Macroevolution of hoverflies (Diptera: Syrphidae): the effect of using higher-level taxa in studies of biodiversity, and correlates of species richness

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Abstract

We test a near-complete genus level phylogeny of hoverflies (Diptera: Syrphidae) for consistency with a null model of clade growth having uniform probabilities of speciation and extinction among contemporaneous species. The phylogeny is too unbalanced for this null model. Importantly, the degree of imbalance in the phylogeny depends on whether the phylogeny is analysed at the genus level or species level, suggesting that genera ought not to be used uncritically as surrogates for species in large-scale evolutionary analyses. Tests for a range of morphological, life-history and ecological correlates of diversity give equivocal results, but suggest that high species-richness may be associated with sexual selection and diet breadth. We find no correlation between species-richness and either body size or reproductive rate.

Introduction

Phylogenies can be used in tests to explain patterns of biodiversity as they carry the direct imprints of the processes of speciation and extinction. Together, these processes account for the exact nature of the branching patterns and hence also of present-day diversity. Complete phylogenies (by which we mean phylogenies that permit enumeration of the species at every tip of the tree) allow us to use recently developed tests of macroevolutionary hypotheses (Harvey *et al.*, 1996; Nee *et al.*, 1996; Purvis, 1996; Mooers & Heard, 1997). We can compare these phylogenies against simple null models to attempt to describe the branching process. If they do not fit these null models, we can look for factors that may correlate with species richness.

It is common in some fields to use genera as if they are comparable units in studies of biodiversity. This is particularly true in palaeobiology, where workers have little choice but to use higher taxa, as the fossil record often contains only a small proportion of the total number of species that have existed (Foote, 1996). Using higher level taxa such as genera or families may, therefore, describe patterns of biodiversity more accurately. It has been argued on empirical and theoretical grounds that higher taxa can safely be used as surrogates for species in studies of biodiversity (Sepkoski & Kendrick, 1993; Williams & Gaston, 1994). Higher taxa have also been used as comparable units in neontological studies (Ricklefs & Renner, 1994). We use the hoverflies as a study group to assess whether genera are adequate surrogates for species.

Hoverflies (Syrphidae) are one of the most diverse families of the Diptera, comprising about 200 genera and over 5000 species. As well as taxonomic diversity, hoverfly adults display a wide range of lifestyles and adaptations (Gilbert, 1990, 1993; Gilbert *et al.*, 1994). They have a 400-fold range in weight, from *Neoascia* at 0.5 mg to the bumblebee-sized *Volucella* or *Milesia* at 200 mg or more, and females have from 8 (*Melanostoma*) to 800 (*Criorhina*) ovarioles. Adults feed on nectar and pollen from flowers, and can be specialists (e.g. *Rhingia* on blue or purple flowers with deep corolla tubes) or,

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more usually, generalists. Conspicuous and charismatic, hoverflies are widely collected and their natural history is better known than for many other insect taxa, making them particularly suitable for testing comparative hypotheses regarding the evolution of morphological, ecological and life-history traits.

Rotheray & Gilbert (1999) have produced a near complete phylogeny of genera of Palaearctic hoverflies, based on a cladistic analysis of morphological characters. We have added the remaining world genera, except for two whose affinities are unknown. We first consider whether the shape of the phylogeny is compatible with a null model in which specification and extinction probabilities are uniform among all contemporaneous species (Raup *et al.*, 1973: henceforth the Markovian model). Rejection of the Markovian model invites study of what factors promote diversification. First, we examine nodes in the phylogeny where the difference in species-richness between sister taxa is surprisingly large, to look for a pattern in the synapomorphies (shared derived characters) leading to diverse or species-poor clades. Then, we test some hypothesized morphological, ecological and life-history correlates of diversity, looking for a repeated association between trait and species-richness (Williams, 1992; Barraclough *et al.*, 1998a). We do not consider geographical influences on species richness, although preliminary results suggest that the invasion of the neotropics has not led to a significant increase in species richness in the hoverflies (A. Katzourakis, unpublished data). We consider the following proposed predictors, for which comparable measures were available for many species.

Body size: Habitats might contain more niches for small organisms than for large ones (Hutchinson & MacArthur, 1959), or a correlate of small body size (such as reproductive rate: Marzluff & Dial, 1991) might drive species-richness differences. Small size is correlated with high diversity in some mammalian groups (Gittleman & Purvis, 1998; Gardezi & da Silva, 1999).

Life history: High reproductive rate has been argued to raise speciation rates and lower extinction rates (Marzluff & Dial, 1991). Reproductive rate is not always tightly correlated with body size in insects (e.g. aphids, Dixon, 1998, p. 79; water-striders, Klingenberg & Spence, 1997), raising the possibility of distinguishing clearly between effects of life history and body size.

Mating system: Reproductive isolation is facilitated by female mate choice, and indices of the strength of sexual selection have been shown to correlate with species-richness in passerine birds (Barraclough *et al.*, 1998b). A more recent study has shown that insect taxa in multimale groups have higher speciation rates than insects that mate only once (Arnqvist *et al.*, 2000). Female hoverflies mate multiply and store sperm in virtually every species studied to date (e.g. Benestad, 1970; Conn, 1971; Duffield, 1981; Simmons & Siva-Jothy, 1998), making sperm choice and strong sexual selection possible. This makes it possible to determine whether the degree of sexual selection within a clade of insects that all display some sexual selection has an effect on species richness, providing a more precise and refined test of this hypothesis.

Diet breadth: The relationship between feeding specialization and rates of speciation and extinction was reviewed by Kelley & Farrell (1998): most authors agree that specialists have higher extinction rates than generalists (e.g. Stanley, 1979; McKinney, 1997), but the situation with speciation rate is less clear.

Methods

Phylogeny

Rotheray & Gilbert's (1999) phylogeny of the Syrphidae includes 82 genera for which the larval stages could be studied. This is the largest and most robust phylogeny of hoverflies currently available. We used this phylogeny as the main basis for our tree, and enlarged it to include the 198 world genera (omitting only two, *Pia* and *Stenopipiza*, whose affinities are unknown). Not all hoverflies are known in their larval stage. This rules out creating a morphological phylogeny for all of the genera based on larval characters, so we combined phylogenetic information from different sources. Our list of genera is based on F. Christian Thompson's world list (on computer only, 1989), modified to reflect recent changes in generic boundaries. It includes some unpublished new genera, and the numbers of species within each genus. The extra genera were placed using suggestions in the literature (Thompson, 1972, 1991; Knutson *et al.*, 1975; Thompson *et al.*, 1976; Hippa, 1978, 1990; Smith & Vockeroth, 1980; Peck, 1988; Thompson & Vockeroth, 1989; Vockeroth, 1992). When placing the additional genera we took the conservative approach of collapsing branches into polytomies when source trees were in conflict, thus excluding branching data that may be ambiguous. The resulting phylogeny had 127 nodes out of a potential 203 for a fully bifurcating tree, so the tree was 63% resolved. The exact details describing the addition of these extra branches are in appendix A; the complete phylogeny with species numbers is in appendix B (both Appendices can be found at www.blackwell-science.com/products/journals/suppmat/JEB/JEB278/JEB278sm.htm). Rotheray & Gilbert's (1999) phylogeny indicates nonmonophyly for two genera, *Cheilosia* and *Volucella*. The distribution of *Cheilosia*'s 390 species among five clades is not known, leading to uncertainties in the species-richnesses of clades in this portion of the tree. We return to the implications of this for our analyses below. The use of subgenera of these nonmonophyletic taxa results in the tree having 204, rather than 198, terminals. To avoid any bias in our results caused by the method we used to construct the complete phylogeny, we repeated a number of the tree balance tests using only the genera in Rotheray & Gilbert's (1999) phylogeny.

Tree balance

We have used three approaches to assess whether the hoverfly phylogeny is compatible with the null Markovian model.

First, we applied Slowinski & Guyer's (1989) test: for a bifurcation subtending S species, the distribution of species among sister lineages is uniform from (1, S–1) to (S–1, 1). The probability under the Markovian model of obtaining a split at least as extreme as a given observation is therefore $2b/(S-1)$, where b is the species-richness of the less diverse clade. Because this test can yield a significant result only when S is over 40, we applied it only to nodes subtending at least 40 species. Additionally, we excluded nodes rendered ambiguous by the polyphyly of *Cheilosia*. The test was performed on each remaining bifurcation in the phylogeny. To control for multiplicity of tests, we have tested whether the proportion of nodes rejecting the Markovian model at $P = 0.05$ significantly exceeds 0.05.

Second, we used Nee *et al.*'s (1996) generalization of the Slowinski–Guyer test: under the Markovian model, species should be split among any number of equal-age clades according to the broken stick distribution. We simulated (1000 trials) breaking sticks of 5330 species into 204 'genera', assuming genera to be roughly equal in age. If simulations seldom produce genera as diverse as some observed genera, then the distribution of species among genera is not compatible with the broken stick distribution, and hence also the Markovian model.

Finally, we used Fusco & Cronk's (1995) test of tree balance. This method calculates the imbalance, I, of each informative node in the phylogeny (i.e. bifurcations subtending at least four species). I is calculated according to

$$I = (B - m)/(M - m)$$

where B is the species-richness of the more species-rich branch, m is the minimum possible value for B, and M is its maximum value (e.g. if $S = 15$, then $m = 8$, $M = 14$, and B will be an integer in the range 8–14 inclusive). I can range between 0 (maximal balance) and 1 (maximal imbalance), and is independent of the size of a node. The median value of I is then used as the measure of the phylogeny's imbalance, following the procedure of Fusco & Cronk (1995). It can then be compared with the distribution of median I-values resulting from 1000 randomization trials under a Markovian model. These randomization trials result in the construction of confidence intervals (CI) for I. We performed this analysis twice, first considering the species-richness of each genus, then setting all species-richnesses to unity (thereby examining the topology of the genus-level phylogeny). *Cheilosia*'s nonmonophyly is a complication when considering species-richness; however, the median I-value is the same to three decimal places whether the 390 species are spread as evenly (78, 78, 78, 78, 78) or as unevenly (386, 1, 1, 1, 1) as possible among the five clades. We also repeated this analysis using only the genera in Rotheray & Gilbert's (1999) phylogeny to avoid any biasing effect of the method we used to derive the complete phylogeny.

To test whether use of species-richness information had a significant effect on the tree shape statistics, we used a two-sample medians test (Zar, 1984, p. 145) to compare the I-distribution where species-richness is considered with that from the topology alone. In this test we ignored values derived from nodes in the region of *Cheilosia*. Again, we repeated this test using the Rotheray & Gilbert (1999) phylogeny.

Comparative analyses

We used a number of measured traits as indicators of variation in the morphology, ecology and life-history variables that we hypothesize to be associated with species richness. The data were available from F Gilbert (unpublished data):

Body size: We used thorax volume and head width as two measures of body size. Thorax volume is considered a good index of body size for the hoverflies and has previously been used in comparative studies (e.g. Gilbert, 1990). It is calculated as the product of thorax width, length and height. Head width is also used as a simpler surrogate measure of body size.

Life history: Ovariole number and egg volume are used as indicators of reproductive rate. Ovariole number is a direct measure of potential lifetime fecundity (Gilbert, 1990); the tight correlation between lifetime fecundity and number of ovarioles has been demonstrated in parasitoids (Price, 1975). Egg volume is an indicator of the resources devoted to each offspring, and is a sensitive indicator of life-history; in the fast-slow strategic differences in insect life-histories, egg volumes are reduced to the physiological minimum in 'fast' developers, whereas they are much larger in 'slow' developers (Wiklund *et al.*, 1987).

Mating system: We used testis length and spermathecal width as indices of sperm competition intensity. The link between testis size and sperm length has been demonstrated in other insects (Joly & Bressac, 1994; Pitnick, 1996), as has the link between sperm length and sexual competition (Snook, 1997). Spermathecal size is also likely to be related to sperm competition, as spermathecae allow post-copulatory female choice.

Diet breadth: We used tongue length as our measure of diet breadth for nectar feeding hoverflies. Tongue length is a well-known correlate of specialization in flower-visiting insects, and in hoverflies is correlated with corolla depth of flowers and the proportions of nectar and pollen in the diet (Gilbert, 1981, 1985).

Measurements are averages from as many individuals of both sexes as were available (range 1–16 individuals, mean = 3, mode = 1); genus values are averages of species values (range 1–20 species, mean = 4, mode = 1). All traits were log transformed. The number of genera for which data was available for each of the traits were as follows: head width 67, thorax volume 67, ovariole number 62, egg volume 53, spermathecal width 49, testis length 51 and tongue length 66.

We used MacroCAIC (Agapow *et al.* unpublished; Gittleman & Purvis, 1998) to generate phylogenetically independent contrasts in predictor variables and species-richness. For predictor variables, algorithms from Pagel (1992) are used to estimate nodal values from genus averages assuming a random walk model of evolution (Felsenstein, 1985). Differences between sister clades provide the contrasts in predictor variables. Contrasts are not computed at polytomies because of the ambiguity of sister-clade relationships. In the absence of branch length information, we have set all branches to equal length. It has been shown by simulation that setting all branches to equal length reduces the type 1 error rate (Isaac, personal communication, 2000).

Following Gittleman & Purvis (1998), the species-richness contrast at each bifurcation is calculated as $\log_e$ (number of species in clade with larger value of trait/ number of species in clade with smaller value of trait). Under the null hypothesis that the trait value does not predict clade size, the expectation of this contrast is zero (Gittleman & Purvis, 1998). Like Gittleman & Purvis (1998), we used *t*-tests to test whether the mean of these contrasts differed significantly from zero for each trait, and used least-squares regression through the origin to test whether the differences in the value of each trait predicted the species-richness contrasts (Garland *et al.*, 1993; Gittleman & Purvis, 1998). All probability values reported are two-tailed. A recent simulation study (Isaac, personal communication 1999) has shown that these tests give correct Type 1 error rates if character change occurs only at speciation events and is conservative if change is gradual. The simulation results hold for both Markovian and unbalanced phylogenies.

Results

Tree balance

Eight bifurcations in the phylogeny, of 74 tested, are significantly unbalanced at the $P = 0.05$ level, according to the Slowinski-Guyer test. Eight is significantly more than expected from the binomial distribution ($P = 0.03$), indicating that the result is not due to multiple tests. The eight nodes are listed in Table 1. There is a potential problem with this test in that some of the significantly unbalanced nodes may be nested and hence not independent. We return to this point in the discussion.

Simulations of the broken stick model produced a genus of at least 257 species in only one of 1000 trials. However, four genera contain more species than this: *Eumerus* (258), *Ocyptamus* (299), *Copestylum* (324) and *Microdon* (356). Therefore the distribution of hoverfly species among genera is not compatible with the broken stick distribution and hence with the Markovian model. From this we may conclude either that speciation and/or extinction probabilities have varied among clades, or that genera differ importantly in age. Another explanation is that groups of taxonomists working on the different genera have had markedly different views about species boundaries.

Table 2 shows the results of Fusco & Cronk's (1995) test of tree shape. The phylogeny is significantly unbalanced whether or not the generic species-richnesses are considered. The degree of imbalance is markedly and significantly greater, however, when species-richnesses are set to unity (medians test: $\chi^2_1 = 12.21$, $P < 0.001$). The imbalance values obtained using just the Rotheray & Gilbert phylogeny were almost identical (*I*-value of 0.64 when species richness is considered and 0.91 when it is set to unity). Similarly, the degree of imbalance was still significantly greater when species richness was set to unity (medians test: $\chi^2_1 = 17.9$, $P < 0.001$).

Correlates of species-richness

The results of the *t*-test and the regression analysis are presented in Table 3. The *t*-tests, but not regressions, indicate that larger testes, longer tongues and (less strongly) wider spermathecae might be associated with species-richness.

Discussion

The degree of imbalance in the hoverfly phylogeny is too great to be compatible with the Markovian null model of clade growth, in which probabilities of speciation and

Table 1 Bifurcations in the phylogeny that are judged to be significantly unbalanced by the Slowinski–Guyer test.

Position in phylogeny	Bigger clade	Smaller clade	*I*-Value	Cumulative *P*
Fagisyrphus vs. sister clade	485	1	1	0.0041
Pocota vs. sister clade	796	3	0.995	0.0075
Ceriana vs. *Primocerioides*	187	1	1	0.0107
Ferdinandea & *Rhingia* vs. sister clade	4455	49	0.979	0.0218
Lejota & *Cynorhinella* vs. sister clade	753	10	0.976	0.0262
Xanthandrus vs. sister clade	1535	25	0.969	0.0321
Three *Volucella* vs. sister clade	2162	41	0.964	0.0372
Eristalis vs. *Eoseristalis*	81	2	0.975	0.0488

Table 2 Results of applying Fusco & Cronk's (1995) test to the hoverfly phylogeny, including and excluding species-richness. The 95% CIs obtained for *I* by simulation under the null model are 0.41–0.59 when species richness is included and 0.42–0.64 when species richness is excluded. The 99% CIs are 0.38–0.62 when species richness is included and 0.37–0.69 when species richness is excluded.

	Including species richness	Excluding species richness
No. of species	5330	204
No. of terminal taxa	204	204
No. of informative nodes	105	58
Median *I*	0.69	0.87

extinction are uniform among contemporaneous lineages. Similar results have been found in most other investigations of large phylogenies and collections of small ones (reviewed by Purvis, 1996), suggesting that this null model may generally be incorrect. This study, however, is the first to detect a significant effect on tree imbalance of treating genera as units of analysis. The genus-level topology (without considering species numbers) is extremely unbalanced: the median *I* of 0.874 exceeds those in all other applications of Fusco & Cronk's method of which we are aware (Table 4). When species numbers are considered, the phylogeny, although still too unbalanced for the null model, is much more in line with these previous applications (Table 4).

The difference between species- and genus-level analyses, which is not present in angiosperms or birds (Table 4), implies that hoverfly genera are not comparable with each other. Interestingly, there is a marked tendency for species-rich genera of hoverfly to be basal (Fig. 1). Why should this be so? One obvious explanation would be that species diversification is decoupled from change in characters used to demarcate genera: perhaps morphological change has been slower in these basal genera, but speciation has been more or less as rapid as elsewhere, implying at least a partial decoupling between species diversification and morphological change, as demonstrated in several other studies (e.g. Fortey & Briggs, 1996). A rather less straightforward alternative explanation is that, for some reason, basal and distal genera have received systematically unequal taxonomic effort, or their workers had markedly different views about species boundaries. Such a pattern might arise if basal taxa were worked upon by 'lumpers' and distal ones by 'splitters'. The largest genera tend to be the most difficult to deal with and hence revise. Some of the largest genera such as *Merodon*, *Eumerus*, *Cheilosia* and *Microdon* have not been worked upon in decades, and are in need of revision. However, a large proportion of the genera used in this study has been checked recently by a single taxonomist, FC Thompson. He altered a number of boundaries in a systematic attempt to use consistent criteria throughout the worldwide fauna. This reduces substantially the problems caused by different taxonomists holding different views on taxon boundaries.

If either of the above explanations is correct, then higher taxa like genera cannot safely be used as surrogates for species in studies of phylogenetic balance. Studies that use higher level taxa may yield misleading results. Researchers who have to rely on higher level taxonomic units should make some effort to at least estimate the dimensions of the terminal taxa if exact numbers of species per taxon are not known. An obvious avenue for further study is to survey suitable phylogenies to see whether the pattern found in the hoverflies is common. Another possible solution when the dimensions of the terminal taxa are not known, is to use a mixture of taxa at different levels, using as many taxa

Table 3 Results of tests for correlates of species richness. *N*: number of contrasts. *t*: *t*-statistic. *P*: probability (two-tailed). *b*: coefficient of regression (standard error in parentheses). *N* differed among many of the tests because missing values in the data set reduced sample sizes.

	t-Test			Regression		
Character	*N*	*t*	*P*	*b*	*t*	*P*
Body size						
Head width	53	0.73	0.5	0.40 (0.999)	0.40	0.7
Thorax volume	53	0.08	0.9	0.11 (0.341)	0.33	0.7
Life history						
Ovariole number	49	–0.25	0.8	0.06 (0.482)	0.13	0.9
Egg volume	44	–0.1	0.9	0.27 (0.279)	0.95	0.3
Mating system						
Spermathecal width	41	1.78	0.08	0.57 (0.433)	1.30	0.2
Testis length	40	2.57	0.014	0.39 (0.366)	1.07	0.29
Diet						
Tongue length	52	2.01	0.049	0.51 (0.912)	0.56	0.6

Clade	Terminals	Species-richness considered?	Median *I*	Source
Hoverflies	Genera	No	0.87	This study
Angiosperms	Families	Yes	0.81	Fusco & Cronk (1995)
Asterids	Genera	Yes	0.82	Fusco & Cronk (1995)
Rosids	Families	Yes	0.81	Fusco & Cronk (1995)
Birds	Families	No	0.75	Fusco & Cronk (1995)
Birds	Families	Yes	0.74	Fusco & Cronk (1995)
Angiosperms	Families	No	0.74	Fusco & Cronk (1995)
Marsupials	Species	N/A	0.70	Katzourakis (unpublished)
Hoverflies	Genera	Yes	0.69	This study
Carnivores	Species	N/A	0.66	Katzourakis (unpublished)
Primates	Species	N/A	0.58	Katzourakis (unpublished)

Table 4 Median imbalance values from published and unpublished applications of Fusco & Cronk's method. Terminals = taxonomic level of most or all terminal taxa.

containing as few lineages each as possible when sampling is good (Robeck *et al.*, 2000). This may not always be possible, as in the case of the hoverflies the phylogenetic relationships within the larger genera are not known.

A final explanation is that the radiations of these species-rich basal genera are in fact recent events, comparable in age to other genera. This would imply that the processes governing speciation and extinction have not been constant through time; if they had, we would expect self-similarity in the tree, with the imbalance patterns being the same irrespective of the level at which we are analysing the phylogeny (Green, 1991). This explanation is less parsimonious, however, on the current evidence. Molecular phylogenies are required to shed light on the dates of these diversifications: the use of a timescale has been used to reveal a 'phylogenetic fuse' where lineages of different age radiated at approximately the same time (Cooper & Fortey, 1998).

Given the marked imbalance in the distribution of species among genera, the lack of clear, convincing correlates of diversity is frustrating. The nodes identified as significantly unbalanced by the Slowinski-Guyer test in Table 1 have few common features. At least three of them may be artefacts caused by taxonomists favouring splitting, rather than lumping, of taxa based on adult characters. Firstly, the genus *Eoseristalis* is still regarded as a subgenus of *Eristalis* by many authors, and in fact there are no differences in larval morphology between the two groups. Second, the taxonomic status of *Fagisyrphus* is uncertain: it was erected by Dusek & Laska (1967) for the species *cinctus* Fallén 1817 on the basis of the very narrow face of the adult, especially of females; however, many authors now incorporate it into the genus *Meligramma*, or include *Meligramma* (including *cinctus*) as a subgenus of *Melangyna*. The problem with this is that all three do not form sister taxa in the phylogeny based on larval morphology, and therefore we have kept them separate here. Third, the genus *Primocerioides* may well not be distinct from *Ceriana* and be better placed as a subgenus: its larva is unknown.

An important caution when interpreting the results of multiple Slowinski-Guyer tests of imbalance is that the nodes identified as significantly unbalanced are likely to be nested within each other. This is unlikely to be the case with the hoverfly phylogeny, however, as the species rich

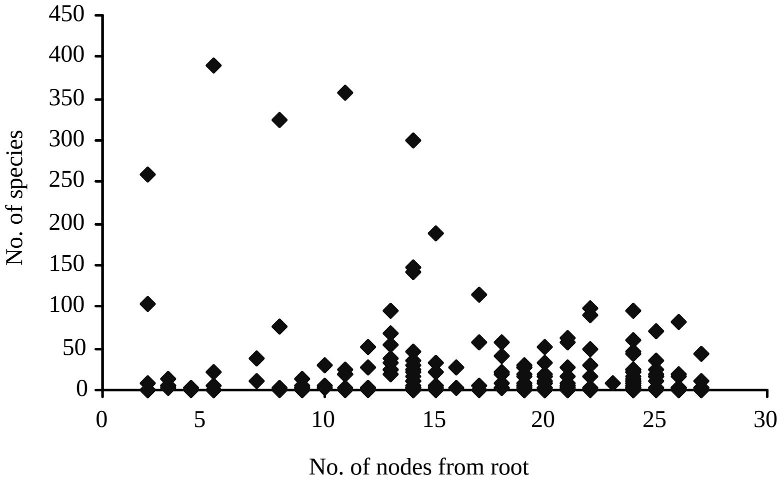

Fig. 1 The species-richness of genera plotted against the number of nodes in the phylogeny separating the genus from the cenancestral syrphid.

clades tend to be basal (see Fig. 1), and their effect will therefore not be amplified down the phylogeny.

Our results suggest the mating system and dietary niche breadth might correlate with species richness, but they are equivocal, with only the *t*-tests being significant. It is important to note however, as mentioned in the methods, that the tests are conservative if characters have evolved in a gradual manner. Furthermore, it may be possible that different causal factors have had an influence on the species richness of different clades within the hoverflies. A way to test for this is to divide the contrasts according to phylogenetic subclades, and analyse each subclade individually (Gittleman & Purvis, 1998). However, due to the highly unbalanced nature of the hoverfly phylogeny it was not possible to divide the contrasts into subclades of a meaningful sample size for this type of analysis.

Testis size, which we find to correlate significantly with high species-richness, correlates positively with the degree of sperm competition, independently of body size, in a wide range of taxa (see Birkhead & Møller, 1998 for recent reviews). Sperm competition leads to sexual conflict and increases effective population size, which in turn is expected to facilitate the rapid evolution of reproductive barriers, and hence increased speciation rates (Gavrilets, 2000). This process is facilitated by high population densities, which might also confer reduced extinction rates (Marzluff & Dial, 1991). A recent broad scale comparative test comparing monandrous vs. polyandrous insect taxa has supported the claim that sexual selection promotes speciation (Arnqvist *et al.*, 2000). Our result suggests that in the hoverflies, all of which display some degree of sexual selection, higher levels of sexual selection are associated with higher species richness. It is worth noting also that testis length is positively correlated with spermathecal diameter (contrasts regression $r^2 = 0.28$, $P = 0.001$), as predicted under the hypothesis that males are selected to fill spermathecae as a safeguard against sperm competition from subsequent males (Simmons & Siva-Jothy, 1998). Spermathecal diameter also shows a near-significant relationship with species-richness, which is not surprising given how closely it correlates to testis length.

We find some evidence that tongue length is associated with species richness. Tongue length is likely to relate to diet breadth in nectar-feeding species. In short-tongued clades, slightly longer tongues might permit utilization of a wider range of flowers. The relationship might not be expected to be linear: some extremely long-tongued species may be more restricted in their niche breadth as they only feed on flowers with long corollae (e.g. *Rhingia campestris*: Gilbert, 1985). However, the relationship between species-richness and tongue length did not depend upon the average tongue length of the lineages being compared (regression $r^2 = 0.02$, $P = 0.139$) reducing the possibility of a nonlinear effect.

Body size and reproductive rate variables were not found to correlate with species-richness, despite their being implicated in several studies on other taxa (see introduction). This ruled out performing a multivariate analysis to distinguish between the effects that these traits have had on species richness. Relatively small sample sizes might have contributed to a lack of significance, and the power of our tests has not yet been assessed systematically, although initial simulations indicate reasonable power varying between 30 and 80% depending on the mode of evolution (Isaac, personal communication, 2000). Our results should, therefore, be regarded as provisional, as they may change in the light of future improvements in the available database or methods. However, we provisionally conclude that any effect of these traits is minor. Interestingly, all other studies based on sister-clade comparisons have either shown weak (Gittleman & Purvis, 1998) or no (Nee *et al.*, 1992; Gardezi & da Silva, 1999) significant effects of body size on diversity. If body size *per se* is an important determinant of species-richness, it seems that it may act more at higher taxonomic levels than those examined so far.

One possible reason for our lack of significant correlates is that the species-richness differences might reflect differences in larval rather than adult characteristics. Several of the unbalanced nodes in Table 1 correspond to marked transitions in the degree of specialization in larval diet. *Fagisyrphus* is one of the most specialized aphidophagous species, only recorded as a larva from seven aphid species, overwhelmingly from beech aphids. The smaller of the other identified pair of sister clades within the Syrphinae is *Xanthandrus*, an unusual and very specialized group feeding as larvae only on gregarious caterpillars. The predatory *Volucella* only feed as larvae on the brood of social wasps and bees, which are not very species-rich groups, and this might, therefore, be legitimately regarded as a specialized diet. Nothing is known about the larval habits of *Cynorhinella*, but *Lejota* larvae develop in sap under tree bark, as does *Ferdinandea*. Thus several of these unequal splits may be connected with the idea of specialization as a dead end for evolutionary innovation (Moran, 1988; Kelley & Farrell, 1998).

In summary, we find that the hoverfly phylogeny is too unbalanced to have been produced under a Markovian null model of clade growth, suggesting that clade-specific factors have played a role in the net speciation process. Most large phylogenies looked at to date reject the Markovian null model (Purvis, 1996; Mooers & Heard, 1997) raising the possibility that the model is generally incorrect. The phylogeny is significantly more unbalanced when the dimensions of the terminal taxa are not considered, strongly suggesting that for the hoverflies, genera are not adequate surrogates for species in studies of biodiversity. The wider implication of this finding is that higher level taxonomic units ought not to be used uncritically as surrogates for species in studies of biodiversity. In our search for correlates of species richness, we find some evidence to suggest that diet breadth and sexual selection may be positively associated with species richness. Body size and reproductive rate variables that have shown to be associated with species richness in other taxa were not significantly associated with species richness in the hoverflies.

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Supplementary material

Appendices A and B are available from www.blackwellscience.com/products/journals/suppmat/JEB/JEB278/JEB278sm.htm