



Patterns of feeding behaviour in adult male riodinid butterflies and their relationship to morphology and ecology

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Adult butterflies are known to visit a wide variety of food substrates, but, with the exception of flower visitation, little is known about what substances are being sought or what determines substrate choice. This is especially true for the Riodinidae, a large family (*c.* 1300 spp.) of almost exclusively Neotropical butterflies. We present adult male feeding records for 124 species in 41 genera of Riodinidae (out of a total of 441 species in 85 genera collected in the study), based on ten months sampling in Ecuador. Records of food substrates visited in this study include flowers, damp sand or mud ('puddling') and rotting carrion. Rotting carrion placed in traps was the most frequently recorded food source in terms of numbers of individuals and taxa, attracting 89 species from 32 genera. A correlation is found between food substrate choice and morphology, specifically wing area to thoracic volume ratio (WA:TV ratio). Our data suggest the possible existence of two adaptive syndromes whose species have significantly different mean WA:TV ratios and differing suites of accompanying ecological traits, with lower ratios being significantly correlated with species that were recorded feeding. Among species recorded feeding, carrion feeders and puddlers have significantly lower mean WA:TV ratios than flower nectarers, and carrion feeders have a lower mean WA:TV ratio than species not recorded on this food source, a correlation that is significant across all tribes and within some tribes (Riodinini and Saratoni). We reanalyse previously published data on flight and morphology for species in other butterfly and moth families and show that the ratio of wing area to thoracic mass is significantly negatively correlated with flight speed and oxygen consumption (a direct indicator of metabolic rate). We suggest that adult male riodinids may puddle and feed at rotting carrion to supplement nutrient stores from larval feeding, not only to increase reproductive success, but also to provide the necessary nutrients to maintain high metabolic rates during rapid flight.

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ADDITIONAL KEY WORDS:—adaptive syndromes – bait trapping – Ecuador – flight speed – Lepidoptera – metabolic rate – food substrate choice – perching behaviour – puddling – wing area:thoracic volume ratio.

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INTRODUCTION

The feeding behaviour of adult butterflies is an often neglected topic in the study of butterfly biology; for example, it was not even mentioned among the many papers in the symposium volume *The Biology of Butterflies* (Vane-Wright & Ackery, 1984). Scoble (1992) provides a recent summary of our knowledge on the subject, drawn largely from general field observations. In temperate regions, butterflies most commonly obtain nutrients from nectar sources, and it is this behaviour which has received the most attention (Watt, Hoch & Mills, 1974; Kingsolver & Daniel, 1979; May, 1988, 1992, 1993). However, in the tropics, butterflies have been observed to feed on a much wider diversity of substrates, including nectar and pollen (Gilbert, 1972; Boggs, Smiley & Gilbert, 1981; DeVries, 1979), decaying fruit and animal matter, and moist surfaces (known as ‘puddling’) (Collenette, 1934; Norris, 1936; Downes, 1973; Sevastopulo, 1974; Ray & Andrews, 1980; Boggs & Jackson, 1991; Austin, Brock & Mielke, 1993; Sculley & Boggs, 1996). An extensive list of recorded feeding substrates for adult Lepidoptera is given by Adler (1982). In the majority of cases, the stimuli for feeding, the substances sought (but see Arms, Feeny & Lederhouse, 1974; Boggs, 1981) and how they relate to adult physiology are poorly understood.

It is well known that members of certain groups, such as the Charaxinae, Limenitidinae, Nymphalinae, Apaturinae, Satyrinae, Morphinae and Brassolinae feed on rotting fruits (DeVries, 1988; DeVries, Murray & Lande, 1997), while those of the Papilionidae, Pieridae, Nymphalidae, Riodinidae and Lycaenidae puddle and/or are attracted to flowers. However, those groups that feed on rotting carrion are less well known, partly due to the scarcity of these substrates in nature and to the reluctance of entomologists to work with such malodorous baits. Nonetheless, rotting carrion seems to be an important lepidopteran food source; in addition to the taxa recorded by Austin & Riley (1995) on carrion baits in the Charaxinae, Limenitidinae, Nymphalinae, Apaturinae, Satyrinae, Morphinae, Brassolinae, Danaidae, Heliconiinae and Riodinidae, we have observed numerous species of Lycaenidae

TABLE 1. The number, and percentage of the total number, of genera and species of male Ecuadorian Riodinidae recorded feeding on different nutrient sources. The sum of the values for each nutrient source does not equal the subtotals for either the feeding or non-feeding categories, because in a small number of cases certain species exploit more than one nutrient source

Nutrient source	No. genera	No. species
rotting carrion (fish)	32 (38%)	89 (20%)
rotting fruit (banana)	0 (0%)	0 (0%)
flowers	16 (19%)	31 (7%)
puddling	14 (16%)	25 (6%)
all feeding categories	41 (48%)	124 (28%)
no feeding categories	44 (52%)	317 (72%)
TOTAL	85	441

TABLE 2. The number and percentage of species of male Ecuadorian Riodinidae recorded feeding on different nutrient sources for each subfamily and tribe. The numbers in parentheses after the subfamily/tribe indicate the number of species analysed in this study. Symbols: frv = forewing radial veins; nr = no records

Subfamily/tribe	Feeding category		
	Rotting fish	Flowers	Puddling
Euselasiinae (59)	17(29%)	nr	nr
Riodininae (382)	72(19%)	31(8%)	25(7%)
Mesosemiini (47)	nr	nr	nr
Eurybiini (19)	nr	11(58%)	nr
<i>incertae sedis</i> - 5 frv (21)	3(14%)	nr	nr
Riodinini (84)	39(46%)	11(13%)	25(30%)
Symmachiini (36)	4(11%)	nr	nr
Sarotini (19)	9(47%)	1(5%)	nr
Helicopini (2)	nr	nr	nr
<i>incertae sedis</i> - 4 frv (44)	14(32%)	1(3%)	nr
Lemoniini (18)	2(11%)	2(11%)	nr
Nymphidiini (89)	1(1%)	5(6%)	nr
Stalactini (3)	nr	nr	nr

and a few species of Ithomiinae (*Tithorea* and *Elzunia*). The phenomenon of riodinids feeding on rotting carrion is virtually unknown, Austin & Riley (1995) only reporting *Rhetus* and *Euselasia*, while DeVries (1988, 1997) and Callaghan (1985) both state that with few exceptions riodinids are not attracted to baits of any kind. However, since 1991 we have been surveying the butterfly fauna of Ecuador and recording adult feeding behaviours for all Papilionoidea, and found more riodinid species attracted to rotting carrion than to any other substrate (see Table 1, Table 2 and Appendix).

The Riodinidae is a large family of tropical butterflies with a worldwide distribution, although their proliferation in the Neotropics, where approximately 1300 (93%) species are found, is unmatched anywhere else (Heppner, 1991; D'Abbrera, 1978, 1980, 1986, 1993, 1994; Bridges, 1994). Since Ecuador contains within its borders three of the main Neotropical biogeographic regions, namely the Transandean,

Andean and Amazonian regions, it undoubtedly harbours one of the richest riodinid faunas, which we estimate consists of 750 to 800 species, and it is thus an ideal location for data collection. From our preliminary observations of riodinid feeding behaviour, it became apparent that those species attracted to rotting carrion seemed to have relatively large thoraces, while those species not recorded feeding from any substrate often had relatively small thoraces. This led us to believe that there might be a relationship between adult feeding behaviour and morphology, and therefore biological correlates of morphology, such as metabolic rate and speed of flight. The purpose of this paper is to explore these possibilities and the potential ecological ramifications of such correlations.

METHODS

Field methods

The data for this study were collected by both authors in Ecuador over a four year period between 1991 and 1995, during a total of ten months field work. Riodinid food substrate choice was recorded at approximately 45 sites, from sea-level to 2000 metres on the western slope of the Andes, and from 250 to 2000 metres on the eastern slope, during both wet and dry seasons. Four nutritional substrates were investigated: rotting fruit, rotting carrion, moist ground (puddling) and flowers.

Approximately 15 Van Someron-Rydon traps (design as figured in DeVries, 1987; Austin & Riley, 1995; Sourakov & Emmel, 1995) were deployed in each site between 07:30 and 16:30 hours in a representative sample of microhabitats that included forest canopy and subcanopy (up to 20 m), light gaps, forest edges, streamsides and understorey. Baited traps were raised above the ground by means of a polyethylene string looped over a branch, and were lowered approximately once every hour to check for butterflies that were either in the trap or resting on the outside. Traps were baited with rotting banana (3–7 days old) or rotting fish (1–2 weeks old). Field experience indicates that adult butterflies are typically generalist feeders within their respective feeding guilds, and thus the use of rotting banana provides a method for identifying species that under natural conditions feed on the wide variety of fermenting fruits encountered either on the trees or on the forest floor, while in a similar manner rotting fish represents any decaying animal matter. Observations on flower visitation and puddling were made when not checking traps. Butterfly puddling is a natural phenomenon that occurs at moist areas along streamsides and on forest trails, and the attractiveness of these places was enhanced by the addition of human urine.

Morphological analyses

As the vast majority of individuals observed feeding in the field, except those visiting flowers, were males and as rotting fish is the substrate of most interest in this study, due to both the poorly known nature of and large numbers of species attracted to it, the morphological analysis was restricted to males. Thoracic volume

was the morphological parameter chosen to test for a correlation with feeding behaviour, in part, because it is directly proportional to thoracic mass, which consists of up to 95% flight muscle mass (Marden, 1989) and is an important factor in determining insect flight performance (Marden, 1987), and thus energy requirements and perhaps nutrients sought. However, it is also clear that larger butterflies are more massive and have larger thoraces to power larger wings, so to control for this we also measured wing area, which is isometrically correlated with total body mass (Dudley, 1990) and thus a convenient measure of the relative sizes of butterflies, to create a wing area to thoracic volume ratio. As wing area is proportional to wing length squared, while thoracic volume is proportional to thoracic length cubed, we used values of thoracic volume raised to the two-thirds power to create a dimensionless ratio (hereafter referred to as WA:TV ratio). While a number of other parameters may appear to be of possible interest (e.g. thoracic mass/body mass, abdominal volume and wing loading; see Marden (1989), Srygley & Chai (1990a), Dudley (1990)), we were only able to make measurements from dried and set specimens, thus restricting our choice of parameters.

Measurements of wing and thoracic dimensions were made using digital calipers, to the nearest tenth of a millimetre, for one male of each of the 441 riodinid species observed and collected by ourselves during the study period in Ecuador. The rarity of many species precluded the possibility of measuring multiple specimens per species. The area of a single forewing was used as a convenient estimate of relative wing area, and was calculated as half the product of forewing length (from wing base to apex) and forewing 'breadth' (shortest distance from tornus to costa). Thoracic volume was calculated as the product of maximum thoracic width, depth and length. While both these sets of measurements are approximations, since there appears to be no correlation between size, and shape of the wings or thorax, the error between the calculated and true values is not expected to increase or decrease systematically in magnitude with increase in thoracic volume or wing area.

In the absence of appropriate data for the Riodinidae, we explore for a relationship between WA:TV ratio and flight speed by reanalysing data published by Dudley & Srygley (1994) for 62 species of non-riodinid Panamanian butterflies. Similarly, we investigate possible relationships between WA:TV ratio and oxygen consumption, and thus metabolic rate, during flight through a reanalysis of data published by Bartholomew & Casey (1978) for 31 moth species.

RESULTS

Feeding categories and the WA:TV ratio

We recorded 124 species of riodinids in 41 genera feeding at rotting carrion, flowers, and/or puddling from a total of 441 species in 85 genera encountered (Table 1, Table 2 and Appendix). Most notably, 89 species from 32 genera were recorded feeding on rotting carrion and no species was recorded on rotting fruit. Species of the subfamily Euselasiinae were only observed on rotting fish, while species of the subfamily Riodiniinae were found on all recorded food substrates (Table 2). Within the Riodiniinae, only the tribe Riodinini, whose component species typically provided a relatively high number of feeding observations (see Appendix),

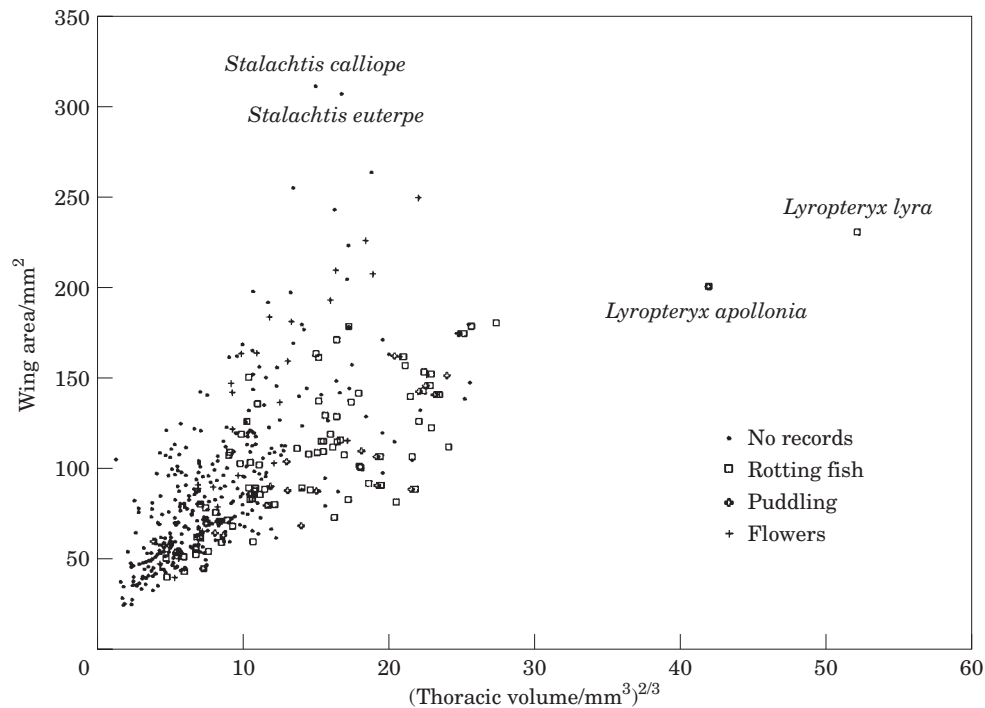


Figure 1. The relationship between wing area and thoracic volume for males of 441 species of Ecuadorian Riordinidae feeding on different nutrient sources. Each point represents a different species, and the slope of the line that joins the origin to the point is equal to the ratio of wing area to thoracic volume for that species; a steeper slope represents a higher wing area to thoracic volume ratio. *Stalachtis* species (high WA:TV ratios) and *Lyropteryx* species (low WA:TV ratios) are indicated on the graph as they illustrate two morphological extremes.

were recorded feeding on all three substrates. Also noteworthy is the fact that no feeding behaviour was observed in the large tribe Mesosemiini.

The majority of species that have been recorded feeding on rotting fish and puddling are in the lower range of WA:TV ratios (Figs 1 and 2). These species belong in genera such as *Lyropteryx*, *Chorinea*, *Rhetus*, *Ancyluris*, *Necyria*, *Lasaia* (Riordinini), *Anteros* and *Ourocnemis* (Sarotini [= Charitini Auctt.]) (see Appendix). Conversely, those species for which there are no feeding records have the highest WA:TV ratios and cluster along the upper edge of the 'shotgun' pattern (Fig. 1). These species are typical of the genera *Leucochimona*, *Mesosemia* (Mesosemiini), *Eunogyra*, *Hyphilaria* (*incertae sedis* - 5 frv), *Mesene* (Symmachiini), *Nymphidium* (Nymphidiini) and *Stalachtis* (Stalachtini). ANCOVA performed on these data (in which the thoracic volume values were log transformed to meet the test's assumptions of normality and equal variance) indicates that the slope of the line for species not recorded feeding ($n=317$) is significantly different from that of fish feeders ($n=89$, $F=19.95$, $P<0.001$), puddlers ($n=25$, $F=11.42$, $P<0.001$) and flower feeders ($n=31$, $F=6.35$, $P<0.02$). While the slopes of the lines for fish feeders and puddlers are not significantly different, those for both of these categories are significantly different to that of flower feeders ($F=26.12$ and 19.77 respectively, $P<0.001$ in each case).

The mean WA:TV ratio for species recorded feeding on rotting fish is significantly

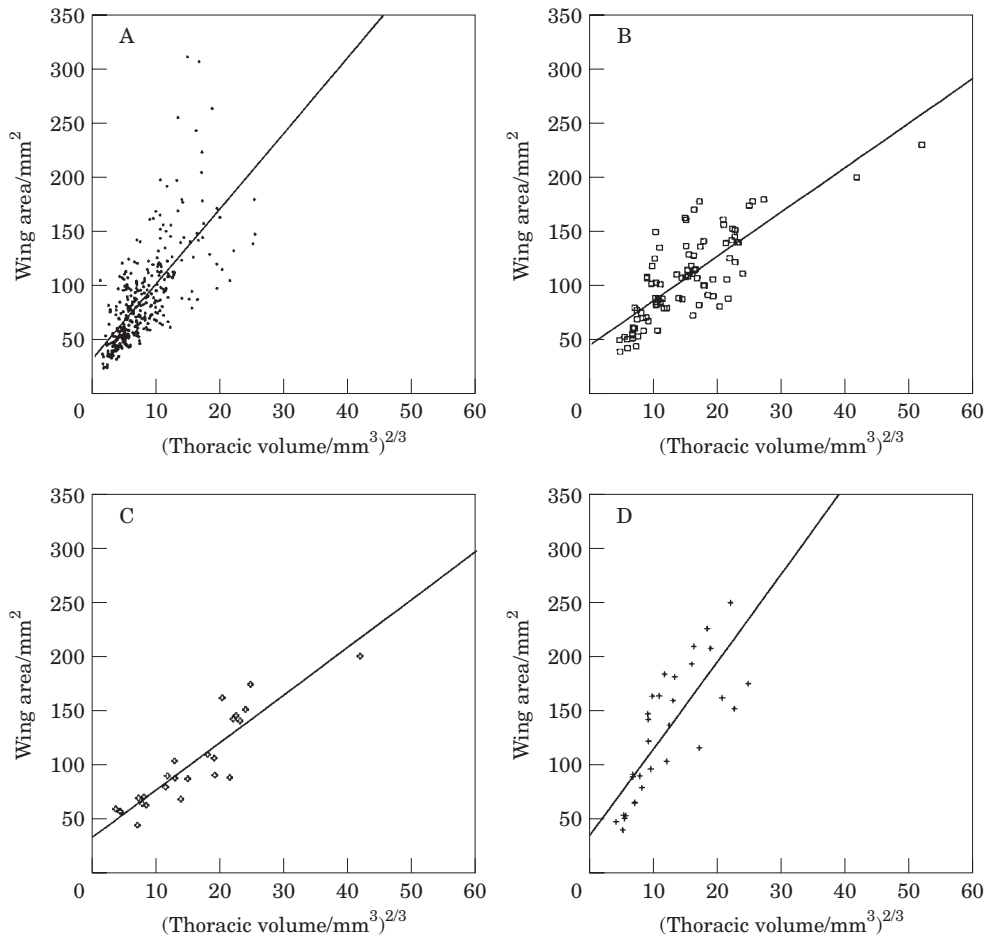


Figure 2. The relationship between wing area and thoracic volume for male Ecuadorian Riodinidae feeding on different nutrient sources. These data sets are individual plots of each feeding category shown collectively in Figure 1. A, no records; B, rotting fish; C, puddling; D, flowers.

lower than that for flower feeders and for those species not recorded feeding, but not does not differ significantly from that for puddlers (Table 3, Fig. 3). Puddlers also have a significantly lower mean WA:TV ratio than flower feeders and non-feeders. However, the mean WA:TV ratio for flower feeders does not differ significantly from that for non-feeders. The mean WA:TV ratio is significantly lower for all species recorded feeding compared with that for species not recorded feeding, for fish feeders compared with non-fish feeders and for puddlers compared with non-puddlers, but is not significantly different for flower feeders compared with non-flower feeders (Table 3).

Effects of phylogeny on the WA:TV ratio

Since no detailed phylogeny of the Riodinidae is available, we could only examine the effects of phylogeny on the observed feeding patterns in a somewhat crude

TABLE 3. Levels of significance for comparisons of mean WA:TV ratio between various feeding categories

Feeding category	<i>n</i>	WA:TV ratio $\bar{X} \pm SE$	Category compared	<i>F</i> value	Significance
Rotting fish	89	7.86 ± 0.23	Puddling ¹	—	NS
			Flowers ¹	—	<i>P</i> <0.01
			Non-feeding ¹	—	<i>P</i> <0.01
Puddling	25	7.47 ± 0.54	Flowers ¹	—	<i>P</i> <0.01
			Non-feeding ¹	—	<i>P</i> <0.01
Flowers	31	10.88 ± 0.54	Non-feeding ¹	—	NS
Non-rotting fish	352	12.20 ± 0.31	Fish ²	46.80	<i>P</i> <0.001
Non-puddling	416	11.56 ± 0.28	Puddling ²	12.82	<i>P</i> <0.001
Non-flowers	410	11.36 ± 0.29	Flowers ²	0.21	NS
All feeding	124	8.67 ± 0.25	Non-feeding ²	43.73	<i>P</i> <0.001
Non-feeding	317	12.37 ± 0.34	—	—	—
All species	441	11.33 ± 0.35	—	—	—

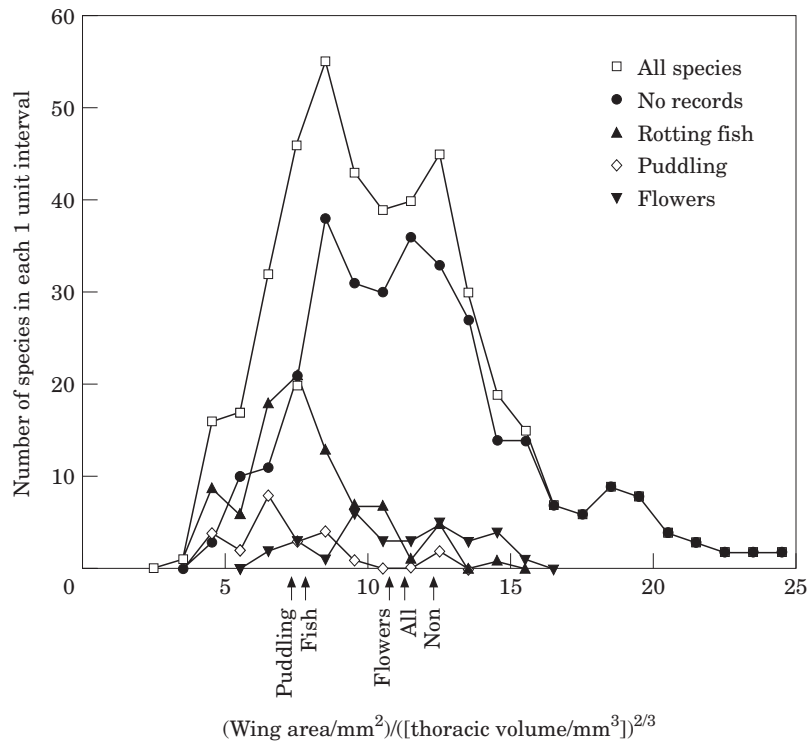
¹ANOVA, Tukey test.²ANOVA.

Figure 3. The frequency of species in each 1 unit interval of wing area:thoracic volume ratio for groups feeding on different nutrient sources. The mean ratio value for each feeding category is indicated by an arrow on the x-axis.

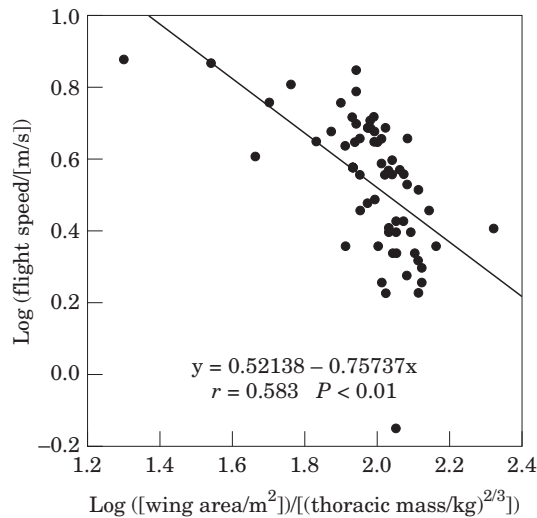


Figure 4. The relationship between flight speed and the wing area:thoracic mass ratio for 62 species of Panamanian butterflies. The data are taken from Dudley & Srygley (1994) and include species from the families Papilionidae (8 spp.), Pieridae (11 spp.), Nymphalidae (39 spp.) and Hesperidae (4 spp.).

manner, by doing step-wise comparisons of mean WA:TV ratios for fish feeders and non-fish feeders at different levels of the taxonomic hierarchy for groups in which this feeding category was well represented. The mean WA:TV ratio for species recorded feeding on fish is significantly lower than that for species not recorded feeding on fish within the tribes Riodinini (ANOVA: $n=39$, mean = 7.18 for fish feeders; $n=45$, mean = 10.99 for non-fish feeders; $F=34.32$, $P<0.001$) and Sarotini (ANOVA: $n=9$, mean = 6.54 for fish feeders, $n=10$, mean = 10.16 for non-fish feeders; $F=19.70$, $P<0.001$). Within the largest genus, *Euselasia*, fish feeders had a lower mean WA:TV ratio than non-fish feeders (ANOVA: $n=16$, mean = 8.83 for fish feeders; $n=42$, mean = 9.69 for non-fish feeders; $F=2.51$, $P=0.118$), although in this case the difference was not quite significant.

The WA:TV ratio, flight speed and metabolic rate

The reanalysis of data presented by Dudley & Srygley (1994) on the morphological characteristics and flight speeds of 62 species of Panamanian butterflies shows that the wing area: thoracic mass ratio (thoracic mass is directly proportional to thoracic volume) and flight speed are significantly negatively correlated (Fig. 4). Thus those species with a low WA:TV ratio have experimentally been demonstrated to have higher flight speeds. The reanalysis of data from the study by Bartholomew & Casey (1978) on metabolic rates during hovering flight and morphology in moths shows that oxygen consumption (indicative of metabolic rate) is significantly negatively correlated with the wing area:thoracic mass ratio (and thus WA:TV ratio), indicating that species with low WA:TV ratios generally have higher metabolic rates in flight (Fig. 5).

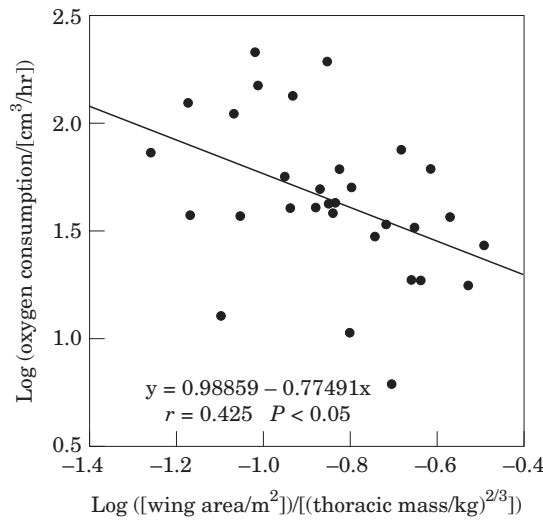


Figure 5. The relationship between oxygen consumption during hovering flight and the wing area: thoracic mass ratio for 31 species of moths. The data are taken from Bartholomew & Casey (1978) and include species from the families Sphingidae (14 spp.), Saturniidae (13 spp.), Megalopygidae (1 sp.), Notodontidae (1 sp.), Noctuidae (1 sp.) and Lasiocampidae (1 sp.).

DISCUSSION

Food substrate choice

Despite the general lack of feeding records for riordinids in the literature, exclusive of flower visitation, it can be seen from Tables 1 and 2 that individuals in almost half the genera and in over a quarter of the species observed by us in Ecuador were recorded feeding. The majority of these were recorded on rotting carrion, a little known adult food source for the Riordinidae. The use of this food substrate in Ecuador has enabled us to compile a more accurate faunal list more rapidly, to considerably extend the known geographic ranges of some very rare species (e.g. *Ourocnemis* spp.), as well as to discover undescribed species (Hall & Willmott, 1995, 1998a, b, c), all elements important in conservation biology.

Based on their very similar mean WA:TV ratios, we regard fish feeders and puddlers as forming a single feeding guild, as first suggested by Downes (1973), the two categories being simply defined by their microhabitat preference rather than by differing nutritional requirements. Most species that puddle are found along forest edges and streamsides, where damp sand is abundant, while those recorded on rotting fish generally inhabit the forest, where most of our trapping has been conducted. This idea was supported during the latter part of the study by more frequent trapping in open areas, where certain genera, previously observed only to puddle, were recorded feeding on rotting fish (e.g. *Siseme*, *Baeotis*, *Cavia*). In addition, several genera were commonly observed feeding at both substrates, including *Lyropteryx*, *Ancyluris*, *Necyria*, *Rhetus*, *Chorinea*, *Lasaia*, *Siseme*, *Notheme* and *Parcella*. This feeding guild is not only the largest in the Riordinidae but probably also in several nymphalid subfamilies and in the Lycaenidae (Hall & Willmott, unpubl. data), although it has been ignored by most authors, including DeVries *et al.* (1997), who

recognized an overly simplistic system of two feeding guilds, one for fruit feeders and one for nectar feeders.

It is certain that the number of species that feed from flowers in nature is underestimated in this study with relation to the number of records for species in the aforementioned feeding guild. While rotting fish, and usually urine, were used as baits in almost all sites, visible nectar sources were present in only a few sites. It is noteworthy, however, that the species composition of the flower feeding guild appears to overlap very little with that of the fish feeding/puddling guild. Thus, although it seems clear, based on the data presented here, that a more complete list of species that visit flowers will still give a mean WA:TV ratio intermediate between species in the fish feeding/puddling guild and species not recorded feeding, their exact position in the continuous spectrum of WA:TV ratios is currently uncertain and the focus of the discussion will be centered on the remaining feeding groups.

The differences in the recorded number of food substrates between the subfamilies Riodiniinae and Euselasiinae (Table 2) is almost certainly an artifact of differing species diversity, since the Euselasiinae contains only three genera, while there are several tribes and numerous genera within the Riodiniinae. However, within the Riodiniinae, the fact that members of the tribe Riodinini have been recorded on all three food substrates appears not to be an artifact of differing species diversity, since even some genera (e.g. *Ancyluris*, 10 spp.) exhibit all three feeding behaviours. It is also noticeable that individuals of a large number of species have not been recorded feeding. One reason for this is that many of the riodinid species in this Ecuadorian sample are very rare, represented by only a handful of specimens in the world's collections, and it should come as no surprise that the sighting or collection of a single specimen would not be accompanied by a feeding record. On the other hand, there are many very common species and genera that still have no feeding records, especially in the Mesosemiini (see Table 2). It is possible that this phenomenon is due to sampling error but the distinct possibility remains that a guild of species genuinely exists that very rarely or never feed as adults.

In the discussion that follows we will offer explanations for these observed differences in choice of exploited nutrient sources, concentrating particularly on what benefits may accrue from feeding on rotting fish, the most numerically important nutrient source in this study. The observed relationship of food substrate choice with WA:TV ratio suggests that one or more biological correlates of the WA:TV ratio might be related to, and in fact might be the physiological factor(s) underlying, the evolution of non-feeding vs. feeding syndromes, and might determine which food substrates are utilised by the species that feed. In particular, the flight speed and metabolic rate during flight are likely to be intimately related to the WA:TV ratio, at the same time having nutritional implications (see below).

The effects of phylogeny and other factors on adult feeding behaviour

First, it is important to assess the effects of phylogeny on and hence the degree of independence of data points in the proposed correlation. It is to be expected that phylogenetic relatedness would contribute to some of the differences observed between species that have been recorded feeding and those that have not in each feeding category, since the independence of each data point is influenced by the

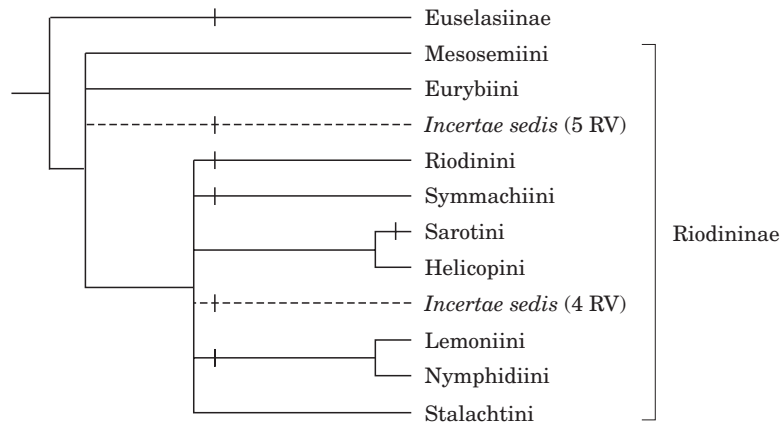


Figure 6. A phylogeny of the subfamilies and tribes of Neotropical Riodinidae (after Harvey, 1987). Solid lines indicate monophyletic groups and dotted lines indicate only loosely related paraphyletic groups. Vertical bars indicate the occurrence of fish feeding behaviour (these are not meant to represent the pattern of evolution for this character).

number of close relatives within the same genus, tribe and subfamily. In other words, species may have the same feeding behaviour and morphology simply because they have both evolved from a common ancestor, rather than independently acquiring similar characteristics due to evolutionary pressures. Indeed, the most widely accepted hypothesis of phylogenetic relationships within the Neotropical Riodinidae (after Harvey, 1987), in Figure 6, clearly shows that certain tribes, most notably the large Mesosemiini and Eurybiini, have, for example, no fish feeding records. Conversely, certain tribes, such as the Riodinini and Sarotini, have a high percentage of fish feeding records and yet others, such as the Symmachiini, Nymphidiini and Lemoniini, have only a few rare records (see Table 2), despite containing a number of species that have low WA: TV ratios. It is notable that only three out of 124 species within the myrmecophilous tribes Nymphidiini, Lemoniini and Eurybiini have been recorded feeding on fish in this study and it seems probable that some phylogenetically shared biological trait, perhaps larval feeding patterns, is important in explaining this observation. Many of these myrmecophilous species feed as larvae on extra-floral nectaries and homopteran honeydew secretions in addition to plant material (DeVries, Chacón & Murray, 1994; DeVries, 1997), and at least one is known to feed solely on the homopterans themselves (Kaye, 1921; Cottrell, 1984; Pierce, 1995), and these unusual behaviours may supply them with the nutrients that other species obtain from rotting fish as adults. Additionally, Smedley & Eisner (1995) suggest that sodium uptake during puddling in the moth *Gluphisia septentrionis* may be necessary because of the unusually low sodium content in its primary larval foodplant *Populus tremuloides*, indicating that perhaps foodplant sodium content may also affect adult food substrate choice in Lepidoptera.

However, the cladogram also indicates that fish feeding does recur frequently at the tribal level and it is certainly not confined only to particular monophyla. In the absence of a fully resolved phylogenetic tree for the entire family, it is not possible to track the state changes of the characters under consideration from one node to the next and we can only provide crude estimates of the independence of data

points. The fact that within the largest fish feeding tribes (Riodinini and Sarotini) the mean WA:TV ratio for species feeding on fish is significantly lower than that for species not recorded feeding on fish indicates that data points are reliably independent at the generic level, and the fact that WA:TV ratios in the largest fish feeding genus (*Euselasia*) are so strongly polarized between fish and non-fish feeders suggests that data points at the species level also show a considerable degree of independence. In conclusion, it is clear that phylogeny plays an important but certainly not exclusive part in determining food substrate choice.

Biological significance of the WA:TV ratio

Flight speed

The patterns of variability of body proportions within the family Riodinidae can be seen in Figure 1. Wing area is positively correlated with thoracic volume, but when food substrate choice is considered, the data seem to fall into two main groups: one in which there are few feeding records, characterized by high WA:TV ratios ('*Stalachtis* group'), and another in which there are many feeding records, especially for rotting carrion and puddling, characterised by low WA:TV ratios ('*Lyropteryx* group'). Each group is named for the genus whose morphology epitomises it (see Fig. 1). Our reanalysis of the data presented by Dudley & Srygley (1994) (Fig. 4) suggests that each of these two groups might be expected to differ in mean flight speed, and indeed our anecdotal field observations suggest that species of the '*Stalachtis* group' often tend to be slow flying, with relatively low wing beat frequencies, while members of the '*Lyropteryx* group' are usually rapid flyers, with high wing beat frequencies and erratic flight patterns. Relatively large wings are probably unfavorable for rapid flight due to the greater drag from the air and loss in manoeuvrability resulting from a slower wing beat.

Metabolic rate of flight

Fast flying insect species usually have higher thoracic temperatures while in flight (Heinrich, 1981a,b), thought largely to be due to the generation of heat in the thorax through the inefficient conversion of energy in the flight muscles (Weis-Fogh, 1972; Ellington, 1984d). Metabolic rate is thus thought to be positively correlated with thoracic temperature, assuming a constant muscle efficiency (Kammer & Heinrich, 1974), though this relationship was questioned by May (1985). Chai & Srygley (1990) noted that fast flying species of Panamanian butterflies had higher thoracic temperatures, suggesting that they might also have had higher metabolic rates.

A more reliable measure of metabolic rate during aerobic exercise, as characterises insect flight, is oxygen consumption, and Kammer & Heinrich (1974) demonstrated that in bumblebees (*Bombus*) metabolic rate was positively correlated with muscle activity (and, anecdotally, faster flight). Our reanalysis of the data presented by Bartholomew & Casey (1978) on metabolic rates during hovering flight in moths indicates that species with low WA:TV ratios generally have higher metabolic rates (Fig. 5) (see also Casey, 1981). However, the relationship between metabolic rates during hovering and forward flight are complex, since an increase in flight speed causes a decrease in the power required to move air downwards in support of the

body weight (induced power), but an increase in the power required to overcome air friction (profile power) on the wings (Dudley, 1991; Dudley & DeVries, 1990). The mean force during steady flight seems to differ little from that in hovering flight (Ellington, 1984b), and in bumblebees (Ellington, Machin & Casey, 1990) and flying vertebrates (Ellington, 1991) there is often little increase in metabolic rate with increase in flight speed, suggesting metabolic rates in forward and hovering flight within species might be similar. However, Dudley & DeVries (1991) demonstrated that in the moth *Urania fulgens* mechanical power output, and thus probably metabolic rate, increased with flight speed, possibly largely due to a high ratio of forward to flapping velocity (the advance ratio; see Ellington, 1984b).

Therefore it remains unclear whether it is valid to extrapolate the relationship between WA:TV ratio and metabolic rate in hovering moths to forward flight but if this is done it would follow that flight speed is probably positively correlated with metabolic rate between species, as both flight speed and metabolic rate are negatively correlated with WA:TV ratio in Lepidoptera. In tentative support of this idea, Dudley (1991) found that in 15 species of Panamanian butterflies the specific mechanical power (power per unit body mass) required to fly increased with airspeed, suggesting that metabolic rate would probably follow the same relationship.

Thus fast-flying species with low WA:TV ratios might be operating at higher metabolic rates than slow-flying species with high WA:TV ratios. A theoretical consideration of power requirements during flight might help explain this, as well as why there appear to be very few species with large wing areas and high thoracic volumes in Figure 1 (i.e. intermediate between the morphological extremes of the 'Stalachtis' and 'Lyropteryx groups'). The power required for flight is usually divided into four components (Ellington, 1984a,d; Dudley & DeVries, 1990): induced power, required to accelerate air downwards to support the body weight; profile power, required to overcome the drag of the air on the wings; parasite power, required to overcome the drag of the air on the body; and inertial power, required to accelerate and decelerate the wing mass and an associated mass of air during each wing beat. A typical member of the 'Lyropteryx group' will have a smaller wing area than a member of the 'Stalachtis group' with similar body mass, and will require a greater induced power to support its body weight (Ellington, 1984c; Dudley & DeVries, 1990). Although the former species experiences a reduced profile power, this may be an unrealized benefit if it is operating at higher airspeeds where the profile drag increases substantially (Dudley, 1991). Inertial power is higher in the species of the 'Stalachtis group', but this effect will be negligible if, as is suspected, the thorax is able to store elastic energy during each wing beat (Ellington, 1984d; Dudley, 1991; Dudley & Ellington, 1990). Differences in parasite power are probably also minimal (Dudley, 1991). If insect flight muscles are operating near their force limit, an increase in wing area requires that the wing acceleration during each wing beat cycle is reduced, and hence wing beat frequency. As a high muscle power output may in fact depend on high thoracic temperatures during flight (Josephson, 1981), maintained by high wing beat frequencies, it may be that species with low wing beat frequencies are also simply physiologically incapable of generating high power outputs.

In addition to flight speed, the flight path will also greatly affect the metabolic rate. Chai & Srygley (1990) showed that many species, particularly fast fliers, also exhibited erratic flight paths with frequent changes in both vertical and horizontal direction, and thus kinetic and potential (gravitational) energy. The energetic costs

associated with this type of flight may be substantial; Dudley (1991) calculated that in 15 species of Panamanian butterflies, an average of 26–43% of the total mechanical power requirement (depending on initial assumptions) was necessary to lift and accelerate the body during erratic flight.

Nutrients sought and their function in adult physiology and reproduction

We propose, therefore, that choice of food substrate in male riodinids is correlated with flight speed and metabolic rate. Those species that have low WA:TV ratios and which puddle and/or are attracted to rotting carrion, appear to have higher flight speeds and very possibly higher metabolic rates, at least during flight, than those species with low WA:TV ratios that typically have not been recorded feeding. This suggestion gives us some clues as to what adult males may be seeking when they feed on certain substrates.

Flight muscle metabolism

Arms *et al.* (1974) appear to have conducted the only study to determine exactly what substance is being sought by adult butterflies when feeding on substrates other than flowers. They found that in the swallowtail butterfly, *Papilio glaucus*, sustained feeding at damp sand by males only occurred when sodium ions were present. While amino acids failed to stimulate puddling, radioactively traced amino acids absorbed during puddling were incorporated into body proteins. In the moth *Gluphisia septentrionis*, Smedley & Eisner (1995) found that the duration of puddling and the total fluid volume ejected were inverse functions of the sodium concentration in the imbibed fluid and that the sodium content of males that had puddled exceeded that of controls for all body parts, providing direct evidence that puddling involves sodium uptake in Lepidoptera.

Given the great similarity in morphology of puddlers and fish feeders, that led us earlier to include them in the same feeding guild, it seems likely that fish feeders may be gaining similar nutritive benefits from rotting fish as puddlers do from puddling (as also suggested by Downes, 1973). Altman & Dittmer (1968) present data showing that the sodium content of fish (0.6 mg/g) is similar to that of human urine (3 mg/g), which is highly attractive to puddling species, although the potassium content is greater in fish. The positive correlation of low WA:TV ratios with high flight speed, and very possibly high metabolic rate, in fish feeders/puddlers strongly supports the suggestion of Downes (1973) and Arms *et al.* (1974) that sodium might be important for maintaining high neuromuscular activity. The observation that virtually all individuals found puddling and feeding on fish are males might also be explained by the greater flight activity of this sex (Downes, 1973). The fact that bananas typically contain only a sixtieth of the sodium content of fish (Altman & Dittmer, 1968) might explain why fish feeders/puddlers were not recorded in this study on rotting banana. Fish has a much higher protein content than banana (Altman & Dittmer, 1968) and based on the evidence of Arms *et al.* (1974) for puddlers, fish feeders might also be incorporating amino acids into body proteins to sustain their large thoracic muscle mass. Adult Lepidoptera are not known to consume lipids for energy metabolism, but so little is known about the nutritional physiology of carrion feeders that this might be an additional potential nutritive benefit to feeding on rotting carrion.

Reproductive success

Boggs & Gilbert (1979) were the first to demonstrate that during copulation, both sodium and nitrogen (as amino acids) were transferred in the male spermatophore to female butterflies, which Adler & Pearson (1982) suggested might explain the significant drop in male sodium levels after eclosion, in comparison to females. It has also been shown that access to sodium and nitrogen increases both male mating success and female reproductive success (Dunlap-Pianka, Boggs & Gilbert, 1977; Pivnick & McNeil, 1987; Lederhouse, Ayres & Scriber, 1990; Boggs, 1990, 1995). It therefore seems clear that puddling behaviour and nutrient acquisition in males is, to some degree, due to the necessity to provide for potential mates, which, through copulation, are able to maintain almost constant sodium levels, despite almost never being observed to puddle (Adler & Pearson, 1982). However, importantly, Sculley & Boggs (1996) have shown that the extent of nutrient transfer between sexes can vary interspecifically. If obtaining nutrients from puddling or feeding on rotting carrion is beneficial to both males and the females with which they mate, we might expect all species to feed at these substrates. One possible explanation of why this is not the case may be that those species with high WA:TV ratios also have larger abdominal volumes (Srygley & Chai, 1990a), enabling them to store sufficient nutrients for both reproduction and flight muscle metabolism during larval feeding, perhaps explaining why the adults of many common riodinid species (e.g. members of the Mesosemiini) have not been observed to feed. Conversely, species with low WA:TV ratios (i.e. large thoraces) and low abdominal volumes may be unable to store large amounts of sodium and amino acids from the larval stage, necessitating that they augment their reserves through frequent adult feeding.

Ecological patterns

As briefly outlined earlier, there appear to be two broadly recognizable morphological groups of riodinids, our '*Stalachtis*' and '*Lyropteryx* groups', and each of these appears to display a distinct suite of accompanying ecological characteristics. We suggest that these groups loosely represent two major adaptive syndromes within the Riodinidae.

We have presented evidence in this study that species that typically feed on rotting carrion and/or puddle have low WA:TV ratios, are fast and agile fliers, and probably have relatively high metabolic rates during flight ('*Lyropteryx* group'). Field observations indicate that these species tend to inhabit sunny subcanopy/canopy and forest edge microhabitats which have the high ambient temperatures essential for maintaining the elevated thoracic temperature necessary for rapid and instantaneous flight. Males of many riodinid species are known to 'perch' at characteristic sites (Callaghan, 1983; Brévignon & Gallard, 1995; Hall, 1998), where they are seen to fly out and investigate passing objects in search of females and to engage in aerial 'combat' with other males (Scott, 1976). Males in the '*Lyropteryx* group' are usually encountered perching as solitary individuals, perhaps indicating that their powerful flight is necessary for defending relatively large territories, a hypothesis consistent with the studies of Wickman (1992) on Swedish butterflies. He found that perching species had higher thorax to body mass ratios, wing loadings and aspect ratios, and were more strongly sexually dimorphic than patrolling species, suggesting that the mating system may exert a strong pressure on male flight characteristics. Conversely, we

have shown that those species which typically have not been recorded feeding have high WA:TV ratios, are slow flying, and probably have relatively low metabolic rates during flight ('*Stalachtis* group'). Field observations indicate that they are usually inhabitants of the shady understorey where ambient temperatures are relatively low. When males are encountered perching, they are often found in numbers on a particular bush, indicating that these species do not maintain large territories.

Chai & Srygley (1990) and Srygley & Chai (1990a, b) studied the morphology, flight behaviour, thermal biology and palatability of butterfly species in the Papilionidae, Pieridae and Nymphalidae in Costa Rica. Their results showed that these butterflies also fell into two groups with similar characteristics to those outlined above for riodinids. Those species with more massive thoraces, faster and more erratic flight and higher thoracic temperature (corresponding to our '*Lyropteryx* group') were also found to be palatable to jacamars (*Galbula ruficauda*); species with less massive thoraces, slower and more even flight and lower thoracic temperatures (corresponding to our '*Stalachtis* group') were generally unpalatable. While virtually nothing is known about the palatability of riodinid butterflies, our field observations suggest that genera which contain aposematic and/or mimetic and possibly unpalatable species include *Ithomiola* (*incertae sedis* - 5 frv), *Themone*, *Pheles* (Riodinini), *Xynias*, *Mesene* (Symmachiini), and *Stalachtis* (Stalachtini), all of which fall into our '*Stalachtis* group'. Furthermore, our field observations suggest that nymphalid species that share similar characteristics with our '*Lyropteryx* group' (e.g. Charaxinae, Limenitidinae) are strongly attracted to rotting carrion whereas nymphalid species that share similar characteristics with our '*Stalachtis* group' (e.g. Ithomiinae, except *Elzunia* and *Tithorea* [4 spp.]) do not generally feed on rotting carrion. It thus seems possible that the correlation between food substrate choice and the morphological and ecological characteristics we have outlined above is a general phenomenon found in butterfly families other than the Riodinidae, and might also occur in other lepidopteran groups.

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