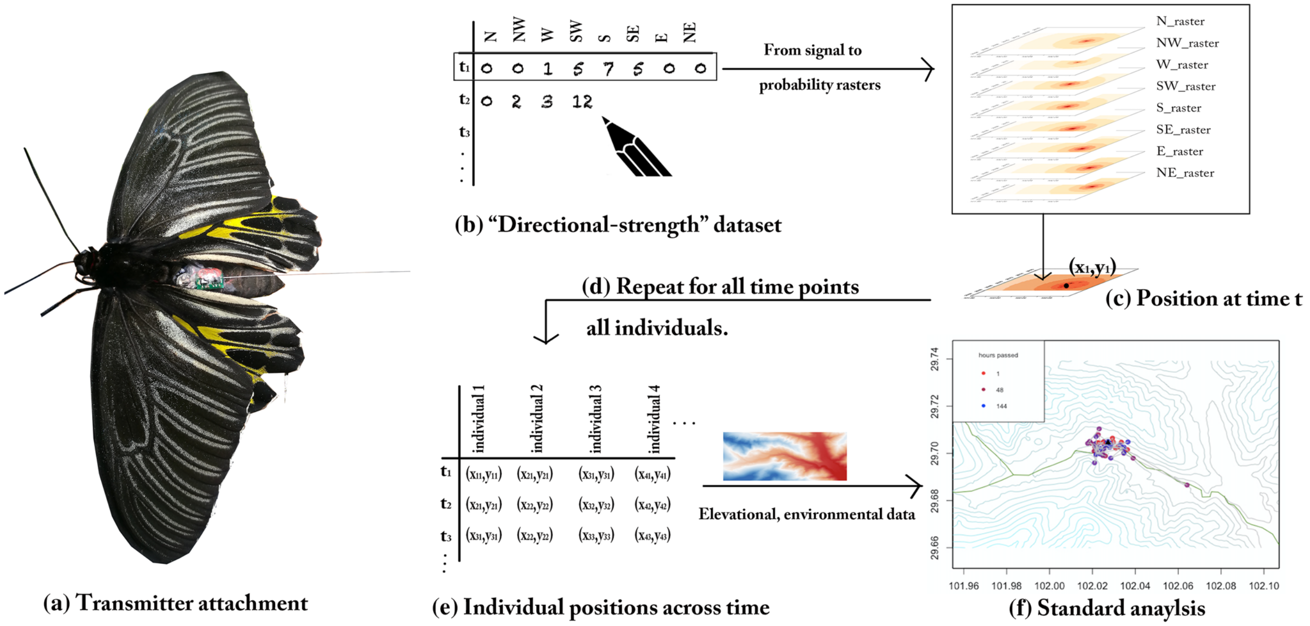


Fig. 2 Schematic representation of methods in this study. **a** LB-2X transmitters (Holohil Systems Ltd., Carp, Ontario, Canada) are attached at the anterior dorsal side of the sample. A female *T. aeacus* is shown. **b** Every 30 min, at the same location as the release point, the signal strength of the butterfly transmitter is noted when detected from eight different directions. **c** From each direction, the position of the butterfly is estimated, and the weighted sum of these layers are used to determine the final position of the butterfly at time t. **d**, **e** Repeat procedure **c** to obtain the most likely position of all individuals across time. **f** Combine elevational and environmental data for analysis of butterfly dispersal. The figure shows the flight trajectory of individual no. 4 released at high elevation release point

the lower end of the valley to the glacier was built along the river, although it is frequently blocked by landslides. Villagers move along the valley either by motorcycle or on foot, tending livestock and collecting wild plants as herbal medicines, including *Gastrodia elata* and *Paris quadrifolia* at mid-level elevations, and the entomopathogenic fungus *Ophiocordyceps sinensis* and flowering plant *Fritillaria cirrhosa* at higher elevations.

Sample preparation

Preliminary observations were conducted from May to July, 2016, to understand the difference in emergence time of *T. aeacus* at different habitats. In the following year of 2017, to ensure butterflies used in the telemetry study were newly enclosed, we started observing both the low and high elevation habitats 2 weeks before any samples were seen. Only fresh specimens with intact wings were captured. At the low elevation release point (Fig. 1), five male *T. aeacus* were captured between June 13th and 14th (average forewing length = 14.02 cm ± 0.40). At the high elevation release point (Fig. 1), four males and one female *T. aeacus* were collected on July 9th (male average forewing length = 14.21 cm ± 0.66; female forewing length = 15.68 cm). Specimen collection stopped after samples with transmitters attached had been released to avoid accidental recaptures.

Transmitter attachment

Once a *T. aeacus* individual was captured, its wings were gently held together with a small clip and the individual was placed in a small cooler for 20 min to reduce activity. Butterflies were not allowed to come into direct contact with the ice in the cooler. The butterfly was then removed from the cooler, and a LB-2X transmitter (Holohil Systems Ltd., Carp,Ontario, Canada) was attached at the anterior-dorsal side of the abdomen with fortified glue (“Gelianghao AB” fortified glue, Fig. 2a). The butterfly was restrained for another 20 min in the shadow to allow the glue to dry and to prevent the possibility that butterfly movements might shift the position of the glue and the transmitter. Each transmitter weighed 0.22 g and included a 140 mm long antenna. Each had a battery life of 7 days and a unique frequency within the range of 148–151 MHz. Before attachment, the transmitter was activated by a solder connection to the battery, and the best reception frequency was verified using an R410 receiver (Advanced Telemetry Systems, Isanti, MN). The butterfly was released after the transmitter was secured and the individual signal’s on the receiver confirmed. Tracking started 30 min after the butterfly was released.

Transmitter calibration

The strength of transmitter signals could be read directly from the screen of the R410 receiver in discrete but arbitrary units from 0 to 18. At signal level 0, nothing appears on the receiver screen, but a constant beeping sound is still emitted. The beeping sound at signal level 0 was manually divided into levels of large, medium and small according to its amplitude, and noted as 0.7, 0.3 and 0.1 accordingly. The receiver was always maintained at maximum radio frequency (RF) gain. The maximum distance at which the signal could still be detected was measured while the transmitter was attached to the dorsal side of a volunteer walking along the valley. From “low elevation release point” (Fig. 1), the volunteer with transmitter walked both upstream and downstream along the valley, then crossed the valley. We monitored how signal strengths changed as the position of the volunteer changed to calibrate our positional inference model.

Data collection

Data of butterfly movements were collected from June 13th to June 18th and from July 9th to July 14th, 2017. Every 30 min from 8:00 AM to 4:30 PM, a “directional-strength” dataset was measured for each butterfly carrying a transmitter, at the location of butterfly release. In other words, data were taken for 5 *T. aeacus* at the low elevation release point from June 13th to June 18th, and for 5 *T. aeacus* at the high elevation release point from July 9th to July 14th. Humidity, temperature and weather were also noted every 30 min (see Supplementary Data). No data were taken during rain to avoid lightning striking the researcher holding the antenna.

A “directional-strength” dataset is composed of the signal strength (21 ordered factors including “small”, “medium”, and “large” as described above, and numbers ranging from 1 to 18) that the target transmitter emitted when the receiver antenna was pointing to the direction of north, north-west, west, south-west, south, south-east, east and north-east (Fig. 2b). To minimize signal obstruction from the mountains, the receiver antenna was pointed parallel to the ground topology (e.g. when detecting for signal from the mountainous north-east direction at the high elevation habitat, the receiver antenna was pointed upwards to avoid directly pointing into the mountains). Our setup is similar to the design of the single automated telemetry system of Kays et al. (2011), but instead of locating the exact bearing by finding the direction of maximum signal, signal strength (with maximum RF gain) is noted at eight fixed directions. At the end of each day, for butterflies that lost signal for the entire day at their release locality, a trans-valley search was conducted in an attempt to relocate them along the valley. The researcher travelled along the valley by motorcycle and several more "directional-strength" measurements were made at upper, middle and lower sites within the valley.

Analysis

All data were processed and analyzed in R v.3.11 (R Development Core Team 2015). Each "directional-strength" dataset (eight measurements) was converted into a single coordinate on the map with a probability estimate indicating the butterfly's location (Fig. 2c–e; see Supplementary Material for detailed algorithm). After obtaining a time-labeled coordinate series for each butterfly, basic dispersal statistics such as flight path, dispersal distance, movement speed and directionality were calculated. A 90 m resolution elevational map of the study region was obtained from the NASA Shuttle Radar Topographic Mission (SRTM) (Jarvis et al. 2008) to relate coordinate changes to elevational changes. We used general independence tests (in R package "coin", Hothorn et al. 2006) to test whether sex has a significant influence on individual butterfly flight statistics and whether individuals collected at high and low elevations differed in their flight pattern. Pairwise correlation tests using Pearson's product moment correlation coefficient (Pearson 1895) were used to assess the relationship between individual forewing length and flight statistics, and examine the relationship between dispersal statistics and temperature, humidity, and time of day, as well as verifying whether butterfly activity levels showed any diurnal patterns. The correlation of these variables with previous dispersal statistics and environmental statistics was also tested. We built a regression model using all of these variables (Chambers 1992). R "phuassess" package (Fattorini et al. 2017) was used to test for habitat preference of the butterflies. Habitat type was labeled as "disturbed farm land" or "undisturbed forest" according to our preliminary field survey.

Results

Transmitter detection and calibration

When RF gain of the receiver was set to the maximum and the antenna was pointing in the direction of the volunteer fixed with transmitter, the maximum signal detection was around 1500 m regardless of whether the volunteer was walking upstream or down stream from the valley. When the volunteer crossed the valley, the signal strength was maximized when receiver was pointed at the direction of the volunteer. The volunteer could not move more than 1500 m away from the receiver when walking perpendicular across the valley. Accordingly, we modeled the distribution of our distance-signal strength relationship by the inverse square law with a maximum detection range of 1500 m at a fixed point. We found no significant correlation between butterfly activity level and time passed since release of the butterfly (Supplementary Fig. 3). During the week-long data collection period, an average signal lasted 78.13 h (n = 10, sd = 49.56) after the release of individual. A total of 991 "directional strength" datasets were recorded (see Supplementary Data), 376 of which provided strong signals that were then converted to coordinate positions according to our model. Detection signals were distributed evenly throughout the day and evenly through the entire detection period (Supplementary Figs. 1, 2). Individual forewing length and sex were not significantly correlated with any butterfly flight pattern data. One male from the low elevation site was not detected and apparently lost after release, and this specimen was excluded from subsequent statistical analyses of butterfly flight patterns.

Flight pattern and dispersal statistics

We analyzed the flight patterns of the ten individual butterflies visually (Supplementary Fig. 8; dispersal statistics in Table 1). Individuals on average moved 876.10 m over the 4 day observation period (n = 10, sd = 1258.79, median = 489.89), and the maximum distance traveled from the starting location was 4314 m. During this time, the average dispersal rate, calculated as final sample displacement over observation period, was 38.07 m/h (n = 9, sd = 85.11, median = 5.60); average movement speed, calculated as sample displacement between two intervals of signal detection, was 293.48 m/h (n = 9, sd = 121.45, median = 305.02). Individuals collected from high and low elevation sites exhibited no statistically significant differences in flight pattern (Table 2).

Environmental influence on butterfly activity

Speed of individual butterfly movement during a detection period was used as a proxy for the current activity level of the individual. Activity level of butterflies from both low and high elevations tracked the diurnal fluctuation in temperature (Fig. 3). Flight activity is significantly positively correlated with temperature (Pearson's product-moment correlation = 0.13, t = 2.46, df = 347, p-value = 0.01) and (not surprisingly, since humidity is also negatively correlated with temperature) negatively correlated with humidity (Pearson's product-moment correlation = − 0.09, t = − 1.70, df = 347, p-value = 0.09) (Supplementary Figs. 4, 5, 6, 7). For individuals released at the high elevation release point, the temperature of the release location was positively correlated with the elevation of the individual butterfly being tracked (Pearson's product-moment correlation = 0.19, t = 2.66, df = 186, p-value < 0.01). A similar positive trend holds for butterflies released at the low elevation point, although this

Table 1 Flight statistics of ten *T. aeacus* observed in the study

ID	Detection time (h)	Number of detections	Final distance moved (m)	Final direction moved (°)	Final elevation moved (m)	Direction moved per step (°)		Elevation moved per step (m)		Movement speed per step (m/h)		Dispersal rate (m/h)
						Mean	sd	Mean	sd	Mean	sd	
Low_1	88.76	40	387.22	151.61	−97	−22.9	108.18	−2.49	68.98	321.5	232.67	4.36
Low_2	0	1	0	0	0	NA	NA	NA	NA	NA	NA	NA
Low_3	102.75	81	362.93	147.39	7	−7.22	106.98	0.09	64.75	374.72	236.27	3.18
Low_4	2.25	6	592.55	−90.62	−163	−70.31	89.8	−32.6	67.64	208.8	130.83	263.35
Low_5	121.75	48	1215.52	−30.65	−185	−5.31	102.3	−3.94	72.59	300.75	249.41	9.98
High_1	53.25	15	825.58	−116.97	183	22.21	117.15	13.07	121.23	441.97	358.89	15.5
High_2	122.5	83	685.47	−25.67	−119	0.8	107.4	−1.45	122.61	301.21	218.05	5.60
High_3	123.5	5	4314.03	−30.91	−238	−93.93	69.28	−59.5	152.65	18.78	27.00	34.93
High_4	121.5	67	246.45	−178.94	62	10.78	104.22	0.94	135.25	305.02	221.80	2.03
High_5	45	30	167.26	−135.9	−57	5.71	106.56	−1.97	89.76	368.59	226.31	3.72

was not statistically significant. The activity levels of butterflies also significantly increased with the elevation of its current estimated position (Pearson's product-moment correlation = 0.19, t = 2.64, df = 193, p-value < 0.01). Our best fit model to explain individual activity level involved modeling time as a quadratic polynomial, with time being the only significant regressor (Adjusted R-squared: 0.02058, F = 5.72, df = 343, p-value = 0.004) (Supplementary Table 1 for model selection; Supplementary Tables 2, 3 for parameters of the selected model). When individual sample variance is considered a mixed effect in the selected model, it does not make a significant difference (Chi square = 2.0615, p = 0.1511).

Habitat preference

While only 27.4% of our 28.5 km^2 detection area was categorized as "disturbed habitat" (Fig. 1), a significantly higher 60.74% of our detections were made in this habitat (1000 bootstrap followed by student *t* test, 95% mean confidence interval = 0.56–0.66, t = 417.12, df = 999, p-value < 0.001). Permutation tests of habitat usage (Fattorini et al. 2017) show significantly higher preference for disturbed habitat (512 permutations, p < 0.01).

Discussion

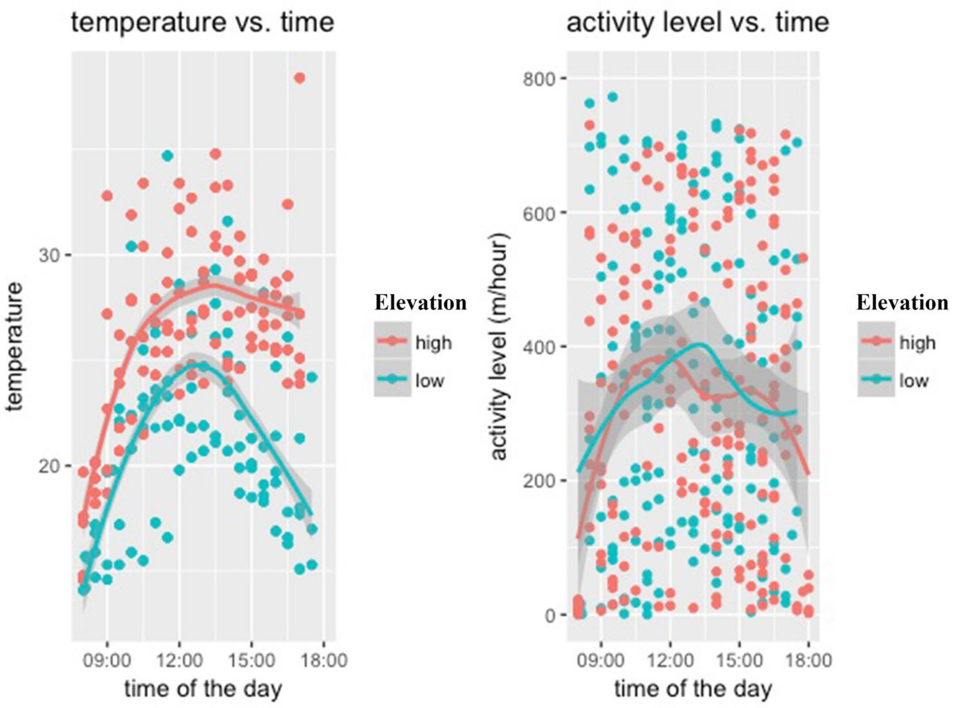
Advantages and limitations of telemetry without triangulation

In our telemetry study, we assumed that individuals did not disperse to other valleys. Mountain peaks separating the valleys are at least 3600 m high (Fig. 1); *Troides* have never been recorded at such a high elevation. Thus we assumed that our telemetry search area across the valley covered both the home range and potential dispersal range of our sampled populations.

The effect of the transmitter on butterfly flight behaviour was not directly tested for logistic reasons: once released, recaptures of the tested individuals required for measuring metabolic costs are difficult. Although Hagen et al. (2011) suggested that transmitter attachment on bumblebees might decrease their rate of flower visitation, Liégeois et al. (2016) tested similar cases using a much smaller lepidopteran, *Paysandisia archon*, flying in a wind tunnel while carrying a 0.27 g transmitter, and found no observable difference in flight behaviour. Srygley and Kingsolver (2000) added weight up to 15% of a banded peacock butterfly's (*Anartia fatima*) body weight and found no effect on its flight speed and ability to avoid capture. In other telemetry studies, standard transmitters can sometimes account for one third of the body weight of the target (Kissling et al. 2014), while our transmitter only accounted for approximately 20% of

Table 2 Results of general independence tests for differences between the flight statistics of low and high elevation samples

	Low elevation mean	High elevation mean	n	Z-value	p-value
Detection time (h)	63.10	93.15	10	0.95853	0.3378
Number of detections	35.20	40.00	10	0.24145	0.8092
Final distance moved (m)	630.56	1247.76	9	0.7107	0.4773
Final direction moved (°)	− 31.37	− 97.68	9	− 1.0025	0.3161
Final elevation moved (m)	− 109.5	− 33.8	9	0.85092	0.3948
Direction moved per step (°)	− 12.35	4.50	376	1.5155	0.1296
Elevation moved per step (m)	− 2.56	− 0.87	376	0.16092	0.8722
Movement speed per step (m/h)	337.40	316.84	376	− 0.82726	0.4081
Dispersal rate (m/h)	70.22083	12.35524	9	− 1.0135	0.3108


temperature vs. time

activity level vs. time

Fig. 3 Temperature and butterfly activity tracked over time. Red dots indicate data collected at the "high elevation release point" in Fig. 1; blue dots indicate data collected at the "low elevation release point" in Fig. 1. Lines indicate Lowess-smoothed conditional means. (Color figure online)

the weight of a typical *T. aeacus* butterfly. A newly captured *T. aeacus* male with 6.43 cm forewing length weighed 1.00 g, and a female with 8.40 cm wingspan weighed 1.11 g. In Malaysia, male *Troides helena cerberus* weigh 1.9–2 g, and female *Trognoptera brookiana* weigh 1.3–2 g (Barlow 2018, Pers. Comm.). These studies and measurements give us confidence that handling the butterflies and attaching transmitters to them did not have a significant impact on their flight performance, but any measurements provided here must necessarily provide only an underestimation of the true flight abilities of these butterflies. We note that Li et al. (2010) found that nectar resources were more important than *Aristolochia* larval food plants to explain the movement of *T. aeacus*. More than 50 flowering plants have been found in the habitat we studied (for a study in vegetation see Cheng et al. 2018). If attaching transmitters have additional energetic costs, this will lead to more frequent nectaring behaviour of *T. aeacus*. In the habitat we have observed *T. aeacus* nectaring on flowers of *Toxicodendron succedaneum, Elaeagnus umbellata* and *Vibernum* sp., but individuals of *T. aeacus* carrying a transmitter could not be visually distinguished from those not carrying one. A positive correlation between butterfly activity level and time passed since capture might indicate increased nectaring behaviour; conversely, a negative correlation might indicate that the transmitter was dragging down the carrier; however, we found no evidence for neither scenario in our analyses (Supplementary Fig. 3). The nectaring behaviour of *T. aeacus* requires further investigations.

The methods developed in this study were specifically designed to be used in terrains where triangulation would be difficult. Instead of obtaining multiple bearings at different localities, our method leverages the fact that although a single signal strength measurement might be uninformative, a set of such measurements from a fixed point can inform the observer both of its distance from the target and its bearing to the target (by the Inverse Pythagorean theorem, see Supplementary Material) (Wastlund 2010). In our analyses, signal strength was used to reflect both the distance of the transmitter conditioning on a single direction, as well as to give statistical weight to the set of likely positions obtained.

The maximum reception distance may vary depending on the transmitter–receiver pair used and on the specific topology of the study area, so to build our model, this distance was measured at the beginning of the experiment in order to obtain topology-specific parameters for the valley. When the butterfly was hidden in dense vegetation, our signal might be significantly obstructed. This might be a major reason of not getting any signal for several measurements. Our data thus only represent a measure of *T. aeacus* location when moving across and above the canopy.

The biggest limitation of the current method (i.e. not taking multiple bearings) is that our positional estimate perpendicular to the valley might be inaccurate due to signal obstruction of the mountains. Our model assumed that the reception range of a transmitter is constant regardless of the movement direction of the object in relation to the direction of the valley. Further studies should aim at providing better calibration between signal strength and transmitter distance when movements are perpendicular to the direction of the valley.

An alternative approach when triangulation is not possible would be to take the bearing of the target and its signal strength, and then estimate distance from the inverse square law, but our current procedure had the advantage of being faster and easier to standardize in a low-budget conservation monitoring program. It is faster for a single observer to turn in a 360° circle and record eight data points than to turn back and forth to try to find and record a bearing; this was especially true in situations when the observer was monitoring multiple butterflies simultaneously.

On average our transmitter signals lasted for 4 days, which is comparable to the monitoring time span obtained in telemetry studies using similar types of transmitters (Hagen et al. 2011; Svensson et al. 2011; Liégeois et al. 2016). However, the current study did not require costly aerial flights or significant movement from the researcher. Signals were distributed evenly throughout the day and evenly throughout the entire monitoring period, suggesting no special signal detection window (Supplementary Figs. 1, 2). A transmitter's signal could be lost because: (1) the individual flew out of the 1500 m detection range—this did not happen in our case since we surveyed the entire valley at the end of each data collection day; (2) signal obstruction, either because the individual was hidden in the bushes or the transmitter became damaged due to predation; (3) the battery ran out. The cost of not manually triangulating the individual was that transmitters were permanently irretrievable for each individual.

Troides aeacus ecology

In preliminary fieldwork conducted in the summer of 2016, we noted that *T. aeacus* adults could be seen at the "low elevation point" of Yanzigou Valley in early June, but did not occur in the "high elevation point" in the Valley until mid-July. This could be interpreted to suggest that individuals of *T. aeacus* occurring at different elevations in the valley belonged to two different populations with a 1 month difference in eclosion time between them because (1) the recorded lifespan of adult *T. aeacus* is 9–14 days (Li et al. 2010), while the difference in occurrence time of the two populations in our study was more than one month; (2) *T. aeacus* found at higher elevations in July had fresh and complete wings, suggesting that they were newly emerged adults. In this interpretation our analysis did not show significant differences in the flight patterns and dispersal patterns of these two populations. Interestingly, the hostplants of *T. aeacus*, a species of *Aristolochia,* were only found at the "high elevation release point" inside the valley, and not at the "low elevation release point" in the valley. This suggests that in early June, the low elevation population emerges from the high elevation habitat and migrates to the lower end of the valley, possibly because it is warmer at the lower elevation site. Another interpretation not inconsistent with the "two populations" hypothesis is that between June and July, individuals from a single population continuously emerges from the high elevation habitat, where hostplants are present. Early-emerged butterflies of this single population fly at low elevation only, while later-merged butterflies, consisting of females, visit the high elevation habitat more often. In this scenario, no difference in any dispersal statistics between "populations" are expected to be found. Our movement visualization have also shown that individuals are clearly capable of flying between the distance of "low" and "high" habitats.

Although no estimates have previously been made of the dispersal distances of birdwings, the 38.07 m/h dispersal rate obtained in our study corresponded to the high end of the range of butterfly dispersal distances compiled by Sekar (2012). The same study also found that dispersal ability positively correlated with wing span. We noticed in our study that a few high elevation individuals dispersed more that 4 km along the valley within a few hours of their release. This suggests that individuals of *T. aeacus* have strong dispersal capabilities across the landscape. Li et al. (2010) treated *T. aeacus* populations from microhabitats as distant as 6 km apart as a single metapopulation based on habitat measurements and mark-recapture. Overall, a combination of telemetry data, mark-recapture studies (Roland et al. 2000; Beirão et al. 2012; Li et al. 2013, 2016) and a careful modeling approach (Schultz and Crone 2001; Brown and Crone 2016) would be the best approach in elucidating the dynamics of butterfly population dispersion in this species.

Our results support the hypothesis that butterfly activity levels reflect change in time (Fig. 3; Supplementary Figs. 4, 5, 6, 7). Niitepõld et al. (2009) found similar results using harmonic radar tracking and time series modeling of Glanville fritillary butterflies (*Melitaea cinxia*) for 5 min intervals: flight metabolic rates of *M. cinxia* increased with temperature. Since both humidity and temperature followed a cyclic relationship with time, peaking and dropping at noon, time was selected as a second degree polynomial in our regression model and significantly explained variation in butterfly activity levels (Supplementary Tables 1, 2, 3). Although time of day, temperature, and humidity were correlated, our data suggest that it is probably the circadian cycle rather than simply the temperature that influences the activity level of the butterflies. Temperature measured in this study was the temperature at the focal individual's release location (that is, "high elevation release point" or "low elevation release point" in Fig. 1) rather than the temperature of the butterfly's current position. We noticed a positive correlation between the temperature of the release location and the elevation of the butterfly's current position—suggesting that butterflies might fly to higher elevations when temperature increases, possibly to modulate body temperature.

A significantly disproportionate number of butterflies were observed in disturbed habitats. Although this might have been confounded by the fact that (1) habitats along the valley were disproportionately disturbed due to ease of human access, and (2) butterflies were captured and released in disturbed habitats (due to ease of capture), this result was nevertheless consistent with the habitat modeling results of Li et al. (2010), which suggest that *T. aeacus* prefers open habitats to dense canopy. Similar behaviour has been noted in other accounts of birdwing sightings and breeding projects (D'Abrera 1975; Matsuka 2001; Sands and New 2013). This can be attributed to the abundance of *Aristolochia* hostplants in open habitats as well as the availability of nectar sources for the adults.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Research involving human and animal participants No *T. aeacus* was harmed during transmitter attachment. All *T. aeacus* collected for the experiment were released.

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