



## Are all butterflies equal? Population-wise proboscis length variation predicts flower choice in a butterfly

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Intraspecific morphological variation fundamentally influences individual resource exploitation. In plant–pollinator systems, variation in floral morphologies and pollinator mouthparts may affect pollinators' resource use. This relationship has frequently been studied across species, but hardly ever at the intraspecific level in natural circumstances. We studied flower visits of clouded Apollo butterflies, *Par-nassius mnemosyne*. (1) We investigated whether proboscis (mouthpart) length variability influenced individual nectar plant choice within a single population. We hypothesized that flower depths would constrain butterflies' flower visits via their proboscis lengths. (2) We studied whether individual proboscis length constrained feeding on the sticky catchfly, *Silene viscaria*, a species with ample nectar and the deepest corolla among the plants visited. We hypothesized that individuals observed visiting *S. viscaria* had longer proboscides than those not observed on this nectar source. We captured clouded Apollos, then measured proboscis length. We surveyed the population daily, identified marked individuals and recorded feeding on nectar plant species. We compared proboscis length to the flower depth of the six most-visited nectar plants and investigated whether individual visits on flowering plants were related to proboscis length. We found large intrapopulation variation in proboscis length, and high intra- and interspecific variation in flower depth of the six nectar plants. Flower depth of *S. viscaria* largely overlapped with proboscis length, while the other five plants had shorter flowers. Individuals with longer proboscides visited *S. viscaria* flowers more often than those with short proboscides. These results indicate the importance of morphological variation in the interaction between plants and pollinators. We provide the first evidence that individual variation in mouthpart length affects lepidopteran foraging in natural circumstances. We suggest that interactions between species in plant–pollinator systems are partially based on individually different continuous traits, rather than on well-defined discrete traits of different taxa as implied by the pollination syndrome hypothesis.

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Intraspecific morphological and behavioural variation are essential in evolution: interactions of a population phenotype in changing environmental circumstances shape population traits through differential survival and reproduction (Bolnick et al., 2003; De León, Rolshausen, Bermingham, Podos, & Hendry, 2012; Grant & Grant, 2014; Miller-Struttman et al., 2015; Pauw, Stofberg, & Waterman, 2009; Pratt, 2005). Intraspecific morphological

variation fundamentally influences individual resource exploitation (Grant & Grant, 2014; Pauw et al., 2009). Although the number of studies investigating individual level resource use has rapidly increased in the last few decades (Araújo, Bolnick, & Layman, 2011; Dall, Bell, Bolnick, & Ratnieks, 2012; Layman, Newsome, & Gancos Crawford, 2015), these studies are still biased towards vertebrates; relatively little is known about individual level variation in resource use by insects and even less on how morphology influences individual foraging behaviour.

Animals select from available resources for optimal intake, and food resource acquisition determines an animal's survival and reproductive success (Stephens, Brown, & Ydenberg, 2007). Food resource availability impacts foraging behaviour, as well as

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population size and, in consequence, the composition of communities (Stephens et al., 2007). Intraspecific variation in mouthpart morphologies has been proved to be the basis of microevolutionary processes through resource use (gastropods: Watanabe & Young, 2006; birds: De León et al., 2012; Grant & Grant, 2014). Although flower-visiting insect pollinators are suitable model organisms to investigate relationships between resource use and morphological traits, their intraspecific variability in morphological traits and their effect on microevolutionary processes have been scarcely investigated (Miller-Struttman et al., 2015; Pauw et al., 2009). Plant–pollinator networks are appropriate examples of complex bipartite interactions, with highly variable functional traits, including multiple connections formed by coevolutionary processes (Darwin, 1862; Nilsson, 1988; Pauw et al., 2009; Schiestl & Johnson, 2013). Flower-visiting insects have to select from the available floral resources to cover their dietary needs (Goulson, 1999). Variation in the shape and size of flowers and pollinator mouthparts plays an important role in foraging efficiency and in the pollinators' resource use. For example, species with longer tongues are able to feed from deeper flowers (Harder, 1985; Haverkamp, Bing, Badeke, Hansson, & Knaden, 2016; Inouye, 1978; Klumbers, Stang, & Klinkhamer, 2019; Pauw et al., 2009; Rodríguez-Gironés & Santamaría, 2007), while they are less successful at imbibing concentrated nectars available in shallower flowers (Borrell & Krenn, 2006; Harder, 1986; Josens & Farina, 2001; Kim, Gilet, & Bush, 2011). Although resource use based on flower and mouthpart size is relatively well studied across species, it has scarcely been investigated within populations, except in flies in which individual nectar consumption was related to tongue length (Pauw et al., 2009) and in bumblebees in which individual flower choice was also related to tongue length (Inouye, 1980; Johnson, 1986; but see also Dohzono, Yasuoki, & Kazuo, 2011).

Butterflies are ideal study systems to address plant–pollinator morphological compatibilities, since they usually have long proboscides, that is, specialized mouthparts evolved as an adaptation to imbibe floral nectar as a primary food resource at the adult stage in most species (Bauder, Lieskonig, & Krenn, 2011; Erhardt & Mevi-Schütz, 2009; Krenn, 2000). Butterflies consume nectar by active suction that does not allow them to imbibe highly concentrated nectar because of its high viscosity (Borrell & Krenn, 2006; Josens & Farina, 2001; Kim et al., 2011). Adult butterflies select from the available nectar plant species (Erhardt & Mevi-Schütz, 2009; Thomas & Schultz, 2016), and diet choice may vary between species, populations, generations, sexes, age groups and individuals (Erhardt & Mevi-Schütz, 2009; Szigeti, Körösi, Harnos, & Kis, 2019; Thomas & Schultz, 2016; Tiple, Khurad, & Dennis, 2009). Furthermore, nectar consumption, as well as larval food intake, has been proved to affect life span and fecundity in several species (Cahenzli & Erhardt, 2013; O'Brien, Boggs, & Fogel, 2004).

We studied flower visits of a small population of clouded Apollo butterflies, *Parnassius mnemosyne* (Lepidoptera: Papilionidae). The clouded Apollo is an appropriate model species, because adult feeding is particularly important and foraging behaviour of individuals is easy to observe and monitor by mark–resighting in small, closed populations, where lifetime individual resighting probability can be high (Konvička & Kuras, 1999; Szigeti, Körösi, Harnos, & Kis, 2018). Clouded Apollo butterflies select from floral resources and their diets vary between regions and years and within flight periods, following temporal changes in floral resource availability at the population and individual level (Konvička, Vlasanek, & Hauck, 2006; Kudrna & Seufert, 1991; Szigeti et al., 2018, 2019).

Time shifts in the individuals' presence within a flight period and temporal changes in floral resources together partially explain individual resource use in clouded Apollo butterflies, albeit a

considerably large part of the individual differences in resource use remains unexplained (Szigeti et al., 2019). We hypothesized that variation in flower depth of the visited plant species and/or in proboscis length within a population can explain some of the intraspecific differences in resource use. Based on our field experience, we assumed that one of their locally important nectar plants and one of the best-yielding nectar sources in their diet, the sticky catchfly, *Silene viscaria* (Caryophyllaceae; Szigeti, 2018; Szigeti et al., 2018), has a flower (corolla) depth of ca. 12 mm (Jennersten & Nilsson, 1993) similar to the 12 mm clouded Apollo proboscis length (Lara Ruiz, 2011; Paulus & Krenn, 1996). Hence, we hypothesized that *S. viscaria* flowers would be available only for clouded Apollo butterflies with long proboscides, while those with short proboscides would not be able to use this resource.

We investigated whether (1) variation in proboscis length influenced nectar plant choice of clouded Apollo individuals within a single population. We hypothesized that flower depths constrain butterflies in flower visits via their proboscis lengths. (2) We also studied whether feeding on *S. viscaria* was constrained by individual proboscis length. We hypothesized that clouded Apollo individuals observed visiting *S. viscaria* had longer proboscides than those not observed on this nectar source. Specifically, we measured clouded Apollo proboscis length within a single population and the corolla length of the six most visited forbs. (1) We compared proboscis length to the flower depth of these six nectar plant species and (2) investigated whether visits to individual flowering plant species were related to proboscis length, taking into account floral abundance as a confounder.

## METHODS

### Study Site and Period

We carried out field work at Hegyesd, a 0.5 ha meadow in the Visegrádi-hegység, Hungary, Central Europe (47°45'22.7"N, 19°02'53.4"E, at 295 m above sea level), from late April to the end of May 2015. We sampled butterflies and forbs between 0900 and 1800 hours during all days of the clouded Apollo butterflies' flight period, as weather permitted.

### Sampling in the Field

We surveyed the whole meadow several times a day throughout the flight period. We walked through the meadow at a slow pace, recording all clouded Apollo butterflies within a 4 m wide zone on both sides. We aimed to capture all unmarked butterflies with a butterfly net. We measured and marked them individually with a colour combination applied on both forewings' tips with edding paint markers and then released them (Szigeti et al., 2018). We monitored the meadow regularly throughout the day and identified individuals and their nectar plant species if they were observed feeding (Szigeti et al., 2018).

We measured flower depth and flower abundance of the six plant species clouded Apollo butterflies visited the most often: *Ajuga genevensis* (Lamiaceae), *Buglossoides purpurocaerulea* (Boraginaceae), *Dianthus giganteiformis* subsp. *pontederiae* (Caryophyllaceae), *Geranium sanguineum* (Geraniaceae), *S. viscaria* (Caryophyllaceae) and *Vicia cracca* (Leguminosae). The cumulative proportion of visits on these six species amounted to 97.4% of the total visits observed and more than 2% of visits were on the sixth species (*A. genevensis*). In contrast, only 0.4% of the visits were observed on the seventh most-visited species.

To sample flower abundance, we prepared a map of our study site using Google Earth aerial photos and adjusted it in the field. About every 3 days, we drew all flowering patches of the six plant

species on a map and estimated the number of flowering shoots per patches within the study site by either counting the shoots (< 10 shoots per patch), or assigning rough estimates by tens, as 20, 30, ... 100 (> 10 shoots per patch; Szigeti, Harnos, Kőrösi, Bella, & Kis, 2015). We summarized the number of shoots per plant species per sampling event for the entire site. We also counted the flowers per flowering shoot on the sampled forbs. We calculated flower abundance for the entire study site for each of the six most-visited plants by multiplying the number of flowering shoots by the average of the number of flowers per flowering shoot. We used kernel smoothing (bandwidth = 5) to extrapolate abundances for each day from the 3 days of sampling. Floral abundance was estimated to control for the effect of the considerable observed changes in abundance over time on the feeding behaviour of clouded Apollos.

#### Proboscis and Corolla Length Measurements

We measured proboscis length from photo macrographs (Bauder, Handschuh, Metscher, & Krenn, 2013). We mounted live, nonsedated butterflies on a small, scaled board with clips. Then we fixed the board on a tripod under a camera, parallel to the plane of the lens (Nikon d7000 + Micro Nikkor 60mm f/2.8G ED AF-S macro lens). We uncoiled the proboscis and extended it over the board with a hooked pin and we took at least two pictures for each individual. We used Fiji/ImageJ (Schindelin et al., 2012) to measure proboscis length from the photographs and used the average of the lengths measured on the pictures of the same individual.

We measured flower depth with callipers in situ (resolution: 0.1 mm). This was the distance between the bottom of the corolla tube, where it meets the receptacle, and the orifice of the flower tube. We defined the orifice as the point where the butterfly can insert the proboscis into the flower.

#### Ethical Note

The clouded Apollo is a robust butterfly species and we did not observe any injuries caused by our protocol (proboscis measurement and individual marking). Our field work was licensed by the Hungarian Nature Conservation Authorities: KTVF: 31430/2014.

#### Data Analysis

We compared proboscis length to flower depths of the six most visited nectar plant species with a Dunnett's test and differences between flower depths with a Tukey test. To analyse the relationship between visit and proboscis length, we used generalized linear mixed models (GLMM) with binomial distributions (Zuur, Ieno, Walker, Saveliev, & Smith, 2009), taking into account the effect of flower abundance and the repeated observations on the same butterfly individuals. We fitted binomial models for the six most often visited species separately, so we obtained six different models. The response variable was a visit on a focal plant species (value: 1) or on any of the other visited species (value: 0) at a given visit observed. The explanatory variables were proboscis length and flower abundance of the focal plant species. We included butterfly individual identifiers as a random factor. We used log<sub>10</sub>-transformed kernel-smoothed daily estimates of the number of flowers of the focal plant species. Note that the results of the six different models are not independent; hence, *P* values were corrected for multiple comparisons according to Benjamini and Hochberg (1995).

We analysed all data in the R 3.4.4 statistical environment (R Core Team, 2018), using the 'chron' 2.3–52 package (James & Hornik, 2018) for calculating dates, the 'KernSmooth' 2.23–15

package (Wand, 2015) for kernel smoothing, the 'DescTools' 0.99.31 package (Signorell et al., 2019) for the Dunnett's test, the 'agricolae' 1.2–8 package (de Mendiburu, 2017) for the Tukey test, the 'lme4' 1.1–21 package (Bates, Maechler, Bolker, & Walker, 2015) for GLMM and the 'ggeffects' 0.12.0 package (Lüdtke, 2018) for visualizing GLMM.

## RESULTS

We observed 1077 flower visits by 113 clouded Apollo individuals, for which proboscis length data were available. We observed  $9.5 \pm 7.5$  (mean  $\pm$  SD; range 1–39) visits per individuals. Clouded Apollo butterflies most often visited the flowers of *D. giganteiformis* (69.5%), *B. purpurocaerulea* (8.9%), *S. viscaria* (7.4%), *V. cracca* (6.1%), *G. sanguineum* (3.6%) and *A. genevensis* (2.2%). Flower abundances and visits changed considerably across species during the flight period (Appendix Fig. A1).

We measured proboscis length in 169 individuals. This varied considerably between individuals (minimum–maximum: 9.98–13.52 mm; mean  $\pm$  SD:  $12.13 \pm 0.58$  mm; Fig. 1). The difference between the longest and the shortest proboscis was remarkably large compared to the mean (range 3.53 mm, 29% of the mean). We observed 113 individuals visiting flowers (proboscis length range 10.51–13.52 mm; mean  $\pm$  SD:  $12.19 \pm 0.54$  mm).

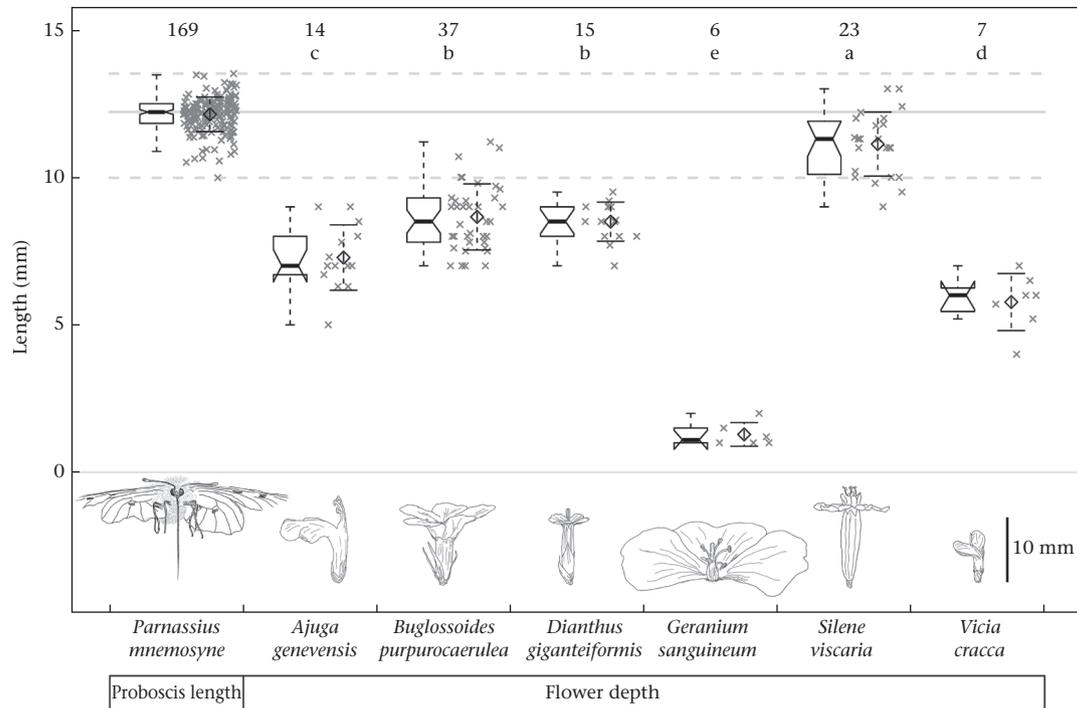
The proboscis was significantly longer than the flower depth for each of the six most-visited plants (Fig. 1; Dunnett's test:  $P_{\text{adjusted}} < 0.001$  for each comparison). Flower depths differed between the six most-visited plants and varied considerably within species (Fig. 1, Appendix Table A1). Flowers of *G. sanguineum* were extremely shallow and those of *S. viscaria* extremely deep, within the range of the six species (Fig. 1). The depth range of *S. viscaria* was similar to the range of proboscis length of clouded Apollo butterflies (Fig. 1), and the difference between the deepest and the shallowest *S. viscaria* flowers was large compared to the mean depth (range 4.0 mm, 36% of the mean). Many *S. viscaria* and a few *B. purpurocaerulea* flowers were deeper than the length of the shortest proboscides (Fig. 1). Flower depths of the other four species were shorter than any proboscis length (Fig. 1).

The median proboscis length of butterflies observed visiting *S. viscaria* was longer than that of butterflies observed visiting other nectar plants (Fig. 2). Proboscis length significantly influenced visits to *S. viscaria*: individuals with proboscides 1 mm longer than those of their conspecifics were 2.46 $\times$  more likely to visit *S. viscaria* (odds ratio;  $P < 0.001$ ; Table 1, Fig. 2). The individual with the longest proboscis (13.52 mm) was estimated to be 14.96 $\times$  more likely to feed on *S. viscaria* than that with the shortest proboscis (10.51 mm; binomial GLMM; Table 1). Proboscis length did not significantly influence visit probability of the other five nectar plant species (Table 1, Appendix Fig. A2). The odds ratio of visits significantly increased with increasing flower abundance for *B. purpurocaerulea*, *D. giganteiformis* and *V. cracca* (Table 1, Appendix Fig. A2).

In summary, individuals with longer proboscides visited *S. viscaria* more often than those with short proboscides, but there was no such relationship in the other five frequently visited nectar plant species (Table 1, Fig. 2).

## DISCUSSION

We investigated the relationships between flower visits and proboscis length of clouded Apollo butterflies during a single flight period in one population. We found remarkable intrapopulation variation in the length of the butterfly's proboscis, and high intra- and interspecific variation in the flower depth of the six most-visited nectar plant species. Moreover, we showed that the longer



**Figure 1.** Clouded Apollo proboscis length and flower depth of the six most-visited plant species. The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range. Notches show 95% confidence intervals for the medians. Diamond symbols show the means and their whiskers SDs. Grey crosses represent individual butterflies or flowers and are jittered on the horizontal axis for better visibility. The horizontal dashed grey lines show the minimum and maximum and the solid grey line shows the median proboscis length. Letters above the boxes show significantly different flower depths (Tukey test). Numbers above the letters show the number of measured butterflies or flowers. Drawings illustrating proboscis length and flower depths are scaled.

the proboscis, the more likely clouded Apollos were to visit *S. viscaria*, the plant species with the deepest corolla in their diet.

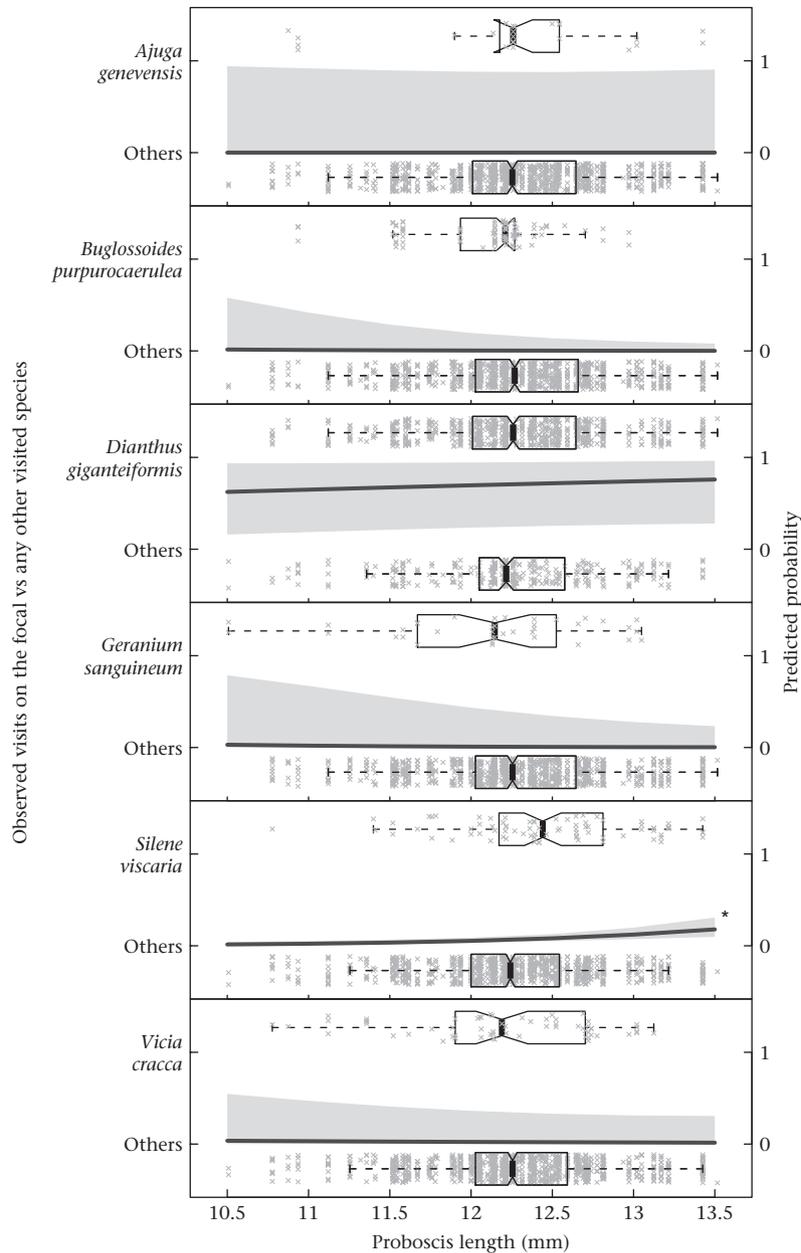
We found large individual differences in clouded Apollo proboscis lengths, and the median (12.2 mm) was similar to those reported by Paulus and Krenn (1996) and Lara Ruiz (2011) (12 mm in both studies). Flower depth also varied within and across species, *G. sanguineum* being extremely shallow and *S. viscaria* extremely deep within the range of the six most-visited floral species. Flower depth of *S. viscaria* was similar (median: 11.3 mm) to that reported by Jennersten and Nilsson (ca. 12 mm; 1993). Many *S. viscaria* and a few *B. purpureocaerulea* flowers were deeper than the proboscis length of butterflies with the shortest proboscides. Butterflies are considered unable to feed from flowers deeper than their proboscis length and interspecific differences in proboscis length explain differences in flower visits of different butterfly species (Corbet, 2000; Haverkamp et al., 2016; May, 1992).

Some of the variation in proboscis length may result from environmental fluctuations during larval development, because abundance and quality of larval host plants, as well as microclimate, determine adult body size in butterflies (Boggs & Freeman, 2005; García-Barros, 2000). Clouded Apollos with longer proboscides also had longer forewings (mean slope  $\pm$  SE:  $0.31 \pm 0.03$ ,  $P < 0.001$ ,  $R^2 = 0.43$ ,  $N = 169$ ; linear regression; Kis, Kőrösi, Szigeti, & Vajna, 2015). Similar results have been reported for other pollinators (within and between species, Agosta & Janzen, 2005; Kramer, Mulvane, Brothers, Gerard, & Lehnert, 2015; Kunte, 2007; Peat, Tucker, & Goulson, 2005). Caterpillars growing in warmer microhabitats and/or places richer in host plants may develop into larger butterflies with longer proboscides. Besides larval nutrition, inherited traits may also influence adult body size in butterflies (Chown & Gaston, 2010; Honek, 1993); thus, genetic variation probably also contributes to proboscis length variation. Similarly, differential development may involve flower depth variability due to environmental factors, such as soil humidity (Galen, 2000) along

time and space, and flower depth variability may also be influenced by genetic factors (Gómez, Abdelaziz, Muñoz-Pajares, & Perfectti, 2009; Klinkhamer & van der Veen-van Wijk, 1999). Interspecific flower depth variation has been found to be an important environmental factor influencing individual diet choice in pollinators (Harder, 1985; Haverkamp et al., 2016; Klumpers et al., 2019; Rodríguez-Gironés & Santamaría, 2007).

Whatever factors determine the morphological variation among foraging individuals, this variation may cause differences in the individuals' food intake as well as in their fitness (Grant & Grant, 2014; Holbrook & Schmitt, 1992; Pauw et al., 2009; Tammaru, 1998). Changes in any of these factors may alter trait distribution in a population (foragers: Grant & Grant, 2014; flower visitors: Miller-Struttman et al., 2015; Pauw et al., 2009; food resources: Lavorel & Garnier, 2002; nectar plants: Leibman, Rowe, Koski, & Galloway, 2018; Little, Dieringer, & Romano, 2005).

Visits on *S. viscaria* were influenced by proboscis length: individuals with longer proboscides visited *S. viscaria* with a larger odds ratio than those with shorter proboscides. Therefore, our results show that individuals with shorter proboscides were less likely to exploit *S. viscaria* as a nectar source. The distribution of corolla tube length in *S. viscaria* implies that a clouded Apollo butterfly with the shortest proboscis could reach only 13.2% of *S. viscaria* flowers. Individuals with at least the lower quantile proboscis length could reach 73.3%, with a median length 86.6%, with an upper quantile length 91.6% and with the longest proboscis 100.0% of the *S. viscaria* flowers. We did not find statistically significant effects of proboscis length on visits to the other five plant species. The visit patterns of *S. viscaria* indicate that variability in proboscis length and flower depth alone may partially explain individual floral choice, although other factors such as flower abundance or nectar quantity and quality are probably crucial as well. Morphological variation may cause differences in the individuals' food intake as well as in their fitness: large variance in proboscis



**Figure 2.** Clouded Apollo flower visit and proboscis length relationships: proboscis lengths compared between butterflies observed on focal nectar plants among the six most-visited species versus those observed on any other species; binomial GLMMs were repeated for all the six most-visited plant species as a focal plant. The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range. Notches show 95% confidence intervals for the medians. Grey crosses represent individual observations and are jittered on the vertical axis for better visibility. Dark grey lines represent regression lines and light grey bands represent 95% confidence intervals for regression lines. The asterisk represents a significant effect ( $P < 0.05$ ).

length may be maintained by a fluctuating environment where floral resource availability changes rapidly (Pauw et al., 2009; Szigeti et al., 2018). Ultimately, intraspecific corolla length variation may be as important in the individual diet choice of nectarivorous organisms as its interspecific variation.

We further discuss a handful of potential alternative explanations of this large variation in proboscis length and its possible consequences for nectar source use. (1) We hypothesize that butterflies with short proboscides access poorer quality *S. viscaria* flowers or have no access to it at all, compared to those with long proboscides. Thus, they learn to avoid *S. viscaria* and look for alternative sources. This could also be true for any similar situations when butterflies face nectar sources with corolla lengths fluctuating around their reach. Several plant species have been shown to include more nectar when their corollas were longer and thus were

richer resources for insect visitors with longer proboscides (Gómez et al., 2008; Lázaro, Vignolo, & Santamaría, 2015). This hypothesis does not predict natural selection for either long or short proboscides or both; it simply considers variation in length and learning. However, selection is likely to happen and may induce various scenarios. (2) Long proboscides might be more advantageous than short ones, because they allow the butterfly to imbibe nectar from both long and short corolla flowers (Inouye, 1980; Rodríguez-Gironés & Santamaría, 2007). (3) Although we did not find any significant relationship between individuals with short proboscides and their visits to short corolla nectar plant species, short proboscides might also be advantageous for various reasons. For example, individuals with shorter proboscides may be better able to consume more concentrated nectars from shallower flowers, since viscosity increases with concentration and more viscous solutions

**Table 1**  
Clouded Apollo visits related to proboscis length and flower abundance: summary of the generalized linear mixed models

| Response variable                   | Explanatory variables                | Slope estimate | SE   | P      | Odds ratio (exp(estimate)) |
|-------------------------------------|--------------------------------------|----------------|------|--------|----------------------------|
| <i>Ajuga genevensis</i>             | Proboscis length                     | -0.08          | 1.11 | 0.94   | 0.92                       |
|                                     | Log <sub>10</sub> (flower abundance) | -2.39          | 2.53 | 0.52   | 0.09                       |
| <i>Buglossoides purpurocaerulea</i> | Proboscis length                     | -0.87          | 0.59 | 0.27   | 0.42                       |
|                                     | Log <sub>10</sub> (flower abundance) | 24.03          | 3.74 | <0.001 | 2.73E+10                   |
| <i>Dianthus giganteiformis</i>      | Proboscis length                     | 0.21           | 0.24 | 0.51   | 1.23                       |
|                                     | Log <sub>10</sub> (flower abundance) | 2.98           | 0.42 | <0.001 | 19.69                      |
| <i>Geranium sanguineum</i>          | Proboscis length                     | -0.81          | 0.58 | 0.28   | 0.44                       |
|                                     | Log <sub>10</sub> (flower abundance) | -1.72          | 0.72 | <0.05  | 0.18                       |
| <i>Silene viscaria</i>              | Proboscis length                     | 0.90           | 0.24 | <0.001 | 2.46                       |
|                                     | Log <sub>10</sub> (flower abundance) | 0.41           | 0.55 | 0.54   | 1.51                       |
| <i>Vicia cracca</i>                 | Proboscis length                     | -0.30          | 0.43 | 0.54   | 0.74                       |
|                                     | Log <sub>10</sub> (flower abundance) | 3.08           | 1.07 | <0.05  | 21.76                      |

The response variable in binomial models was whether the focal floral species or another species had been visited at a specific observation event. We made separate models for the six species. All models included flower abundance of the focal species on the observation day as a fixed factor and visiting individuals as a random effect.

require more force to pump through longer tubes of the same diameter (Borrell & Krenn, 2006; Josens & Farina, 2001; Kim et al., 2011). Shallower flowers (such as *G. sanguineum*) may contain more concentrated nectars than plants with deeper flowers (Borrell & Krenn, 2006; Harder, 1986; Josens & Farina, 2001; Kim et al., 2011). Furthermore, handling times are shorter for shorter proboscides, because less time is needed to uncoil them and take up the same amount of nectar (Borrell & Krenn, 2006; Harder, 1986; Kunte, 2007; but see Klumpers et al., 2019; Peat et al., 2005). (4) Large variance in proboscis length might be associated with within-population resource partitioning: within-population competition may be reduced if butterflies with short proboscides exploit shallower flowers with sparse nectar that has a high sugar concentration and those with long proboscides visit deeper flowers yielding ample, low-concentration nectar. We have no conclusive data to argue for or against these hypotheses. Testing them requires laboratory experiments and conclusions cannot be drawn from observational data, such as those presented here.

To our knowledge, our results provide the first evidence that individual variation in mouthpart length influences diet in Lepidoptera, and generally in solitary nectarivorous insects studied in natural circumstances. Intraspecific relationships between body sizes and diets in insect pollinators have scarcely been investigated and almost exclusively in social forager bumblebees (Dohzono et al., 2011; Johnson, 1986; Peat et al., 2005; Spaethe & Weidenmüller, 2002; Willmer & Finlayson, 2014) and flies (Pauw et al., 2009), but mouthpart length and diet relationships have been thoroughly studied in other taxa (gastropods: Watanabe & Young, 2006; ants: Davidson, 1978; lizards: Schoener, 1968; birds: De León et al., 2012; Grant & Grant, 2014; Pratt, 2005). Note that clouded Apollo butterflies also visited other plant species with short corollas and we found a large scatter in the relationship between visits and proboscis length; hence, we agree with Dohzono et al. (2011) that the morphological fit between proboscis length and flower depth is not the sole determinant of foraging efficiency. Pollinators face a vast range of very different cues regarding whether to land on a plant and probe its flowers (Blüthgen & Klein, 2011; Junker, Blüthgen, & Keller, 2015; Kuppler, Höfers, Wiesmann, & Junker, 2016; Szigeti et al., 2019). For example, the use of different nectar sources by clouded Apollo butterflies varies across the species' distribution range (Konvička et al., 2001; Kudrna & Seufert, 1991; Lara Ruiz, 2011; Szigeti et al., 2018), and even between nearby habitat patches and between consecutive years (Szigeti et al., 2015, 2018). Individuals may encounter different forb species and size distributions of flowers in different habitat patches. Moreover, flower depth may also vary at the intraspecific level due to weather conditions (Carroll, Pallardy, & Galen, 2001; Galen, 2000), and may change during the flowering period (Inouye & Pyke, 1988; Jo, Yi, & Kim, 2014). Our results indicate that

intraspecific morphological variation in both plants and their pollinators is an essential factor in the choice of nectar source; hence, their interactions are at least partially based on continuous trait variability, rather than on well-defined discrete traits of different taxa, as the pollination syndrome hypothesis implies (Blüthgen & Klein, 2011; Ollerton et al., 2009).

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## Supplementary Material

An interactive map associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.anbehav.2020.03.008>.

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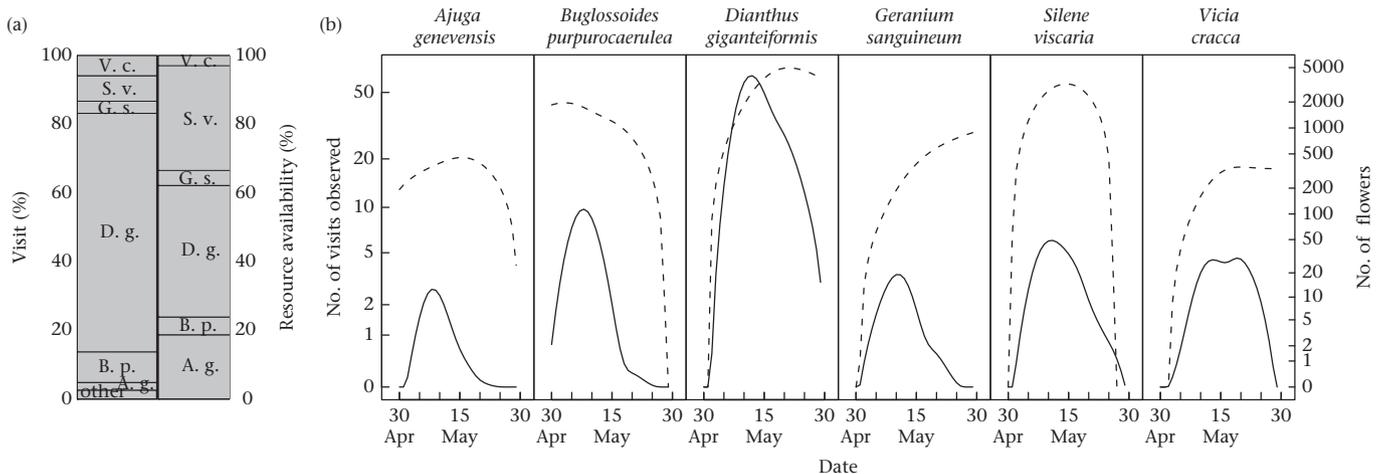
## Appendix

**Table A1**

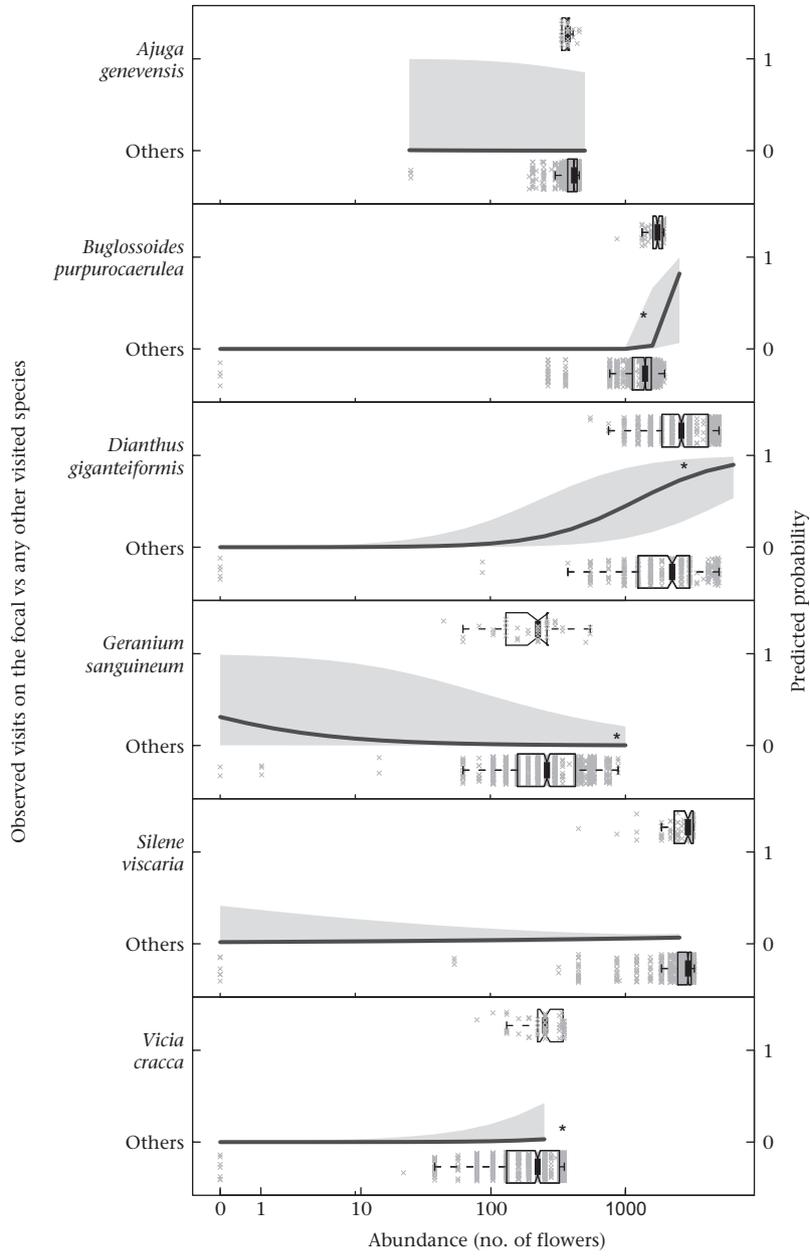
Flower depth comparisons among the six species visited the most by clouded Apollus

| Species pairs compared   | P       |
|--|---------|
| <i>Buglossoides purpuracaerulea</i> – <i>Ajuga genevensis</i>        | <0.001  |
| <i>Dianthus giganteiformis</i> – <i>Ajuga genevensis</i>             | 0.021   |
| <i>Geranium sanguineum</i> – <i>Ajuga genevensis</i>                 | <0.0001 |
| <i>Silene viscaria</i> – <i>Ajuga genevensis</i>                     | <0.0001 |
| <i>Vicia cracca</i> – <i>Ajuga genevensis</i>                        | 0.023   |
| <i>Dianthus giganteiformis</i> – <i>Buglossoides purpuracaerulea</i> | 0.1     |
| <i>Geranium sanguineum</i> – <i>Buglossoides purpuracaerulea</i>     | <0.0001 |
| <i>Silene viscaria</i> – <i>Buglossoides purpuracaerulea</i>         | <0.0001 |
| <i>Vicia cracca</i> – <i>Buglossoides purpuracaerulea</i>            | <0.0001 |
| <i>Geranium sanguineum</i> – <i>Dianthus giganteiformis</i>          | <0.0001 |
| <i>Silene viscaria</i> – <i>Dianthus giganteiformis</i>              | <0.0001 |
| <i>Vicia cracca</i> – <i>Dianthus giganteiformis</i>                 | <0.0001 |
| <i>Silene viscaria</i> – <i>Geranium sanguineum</i>                  | <0.0001 |
| <i>Vicia cracca</i> – <i>Geranium sanguineum</i>                     | <0.0001 |
| <i>Vicia cracca</i> – <i>Silene viscaria</i>                         | <0.0001 |

Adjusted P values are from Tukey tests.



**Figure A1.** (a) Clouded Apollo annual visit rates and resource availability of the six most-visited nectar plants (abbreviations correspond to species names in (b)) and (b) temporal changes during the clouded Apollo flight period in flowering and visits for the six most-visited nectar plants. Dashed curves show changes in flower abundances and solid curves changes in the number of visits observed. All curves are kernel smoothed. Note that both vertical axes in (b) are log<sub>10</sub> scaled.



**Figure A2.** Clouded Apollo flower visit and flower abundance relationships. The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range. Notches show 95% confidence intervals for the medians. Grey crosses represent individual observations and are jittered on the vertical axis for better visibility. Dark grey lines represent regression lines and light grey bands represent 95% confidence intervals for the regression lines. Asterisks represent a significant effect ( $P < 0.05$ ). The x-axes are  $\log_{10}$  scaled.