

Allometry and functional constraints on proboscis lengths in butterflies

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Summary

1. In generalist nectar-feeding insects such as butterflies, body size and proboscis length show an allometric relationship. Butterflies that deviate from this relationship and have disproportionately long proboscides can access nectar from deep flowers, which is inaccessible to species of similar or larger body size but with shorter proboscides.
2. Despite this selective advantage, few species possess disproportionately long proboscides for their body size, which indicates that there may be developmental, functional or other ecological constraints on very long proboscides. I hypothesized that species with disproportionately long proboscides had a functional cost in terms of higher handling time (amount of time spent per flower); therefore, they were at a competitive disadvantage compared to butterflies that had shorter proboscides and lower handling times.
3. I tested this hypothesis using Costa Rican butterflies. I measured body length, proboscis length and handling time on *Lantana* and *Wedelia*, two nectar plants with generalist pollination systems which attract large numbers of nectar-feeding butterfly species.
4. There was a strong positive relationship between ‘relative proboscis length’ (proboscis length in relation to body size) and handling time per flower on both nectar plants. Species with greater relative proboscis length had up to three times longer handling time per flower. Thus, butterflies with relatively long proboscides should harvest less nectar per unit time from the same flower than butterflies with normal proboscides.
5. Reduced foraging efficiency in the face of competition from other nectarivores may thus be a functional constraint that limits the evolution of disproportionately long proboscides in generalist nectar-feeding butterflies.

Key-words: foraging behaviour, handling time, nectarivory, scaling relationships

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Introduction

Both allometry – scaling relationships in various body structures compared to body size – and adaptive departures from usual allometric relationships are widespread in the animal world (Thompson 1917) and insects provide some of the most intriguing examples of such adaptive departures (Emlen & Nijhout 2000). An important and famous case of adaptive departure from allometric relationships in insects was the discovery of the unusually long-tongued hawk moth *Xanthopan morgani praedicta*, whose existence and proboscis length were predicted by Darwin before its discovery based on his knowledge of the long-spurred Madagascan star orchid *Angraecum sesquipedale* (Nilsson 1998). This species departs strikingly from the allometric relation-

ship between body size and proboscis length seen in most hawk moths (Agosta & Janzen 2005). The diversity and selective advantages of such departures from allometric growth forms have been well-documented (e.g. Schmidt-Nielsen 1984; Nilsson 1988; Emlen 2001).

In butterflies and moths, body size or mass is a strong predictor of proboscis length (Corbet 2000; Agosta & Janzen 2005). Some nectar-feeding species, however, deviate from the usual allometric relationship with their disproportionately long proboscides in relation to body size (i.e. greater relative proboscis length). These examples include both specialist nectar-feeding hawk moths and generalist nectar-feeders such as butterflies. For the purpose of this paper, specialist nectar-feeders are those mutualist pollinators that have closely co-evolved with particular nectar plants, often thereby forming tight plant-pollinator systems. Generalist nectar-feeding butterflies, on the other hand, are ‘nectar thieves’ that take nectar without pollinating flowers

(Inouye 1980), they usually take nectar from a wide variety of plants and have only diffusely co-evolved, if at all, with those nectar plants. In mutualist nectar-feeders, proboscis length co-evolves with flower depth such that the fit between the two increases the fitness of both plant and insect partners, and there is a good match between flowers and feeding structures in a wide range of plant-pollinator associations (Heinrich 1976; Grant & Grant 1983; Kodric-Brown *et al.* 1984; Nilsson *et al.* 1985; Nilsson 1988, 1998; Johnson & Steiner 1997; Alexandersson & Johnson 2002; Temeles & Kress 2003).

Among nectar thieves, longer proboscides confer higher energy gains. This is because species with a longer proboscis can access nectar from deeper flowers (May 1992), which usually have higher standing nectar crops and provide higher energetic rewards (Brown, Calder & Kodric-Brown 1978; Harder 1983, 1985; Kodric-Brown *et al.* 1984; May 1988; Haber & Frankie 1989). Long proboscides of nectar thieves may also enable nectar theft from specialist flowers. Given these important selective advantages, it is puzzling that a disproportionately long proboscis has evolved in only a few, phylogenetically distant species of generalist nectar-feeders. Perhaps some constraints and trade-offs restrict more widespread evolution of very long proboscides. Given the apparent lack of developmental constraints on selective departures from usual allometric relationships in diverse insect body structures (Weber 1990; Emlen 1996; Frankino *et al.* 2005), it appears that energy-allocation (Emlen 2001), sexual selection (Frankino *et al.* 2005) or functional (ecological) constraints are more important in the evolution of these allometric structures in insects. However, functional constraints have rarely been studied.

In this paper I test the functional constraints hypothesis that species with greater relative proboscis length have reduced foraging efficiency. I consider the reduced foraging efficiency or greater handling time per flower as a functional cost of greater relative proboscis length because the number of flowers probed and energy gained per unit time depend on handling time, which is determined by proboscis length and other related parameters (Ranta & Lundberg 1980; Harder 1985, 1988). My functional constraints hypothesis is based on the biomechanical considerations that: (i) butterflies and moths draw nectar through the proboscis by suction created by cibarial dilator muscles; and (ii) the amount of energy required to draw nectar is directly proportional to the pressure differential produced by the cibarial muscles (Kingsolver & Daniel 1979, 1995). Assuming an overall allometric relationship between body size and cibarial muscle mass, these biomechanical considerations lead to a hypothesis that disproportionately long proboscides have reduced nectar uptake rates (i.e. greater handling times) because, for a given body size and cibarial muscle mass, longer proboscides will produce more resistance to incoming nectar due to their greater inner surface area. Thus, under this functional constraints hypothesis we predict a *positive* relationship

between relative proboscis length and handling time. An alternative hypothesis is that species with greater relative proboscis length also have greater relative cibarial muscle mass to compensate for the increased resistance to incoming nectar, making them *more or equally* efficient nectar-feeders. The alternative hypothesis thus predicts an *inverse or no* relationship between relative proboscis length and handling time.

Cibarial muscle mass is difficult to measure precisely, so the assumption of allometric relationship between body size and cibarial muscle mass is not easy to test. However, the above predictions regarding relative proboscis length and handling time can be tested, which I do here. I proceed by establishing the general allometric relationship between body size and proboscis length of butterflies and then test the functional constraints hypothesis mentioned above. Empirical data from two nectar plants and tropical butterfly assemblages strongly support the prediction of positive relationship between relative proboscis length and handling time. The cost (reduced efficiency) of foraging with greater relative proboscis may thus be important in restricting the evolution of disproportionately long proboscides in butterflies.

Materials and methods

STUDY SITE AND PERIOD

This research was conducted at Sirena Biological Station in Corcovado National Park, Costa Rica, on a small 800 × 40 m air-strip in the middle of a coastal secondary evergreen forest. Observations were taken continuously at the edge of the airstrip throughout a 6-week period from July 3 to August 15, 2003.

NECTAR PLANTS AND BUTTERFLY ASSEMBLAGES

Two non-native nectar plants grew profusely at the field site: *Lantana camara* (Verbenaceae) – a large shrub, and *Wedelia* sp. (most likely *W. trilobata*, Asteraceae) – a small gregarious herb. A major advantage of using these non-native plants was the lack of co-evolutionary plant-pollinator dynamics between them and the native butterfly species. This allowed a benchmark to compare a wide variety of butterfly species. Restricting observations to just two plants but a large set of butterflies avoided confounding factors such as subtle relationships between the flower morphology, floral preference and their combined effects on handling time.

Both plant species attracted a wide range of nectarivores as they have apparently evolved generalist pollination systems. The size of their flowers was substantially different: the corolla tube measured *c.* 10 mm for *Lantana* and *c.* 2.5 mm for *Wedelia*. As a result of this difference in flower size, the nectar plants had distinct butterfly assemblages, albeit with some overlap. The *Lantana* butterfly assemblage was made of a greater proportion of forest species, while the *Wedelia*

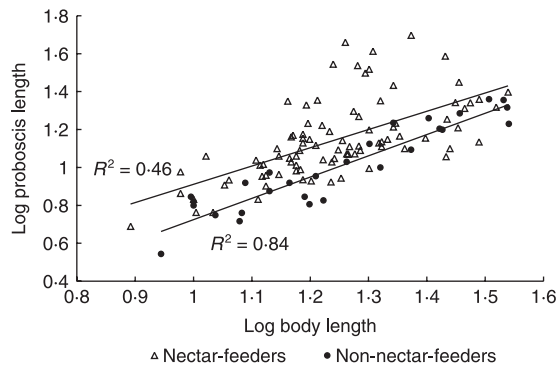


Fig. 1. The allometric relationship between body length and proboscis length in butterflies. The regression lines show that nectar-feeding species ($n = 89$) have significantly longer proboscides for a given body size compared to non-nectar feeding species ($n = 28$).

assemblage was largely comprised of species from non-forest habitats. The complete list of butterfly species recorded on each nectar plant is given in Supplementary Appendix S1.

MORPHOMETRICS OF BUTTERFLIES

An allometric relationship between body size and proboscis length must be established and compared between nectar-feeding and non-nectar feeding butterflies before testing the functional constraints hypothesis. For this purpose I captured and took two morphometric measurements – body length and proboscis length – of 117 species (89 nectar-feeders and 28 non-nectar feeders) encountered during the study period. Body size was not directly measured as the body mass of living butterflies, so body length was used as a surrogate. Proboscis length was measured on live butterflies after inserting a needle in the centrepoint of the coiled proboscis and straightening the proboscis out. The length was then measured as the distance between the base of labial palps to the tip of the proboscis.

After taking the measurements, marking with a felt-tip marker to avoid repeat measurements and photographing the specimens for identification purposes, I released them without noticeable harm. The numbers of measurements for each species depended on its commonness and ease of capture, and ranged from 1 to 10. Averaged morphometric measurements, including relative proboscis length, for each species are given in Supplementary Appendix S1. All the species in Supplementary Appendix S1 were used in the comparison between nectar- and non-nectar feeding butterflies (Figs 1 and 2).

FORAGING BEHAVIOR

To compare nectar-feeders and non-nectar feeders, I classified species of Satyrinae, Morphinae, and some Nymphalinae and Riodinidae as non-nectar feeders. These species feed on plant sap, rotting fruits, animal

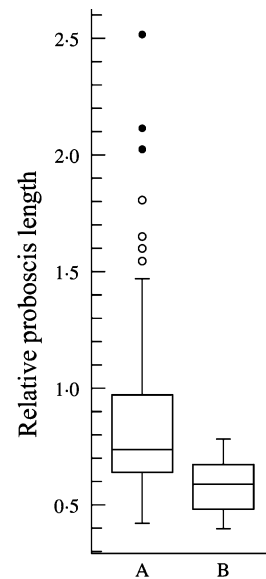


Fig. 2. Box plots of relative proboscis lengths (proboscis length/body length) of (A) nectar-feeding ($n = 89$), and (B) non-nectar feeding ($n = 28$) species. The distribution of relative proboscis lengths of nectar-feeding species is strikingly right-skewed with outliers towards longer proboscides.

faeces or other non-nectar food sources but do not visit flowers. All other species from Supplementary Appendix S1 feed from flowers at least occasionally, and I classified them as nectar-feeders.

To study foraging behaviour in terms of handling time per flower, I selected a subset of nectar-feeding species based on the consistency of their occurrence on the nectar plants, not on their ecology, size, relative proboscis length and foraging behaviour. I calculated handling time as the time spent on an inflorescence in actually probing flowers divided by the number of flowers probed in that inflorescence, assuming that nectar uptake occurred when flowers were probed. I made the observations between 09.00 and 14.00 h, when butterflies were most active. Handling times of the species are given in Supplementary Appendix S2.

STATISTICAL ANALYSIS

For exploring the relationship between body length and proboscis length I log-transformed the data and tested the difference in the slopes of ordinary least-squares regression of nectar-feeders and non-nectar feeders using the analysis of covariance. The use of ratios to normalize for variation in body size has been criticized because the relationship between body size and other body parameters is usually non-isometric and the derived ratios do not completely control for body size (Packard & Boardman 1999). Therefore, for the purpose of testing the functional constraints hypothesis, first I performed the ordinary least-squares regression analysis of body length and proboscis length (values not log-transformed). The residuals from this analysis were then regressed against the handling time. When the proboscis

length to body length ratio was used as an independent variable instead of the residuals, a similar positive relationship between the relative proboscis length and the handling time was found (results not presented here). All statistical analyses were performed using JMP 6 (SAS Institute, Carey, NC, USA) and online statistical packages (Kirkman 1996; Wessa 2007).

Results

RELATIONSHIP BETWEEN BODY SIZE AND PROBOSCIS LENGTH

Both nectar-feeding and non-nectar feeding butterflies showed a positive relationship between body length and proboscis length (nectar-feeders: $F_{1,87} = 23.91$; non-nectar feeders: $F_{1,26} = 192.33$; both $P < 0.0001$). Nectar-feeders had a higher y -intercept than non-nectar feeders and the difference between the two regressions was significant ($y = 0.8927x^{1.1031}$ for nectar-feeders and $y = 0.7261x^{1.4157}$ for non-nectar feeders, ANCOVA for different slopes: $F_{3,113} = 18.48$, $P < 0.0001$; Fig. 1). Also note that many nectar-feeders deviated considerably from the regression line whereas non-nectar feeders were much more tightly clustered around it (nectar-feeders: $R^2 = 0.46$; non-nectar feeders: $R^2 = 0.84$; Fig. 1), pointing to the tendency of nectar-feeders to produce disproportionately long proboscides.

When the variation in proboscis length relative to body length was compared, nectar-feeders had significantly greater relative proboscis lengths than non-nectar feeders (nectar-feeders: mean 0.863 ± 0.40 (range 0.42–2.52), $n = 89$; non-nectar feeders: 0.580 ± 0.11 (range 0.39–0.78), $n = 28$; $t = 3.71$, $df = 115$, $P = 0.0003$; Fig. 2). Also note from the boxplots in Fig. 2 that there was a general tendency among nectar-feeders towards having relatively longer proboscides as evidenced by: (i) the right-skewed distribution of relative proboscis lengths; (ii) more species (longer whiskers) having higher values of relative proboscis length than lower values; and (iii) no outliers towards shorter proboscides but seven towards longer proboscides.

EFFECT OF RELATIVE PROBOSCIS LENGTH ON HANDLING TIME

There was no relationship between raw proboscis length and handling time (*Lantana*: $F_{1,17} = 0.20$, $R^2 = 0.043$; $P = 0.4$; *Wedelia*: $F_{1,13} = 0.34$, $R^2 = 0.12$; $P = 0.21$), indicating that raw proboscis length was not a simple predictor or correlate of handling time. There was, however, a significantly positive relationship between the residuals of the body length-proboscis length regression (i.e. the relative proboscis length) and the handling time (*Lantana*: $F_{1,16} = 10.7$, $R^2 = 0.39$; $P = 0.004$; *Wedelia*: $F_{1,12} = 6.65$, $R^2 = 0.34$; $P = 0.023$). Thus, butterflies with relatively longer proboscides (positive residuals) had up to three times longer handling times than butterflies with shorter proboscides (negative

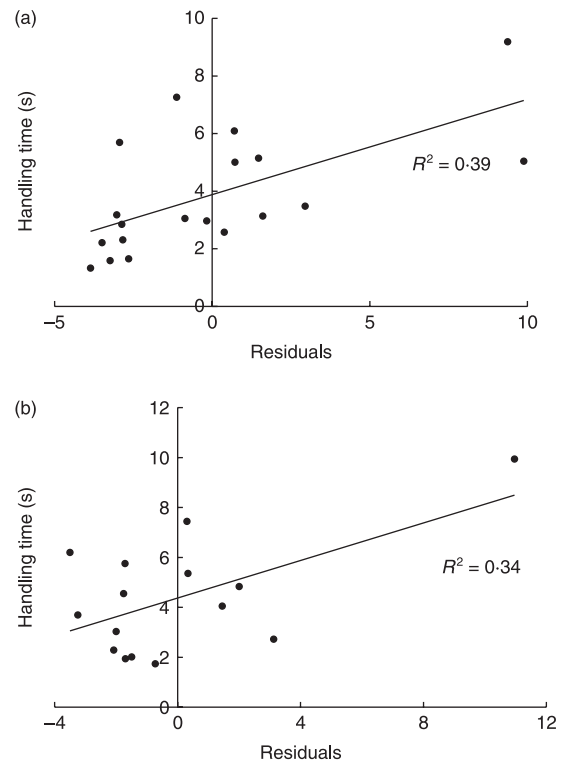


Fig. 3. The relationship between relative proboscis length and mean handling time in seconds for butterflies feeding on (a) *Lantana* ($n = 19$ spp), and (b) *Wedelia* ($n = 15$ spp). The residuals are from a regression between body length and proboscis length. On both nectar plants, butterfly species with greater relative proboscis length had higher handling times, indicating that longer proboscides had a functional cost.

residuals; Fig. 3). This positive relationship is extremely important as it suggests that a relatively longer proboscis has a functional cost in terms of reduced foraging efficiency.

Discussion

Few studies have considered biomechanical constraints on foraging efficiency (e.g. Kingsolver & Daniel 1979, 1983; May 1985; Borrell 2006, 2007) or functional constraints on the evolution of foraging-related adaptive traits such as proboscis lengths. The finding of this study that raw proboscis length did not have any relationship with foraging efficiency but *relative* proboscis length did have a significantly negative relationship with foraging efficiency (foraging efficiency and handling time are inversely related) is important. It demonstrates that allometry and relative proboscis length are useful means of explaining the variation in proboscis lengths and foraging efficiency in butterfly nectar thieves. Also, my data suggest that body size may interact indirectly with proboscis length through the allometric relationship with cibarial muscle mass to influence foraging efficiency.

The biomechanical constraint on foraging efficiency proposed in the introduction assumes an allometric relationship between body size and cibarial muscle mass. The positive relationship between relative proboscis

length and handling time indeed suggests that cibarial muscle mass may not correlate positively with relative proboscis length. This assumption, however, should be directly tested. It is conceivable that at least some species that depend heavily on nectar may have greater cibarial muscle mass to increase the rate of nectar uptake and reduce handling time. Further morphological and behavioural studies would be informative in this regard.

It could be argued that species with greater relative proboscis length had higher handling times because they extracted more nectar from flowers. The increased handling time, however, could not have been due to an increased amount of nectar extracted because all butterflies feeding from the two nectar plants had proboscides at least as long as the mean flower depths (Supplementary Appendix S1). Thus, all species could easily harvest even trace amounts of nectar deep in the flowers. Therefore, relatively long proboscides did not offer access to more nectar in these species and the nectar harvest could not have been higher. The increased handling time thus probably represented a genuine reduction in foraging efficiency. The selective pressures on relatively long proboscides in butterfly nectar thieves apparently balance ecological parameters such as the relative abundance of deep vs shallow flowers and access to large standing nectar crops in deep flowers vs reduced foraging efficiency on shallow flowers in the face of competition for nectar.

One shortcoming of this study is that I have not tested the patterns presented with explicit phylogenetic tests. The reasons for this are twofold. First, currently there is no phylogeny representing most of the species – or even a good sample – used in this study. Second, the species with very long proboscides belonged to phylogenetically distant groups, which may reasonably be treated as phylogenetically independent. Examination of the data in Supplementary Appendix S1 further reveals that species within families had remarkably different ratios of proboscis length to body length. For example, within Riodinidae, *Eurybia* spp. have much higher values of relative proboscis length compared to *Metacharis* and *Charis* spp. Similarly, within Pieridae, *Eurema* and *Phoebis* have longer proboscides for their body length compared to *Ascia* and *Melete*. Such comparisons can also be drawn between species within Nymphalidae, HesperIIDae and Papilionidae. Moreover, there was considerable morphometric variation within genera (e.g. compare species of *Urbanus* and of *Heliconius*, Supplementary Appendix S1), which shows that there is abundant interspecific variation in the traits studied here. These patterns indicate that disproportionately long proboscides have evolved multiple times in neotropical butterflies and phylogenetic constraints on ecomorphology may not be very strong in these butterflies. Therefore I have treated the data points as phylogenetically independent samples. Future work should be aimed at sampling butterfly species more exhaustively and testing differences in relative proboscis length and foraging efficiency with explicit phylogenetic methods.

Among butterflies and moths, departures from allometric relationships are seen in many body structures such as relative wing size, thoracic mass and proboscis length (e.g. Deinert, Longino & Gilbert 1994; Agosta & Janzen 2005). Although direct investigations into the evolution of such structures and their selective advantages are very useful, studying constraints on the evolution of these structures will be equally illuminating. The findings of this paper add functional (ecological) constraints to recent evidence (Emlen 2001; Frankino *et al.* 2005) that sexual selection and functional constraints are more important than developmental or phylogenetic constraints in limiting the evolution of non-allometric structures in insects.

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Supplementary material

The following supplementary material is available for this article.

Appendix S1. Morphometric measurements and feeding habits of butterfly species in this study

Appendix S2. Handling time of butterflies

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2435.2007.01299.x>

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