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Title: A comparative analysis of the evolution of imperfect mimicry

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Running title: Imperfect mimicry in hover flies

Summary

Although exceptional examples of adaptation are frequently celebrated, some outcomes of natural selection appear far from perfect and it is important to establish why this is so. For example, many hover flies (Diptera: Syrphidae) are harmless (Batesian) mimics of stinging Hymenoptera [1]. However, while some hover fly species are considered excellent mimics, other species bear only a superficial resemblance to their models [2]. Here we use a comparative approach to evaluate a series of largely untested hypotheses that have been put forward to explain inter-specific variation in the mimetic fidelity of Palearctic Syrphidae. The degree of mimetic perfection was quantified for each of 38 syrphid species using both human and multivariate morphometric rankings. The long-term relative abundance of each of these species was estimated from 11 independent field studies. Finally, a novel phylogeny based on COI was constructed to control for evolutionary relationships between these species. Our findings, in combination with previous results, allow us to reject several key hypotheses for imperfect mimicry: (i) human ratings of mimetic fidelity are positively correlated with both morphometric measures and avian rankings, indicating that variation in mimetic fidelity is not simply an illusion based on human perception [3], (ii) no species of syrphid maps out in multi-dimensional space as intermediate in appearance between several different hymenopteran model species, as the “multi-model” hypothesis [4] requires, and (iii) we demonstrate no evidence for a negative relationship between mimetic fidelity and abundance, which calls into question the "kin selection" [5] hypothesis. By contrast, a strong positive relationship between mimetic fidelity and body size supports the "relaxed selection" hypothesis [6,7], suggesting that reduced predation pressure on less profitable prey species limits the selection for mimetic perfection.

Keywords: flower flies, syrphid, Batesian mimicry, inaccurate mimicry, comparative analyses, behavioural mimicry

Main text

Much of evolutionary theory relating to mimicry has been based on the assumption that the fidelity of mimicry in any given system is extremely high (see [8] for a review). Of course, if mimicry were poor, then one might intuitively expect that signal receivers would learn be able to distinguish mimics from their models and (depending on context) accept or reject them. In reality however, there are many examples of inaccurate or low fidelity mimics [2,4,5,7,9]. For example, the relative composition of key odour compounds of specific non-rewarding orchids differ markedly from the bees they have evolved to resemble [9]. Likewise, while mimetic spiders of the genus *Cosmophasis* bear some resemblance to ants, they are readily visually discriminated by the human observer [4]. Perhaps the best examples of imperfect mimics are found in hover flies (Diptera: Syrphidae), which are considered Batesian (harmless) mimics of hymenopteran models [1] but which appear to vary markedly across species in the degree of mimetic perfection [2,10] (see **Figure S1)**.

There have been numerous hypotheses proposed to explain the evolution and maintenance of "imperfect" mimicry, but despite calls for study there have been no comparative tests of their validity [5,11]. Common (and inter-related) explanations include: (i) "eye of the beholder", such that poor mimics to human eyes remain good mimics to natural predators [3], (ii) "multi-model", such that mimics gain most benefit from imperfect similarity to multiple models [4], (iii) kin selection, such that imperfect mimicry is maintained through its benefit to conspecifics carrying the same trait [5], (iv) "constraints", such that the evolved degree of mimetic perfection represents a trade-off between selection for mimicry and selection acting on other aspects of life-history [12], such as thermoregulation, and (v) "relaxed selection", such that selection for mimicry gradually weakens to a point where it is readily counteracted by weak selection or mutation [6,7] (see **Supplementary Information A** for additional hypotheses). Below we describe new comparative morphological and genetic data that allows us to evaluate which of these hypotheses are best able to explain the range of mimetic perfection seen in hover flies.

Phenotypic mapping

A long-standing challenge in elucidating the ultimate causes of imperfect mimicry is quantifying the extent of mimetic fidelity between mimics and models, which frequently differ in multiple trait dimensions ranging from colour to shape. Previous measures of mimetic fidelity have used human rankings [13], pigeon responses [10], pixel mapping [10], neural networks [13] and multivariate analyses [14]. We employed subjective human rankings of mimetic fidelity (hereafter "fidelity$_{HR}$", see Methods) across a range of species which were compared for consistency against a measure derived from a multivariate analysis of trait values (hereafter "fidelity$_{MD}$", see Methods).

Overall, our morphological analysis of 38 syrphid species and 10 hymenopteran model species indicated that there was a clear statistical difference in appearance between the 2 taxa (Syrphidae vs. Hymenoptera) (nested MANOVA: taxon, $F_{1,427}=797.77$, $p<0.001$; species, $F_{47,427}=11.03$, $p<0.001$). The first three canonical variates in a generalized canonical discriminant analysis (GCDA) explained 80.6% of the variance among the species in terms of their morphological features (individually: 41.1, 20.4 and 19.2%).

The Mahalanobis distances between each of the syrphid species and each of the Hymenoptera groups were calculated from these three canonical variates. This measure was multiplied by -1 to give a quantity, $fidelity_{MD}$, that is positively related to mimetic fidelity. Syrphids and hymenopterans tend to cluster with their respective orders, largely on the basis of relative antennae length (RELAntL), a feature that is thought to be used in discrimination by birds [13]. The "multi-model" hypothesis [4] would predict that mimics fall between several models, gaining greater benefit from multiple, weaker associations. Our analysis clearly indicates that there are no mimetic phenotypes in our sample that could be considered as falling morphologically between two or more distinct model phenotypes (**Figure 1**).

The "eye of the beholder" hypothesis recognizes that the natural predators of mimics (such as birds) and humans differ in both their perception and cognitive abilities, and argues that the apparent variation in mimetic perfection is therefore illusory and/or misleading. However our multivariate measure of mimetic fidelity correlated well with our human ranking ($r= 0.555$, $df = 36$, $p < 0.001$, **Figure 2**), while similar work indicates that trained pigeons rank mimetic fidelity of hover fly species in much the same way as humans do (**Figure S2**). Additional results suggest that behavioural mimicry (antennae waving, mock stinging, wing wagging) only occurs in species that humans classify as high fidelity mimics (Penney *et al.*, in prep), further suggesting that the human-based quantification of mimetic perfection is ecologically relevant. Collectively, these findings suggest that we can discount the "eye of the beholder" hypothesis as an explanation for inter-specific variation in hover fly fidelity.

Mimetic fidelity and abundance

It has been stated frequently that, within hover flies at least, poor mimics tend to occur at higher population densities than good mimics [2,4,10]. While this relationship is plausible, it remains entirely anecdotal. The kin selection hypothesis for imperfect mimicry not only assumes a degree of family grouping (unlikely in hover flies [2]), but also predicts that the evolved degree of mimetic perfection will be lowest when mimics are relatively common and/or relatively beneficial to attack compared to their models. This prediction arises from the assumption that predators that are largely unable to distinguish mimics from models will sample those high fidelity mimics at a greater rate when the incentive to attack is greater. The constraints [12] and relaxed selection [6,7] hypotheses predict the opposite, namely that the evolved degree of perfection will be highest when mimics are relatively common and/or relatively beneficial to attack simply due to the increased selection pressure to avoid predation through mimicry. Meta-analysis of 11 independent studies (**Table S1**) demonstrated no evidence of a strong correlation between relative abundance and either measure of mimetic fidelity in our 38 focal species, either before controlling for phylogenetic autocorrelation ($fidelity_{HR}$: r-bar = 0.065 (95% CI: -0.052 – 0.181); $fidelity_{MD}$: r-bar = 0.001 (95% CI: -0.149 – 0.152)) or after controlling for phylogeny using phylogenetic generalised least squares regression (PGLS) for a subset of 31 species (**Figure 3**) ($fidelity_{HR}$: r-bar = -0.083 (95% CI: -0.031 – 0.198); $fidelity_{MD}$: r-bar = 0.223 (95% CI: 0.058 – 0.389)). Note that this latter correlation between $fidelity_{MD}$ and abundance was significant (95% CI did not overlap zero) and positive, indicating that in this case poor mimics tend to be less common. Therefore, based on our sample of species (i.e. those sufficiently common to appear in systematic field surveys) we find no evidence that good mimics tend to be rarer (**Figures S3** and **S4**).

Mimetic fidelity and body size

The constraints [12] and relaxed selection [6,7] hypotheses suggest that smaller-bodied (and thus less nutritionally profitable [15]) species will endure low levels of predation, even if they are poor mimics, which produces weaker selection for improved mimicry; the "kin selection" hypothesis predicts the opposite (see above). Therefore the relationship between hover fly species body size and their mimetic fidelity was assessed. There was a highly significant relationship between body size (-PC1) and $fidelity_{HR}$ both before controlling for phylogeny (Pearson's correlation, $r = 0.680$, $df = 36$, $p < 0.001$) and after controlling for phylogeny (PGLS, $t = 4.693$, $p < 0.001$). The relationship between body size and $fidelity_{MD}$ was also highly significant before controlling for phylogeny ($r = 0.632$, $df = 36$, $p < 0.001$) and after controlling for phylogeny ($t = 3.005$, $p = 0.005$) – see **Figure 4**. Finally, our meta-analysis indicates that the relative abundance of hover fly species was only weakly (negatively) correlated with their body size before controlling for phylogeny (r-bar = -0.132 (95% CI: -0.239 – -0.024)) and after controlling for phylogeny (r-bar = -0.240 (95% CI: -0.476 – -0.005)), and it is clear that this relationship is not consistent among studies (**Figure S5**).

The constraints and relaxed selection hypotheses both suggest that larger, more profitable species will tend to achieve a higher degree of mimetic fidelity at equilibrium, due to the greater underlying incentive on predators to attack them. Other dimensions of profitability might include evasive flight behaviour, but predation of hover flies by birds takes place largely on flowers [2]. Of course, the predicted evolutionary trajectory for small and large mimics is less obvious if larger-bodied species are rarer than smaller-bodied species [14,16], but as noted above, there is no consistent evidence that this is the case. Likewise, our expectation that selection might be less intense on small species because they are less valuable prey might not hold if predators rely heavily on body size as a trait to distinguish mimics from models [17] (hymenopteran models tend to be larger). At the extreme, if predators were highly sensitive to size then there might be a complete relaxation of selection on mimicry in small species (since they are always attacked regardless of mimetic fidelity), leading to the same general outcome we have observed. Alternatively, small body-size could conceivably favour higher mimetic fidelity as a way to counteract size-based discrimination. Nevertheless, there is evidence that predators cannot discriminate perfectly between mimics and models on the basis of body size [17], and our general arguments remain valid.

Conclusion

Mimicry provides a textbook example of adaptation, but researchers have long debated why the fidelity of many imperfect mimics is not further improved by natural selection. Our study represents the first attempt to evaluate multiple hypotheses for imperfect mimicry in the group best known for it, and the first to reveal a significant pattern. Of the five primary hypotheses that we evaluated, our comparative study is only consistent with the "constraints" and "relaxed selection" hypotheses while questioning the assumptions and predictions of the kin selection, eye of the beholder, and multi-model hypotheses. Our revelation of a strong positive relationship between body size and mimetic fidelity is readily explained if body size influences predation behaviour and thereby the intensity of selection for more perfect mimicry. Indeed, relationships between body size and the evolution of aposematic colouration in dendrobatid frogs [18] and putative snake mimicry in Lepidoptera [19] may also be explained by the kinds of processes we have invoked. The fact that we can explain the variation in mimetic fidelity on the basis of

a relaxation of selection on mimetic fidelity alone without the need to invoke a specific constraint to generate counter-selection, renders the relaxed selection hypothesis entirely sufficient to explain the variation we have documented, but we cannot discount the constraints hypothesis. Whether the patterns we have revealed are observed in other mimicry complexes remains to be seen. However it is clear that the comparative method will play an important role in evaluating the various explanations not only for imperfect mimicry, but limits to adaptation in general.

Methods

Mimetic fidelity

Specimens

We focused on the hover fly species recorded in the most extensive (>40,000 specimens) multi-annual (15 years) abundance dataset available [20]; see **Table S2** for a species list. We took photographs of the dorsal and lateral aspects of pinned specimens of 35 species which were included in this focal dataset and present in sufficient numbers at the Canadian National Collection of Insects and Arachnids (CNC), Ottawa, Canada. Three additional hoverfly species were included to increase the number of high fidelity mimics, while ten hymenopteran species representing a broad array of potential models (vespid wasps, polistine wasp, honey bee, bumble bees) were also photographed. Photographs were taken of 10 individuals (5 males, 5 females) for each of the 38 syrphid species and 10 individuals of each hymenopteran species (all female). All the photographs were taken using a Canon EO5 50D camera with macro lens (100 mm) and microtwin light (MT-243X).

Human rankings

A sample of the photographs, all dorsal view, representing 2 different individuals of each of the 38 syrphid species were collated. Human volunteers (n=21) were shown each photograph in random order on a projector screen for 20 seconds, alongside the same images of a wasp (*Vespula vulgaris*), honeybee (*Apis melifera*) and bumblebee (*Bombus impatiens*). Each hover fly and model image was presented at magnifications such that they had the same projected body length. Human subjects were asked to rank each syrphid on a scale of 1 (very poor mimic) to 10 (excellent mimic) for each of the 3 potential models (wasp, honey bee and bumble bee). The human rank of mimetic fidelity identified the model type to which the potential mimic bore the closest resemblance (based on overall mean score for images of that species) and provided a measure of mimetic fidelity, $fidelity_{HR}$.

Multivariate ratings

A range of attributes were extracted from individual photographs of specimens of the syrphids and hymenopterans described above, using ImageJ (http://imagej.nih.gov/ij/). Specimen phenotypic characters were selected based on their relevance to avian perception (taken from [13]): antenna length (AntL), abdomen length (AbL), abdomen width (AbW), thorax width (ThW), wing length (WingL) and head width (HeW). Mean red, green, blue (RGB) colour (Red, Green, Blue) and the standard deviation of RGB (sdRed, sdGreen, sdBlue) of the abdomen were also measured using COREL PhotoPaint X3.Finally, the number and colour (classified by the observer as white, grey, silver, yellow, orange or brown) of patches and/or stripes were also recorded (Stripe, Patch, StripePatchcolor). While we did not transform colour measurements into avian colour space the relationship we presented between human and

multivariate measures of mimetic fidelity (see text) remains significant even when we remove RGB and the number of stripes and patches, retaining only measurements of the physical dimensions of specimens ($r = 0.369$, $df = 36$, $P = 0.023$). All of the above size-related values in our analyses were first divided by the width of the head before analysis to create a relative measurement.

A generalized canonical discriminant analysis (GCDA) was used to identify combinations of variables that serve to discriminate among one or more groups of data based on differences among them using the "candisc" library [21] in R [22]. Each potential mimic species is represented by a centroid in multivariate space representing the mean GCDA variates of the individual specimens of that species. Typically each model species centroid clustered closely around its taxonomic group centroid. The distance between species' centroids (the Mahalanobis distance) represents a multi-dimensional measure of the morphological similarity between species. While we cannot confidently assign specific hymenopteran models to each mimic, it is possible to distinguish bee mimics from wasp mimics. Therefore, the average of the distances between each mimic centroid and the centroids of the bee and wasp models was calculated to give a score for mimetic fidelity for each mimic to its putative model group. The smallest mean Mahalanobis distance from the hover fly species to its potential model type (bee or wasp) again provided a measure of mimetic fidelity. Since Mahalanobis distances were negatively related to mimetic fidelity, we invert those distances to give a measure of mimetic fidelity that is easier to interpret: fidelity_{MD}.

Quantification of body size

Body size of each of the 38 syrphid species photographed was quantified by conducting a principal components analysis (PCA) on body dimensions mentioned above. The first principal component (PC1) explained 82.9% of the variation in the data, was strongly negatively correlated to all six body dimensions ($r<-0.81$, $p<0.001$ in all cases), and was taken as a composite measure of body size. Since PC1 was negatively correlated to body size measures, we refer to "-PC1", which is positively correlated with body size, in the results as an aid to interpretation.

Abundance

We identified 11 independent studies that provide estimates of relative hover fly abundance based on a range of trapping and survey methods (see **Table S1** for full details). These studies included between 3 and 34 species for which we had detailed morphological data (hence estimates of mimetic fidelity). Where multiple years of data were presented, this was based on the arithmetic mean count of each species trapped per year over the whole period of recording. These data were considered reasonably indicative of abundance, as there was a general tendency for the relative abundance of hover fly species to correlate between studies based on a range of trapping methods (see **Table S3**).

Phylogenetic analysis

Seventy-seven species of 21 genera of Syrphidae are included in the ingroup (**Table S4**), including 31 species for which we have morphological data (**Figure 3 and Table S3**). To encompass a range of genetic variation, we included multiple exemplars from each genus used in our mimicry analysis. These

specimens represent most major syrphid clades. Four species of *Microdon*, the putative sister group to the rest of the syrphids [23], were used as outgroup taxa.

The 5′ region of cytochrome oxidase *c* subunit I (COI) was sequenced for each specimen following the methods outlined in Gibson *et al* [24]. DNA extraction and sequencing was performed in house and at the Canadian Centre for DNA Barcoding. The resultant sequences, as well as images and related data, can be accessed through the Barcode of Life Data Systems (BOLD) (http://www.barcodinglife.org/) in the public project '*Mimicry* – Skevington (MIMSK)' (http://www.boldsystems.org/views/projectmenu.php?&). In addition, all sequences were deposited in GenBank (**Table S4**).

Bayesian analyses were conducted using MrBayes 3.1.2 [25] with a Markov Chain Monte Carlo (MCMC) method as submitted remotely to the CIPRES computing cluster (www.phylo.org/). MrModeltest v2.3 (JAA Nylander 2004, Uppsala University) was used to determine the best model (GTR+I+G) for analysis. Four chains (three hot, one cold) were run simultaneously for 5 million generations. Trees were sampled every 1000 generations and each simulation was run twice. At 5 million generations the standard deviation was 0.03195. Following the discard of the first 500,000 samples as burn-in, 9002 trees were used to generate a majority rule consensus tree, posterior probabilities for each node, and branch length estimates. The resulting phylogeny is largely congruent with other published results that used nuclear loci [23] and contains multiple taxa per genus which acts as a major control for the single mitochondrial marker. Reassuringly, the resulting phylogeny supported monophyly for all genera apart from identifying two paraphyletic genera that have been suggested as such in the literature (*Cheilosia* [26,27] and *Eupeodes* [27], **Figure S6**). Finally, using additional 28S sequences for a subset of 15 species (see **Table S4** for accession numbers), we find a significant correlation between the phylogenetic distances of the COI+28S and COI-only trees (Mantel test for phylogenetic distances, $r=0.680$, $p<0.0001$) suggesting that our COI phylogeny is an adequate representation of the phylogenetic relationships between the species in our analysis.

Relationships between variables were first evaluated without control for phylogenetic autocorrelation using Pearson correlations. Autocorrelation was incorporated into a second analysis using the "corGrafen" function in the "ape" library [28] in R [22] to create a covariance matrix based on species from the tree structure described above. The "gls" function in the "nlme" package [29] was then used to carry out the test. For the abundance analysis, Pearson correlations between variables were used in the "MetaTable" function in the "psychometric" package [30] in R to calculate the weighted mean correlation, r-bar, for all 11 studies. This statistic does not have an associated p-value, but 95% confidence intervals for the coefficient were calculated and can be used to determine significance. To control for phylogenetic autocorrelation, t-statistics from the PGLS analyses of abundance were converted to Pearson correlation coefficients, where $r=t/\sqrt{(n-2+t^2)}$ followed by the calculation of the weighted mean correlation.

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Carleton University Research Ethics Committee and conducted according to the guidelines set out in the Tri-Council Policy Statement on Ethical Conduct for Research Involving Humans. The work was supported by grants to T.N.S. from NSERC, the Canada Foundation for Innovation and the Ontario Innovation Trust. C.H. was supported by an Ontario MRI Fellowship.

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Author contributions H.D.P. photographed and measured specimens, and collected data on human rankings; J.H.S. provided the novel molecular phylogeny; C.H. analysed the data; C.H., K.R.A. and T.N.S. wrote the paper; T.N.S. conceived the project. All authors discussed the results and provided comments on the manuscript.

Author information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. All new genetic sequences were deposited in GenBank (see **Table S4** for accession numbers). Correspondence and requests for materials should be addressed to T.N.S. (sherratt@connect.carleton.ca).

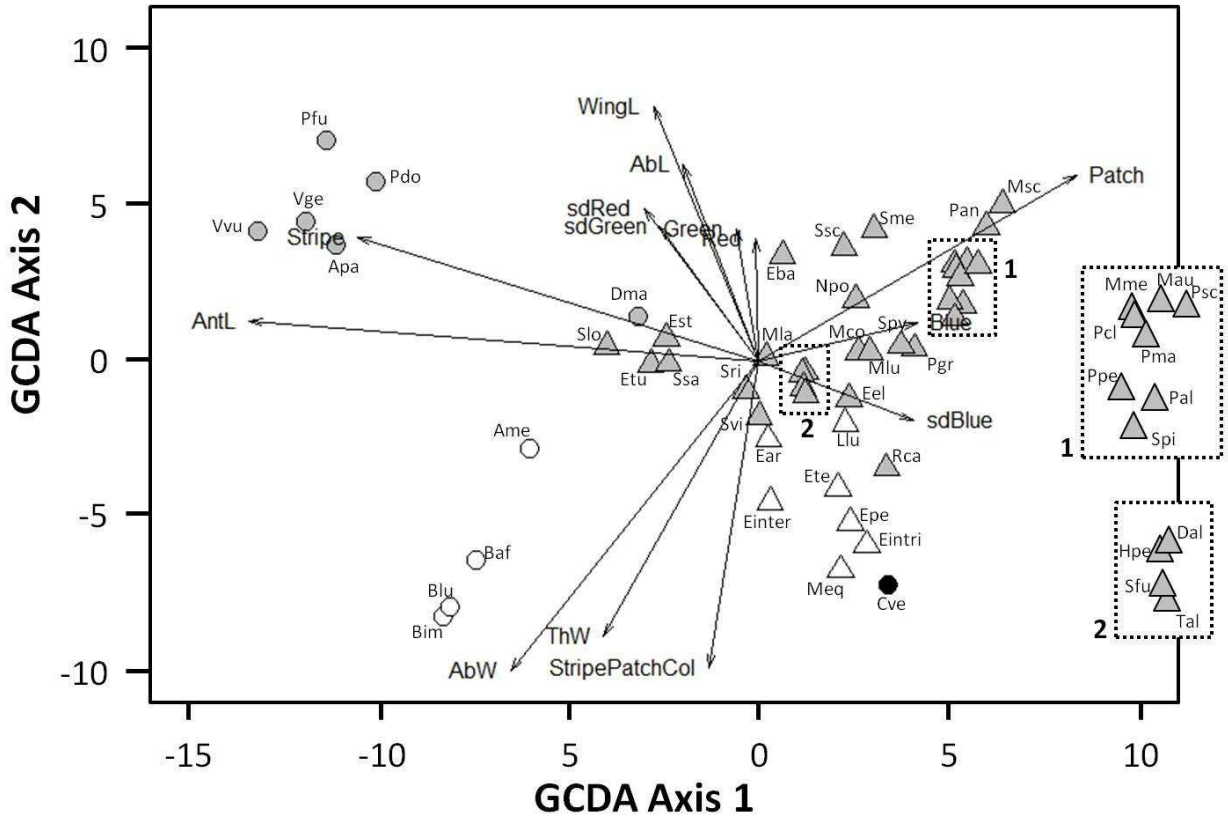

Figure 1: Generalized canonical discriminant analysis plot. Circles are models, triangles are mimics; grey symbols are wasps or wasp mimics, open symbols are bees or bee mimics while the solid black circle is the non-mimetic syrphid, *Cheilosia vernalis*. Species codes can be found in **Table S3**.

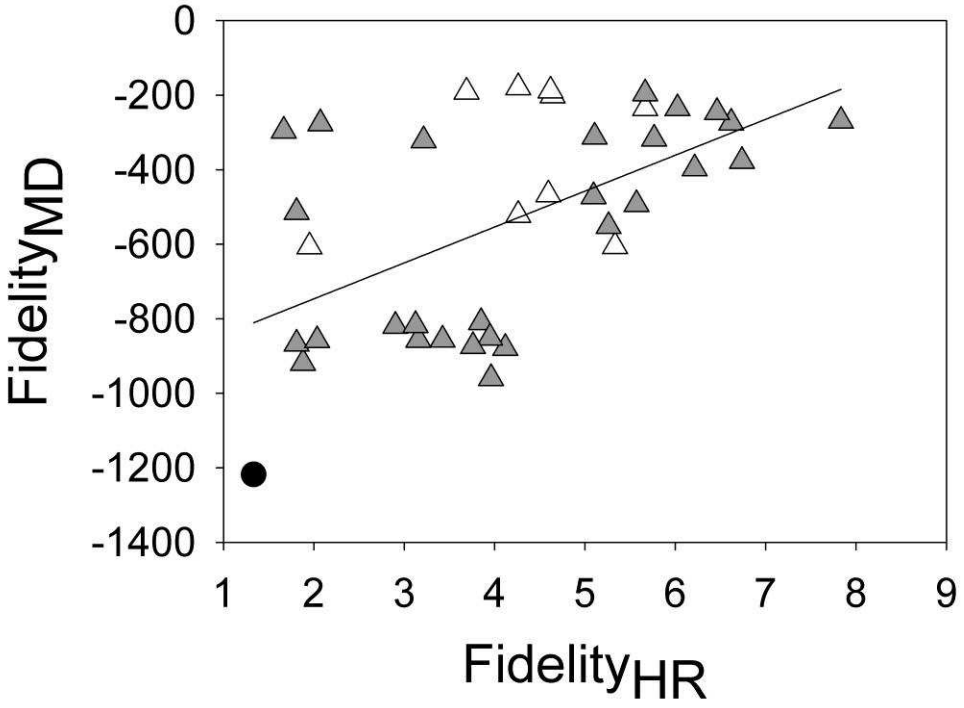

Figure 2: The relationship between two different measures of mimetic fidelity in hover flies using Mahalanobis distances ($Fidelity_{MD}$) and human rankings ($Fidelity_{HR}$). Line shows linear regression. Symbols: wasp mimics (filled triangles), bee mimics (open triangles) and the non-mimetic syrphid, *Cheilosia vernalis* (filled circle).

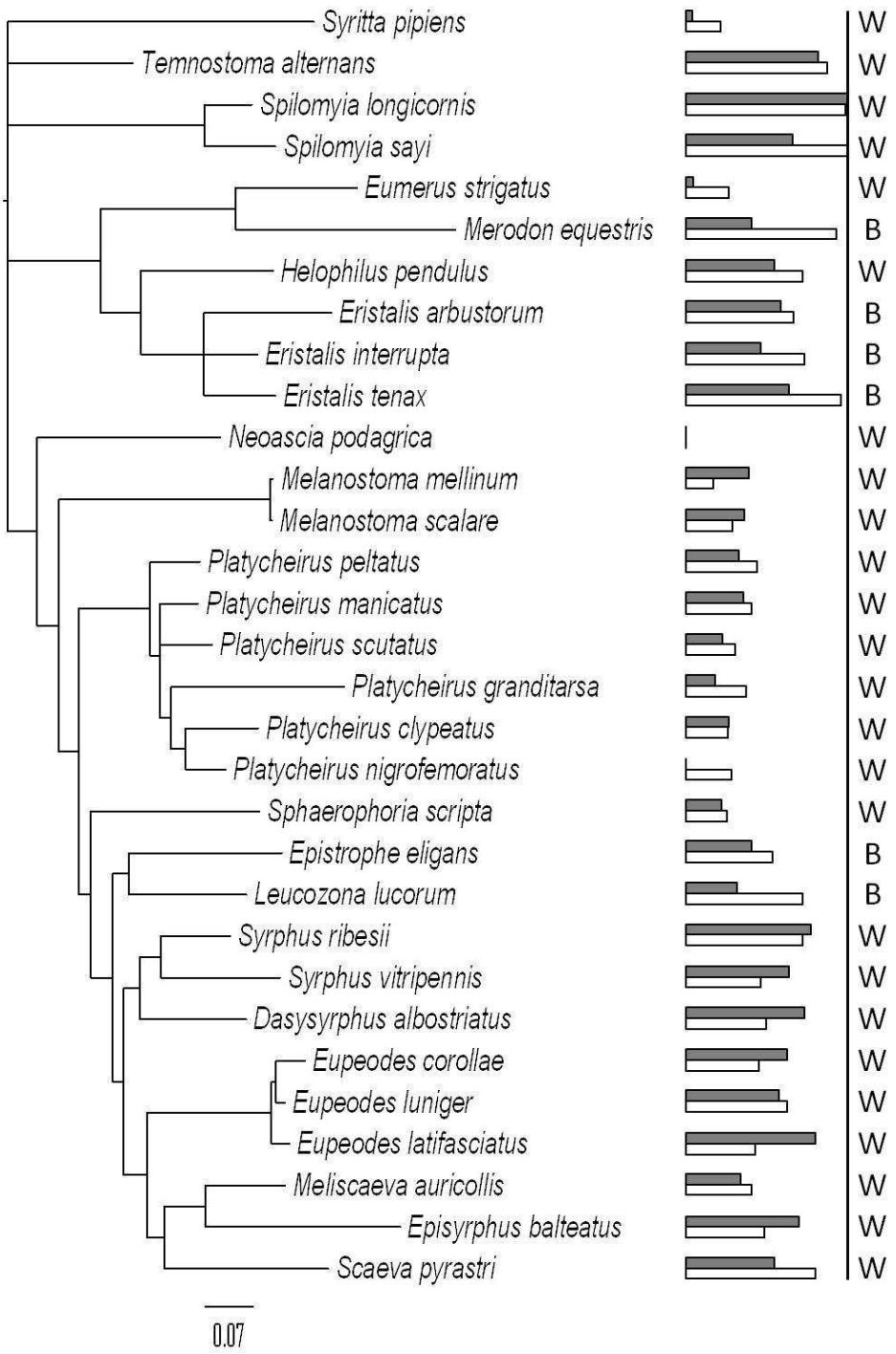

Figure 3: Phylogenetic relationships between the subset (31) of the hover fly species (Diptera: Syphidae) for which fidelity and body size data exists. Shaded bars show the species' mimetic fidelity ($Fidelity_{HR}$), and open bars show the species body size (-PC1). In both cases, the length of the bars is scaled from smallest to the largest score for the species shown. The model for each hover fly species is shown at the right (W = Wasp; B = Bee). See text for details of tree construction methods and **Figure S6** for the phylogeny of all 81 species for which COI genes have been sequenced.

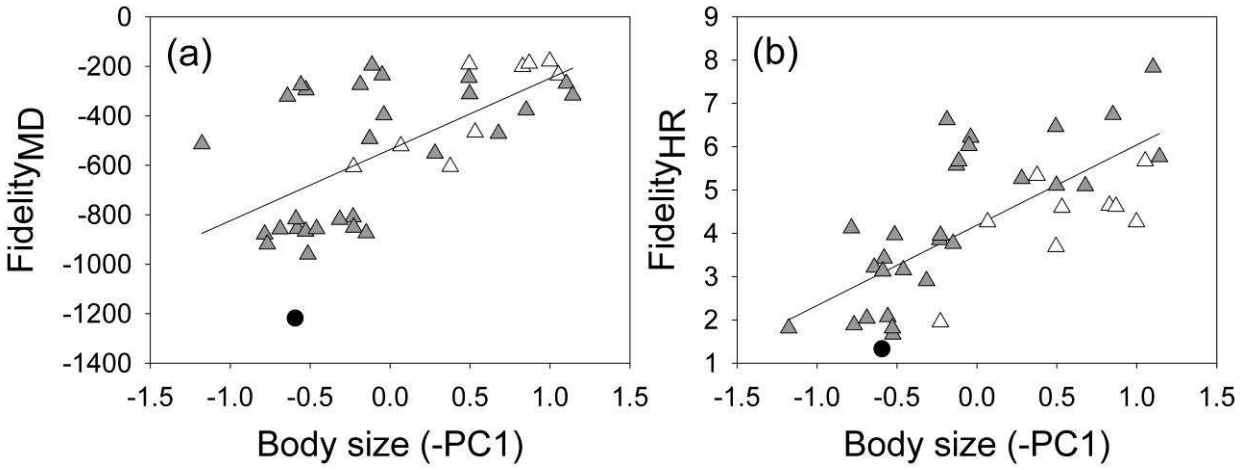

Figure 4a,b: Relationship between body size (estimated as -PC1) and (a) a measure of mimetic fidelity based on Mahalanobis distances (Fidelity$_{MD}$) and (b) human ratings of mimetic fidelity (Fidelity$_{HR}$). Lines show linear regressions. Symbols: Wasp mimics (filled triangles), bee mimics (open triangles) and the non-mimetic syrphid, *Cheilosia vernalis* (filled circle).

Supplementary Information

Figure S1 Illustration of variation in mimetic fidelity in hover flies (Diptera: Syrphidae) with their putative hymenopteran models. HR=human rankings of mimetic fidelity (see text for details).

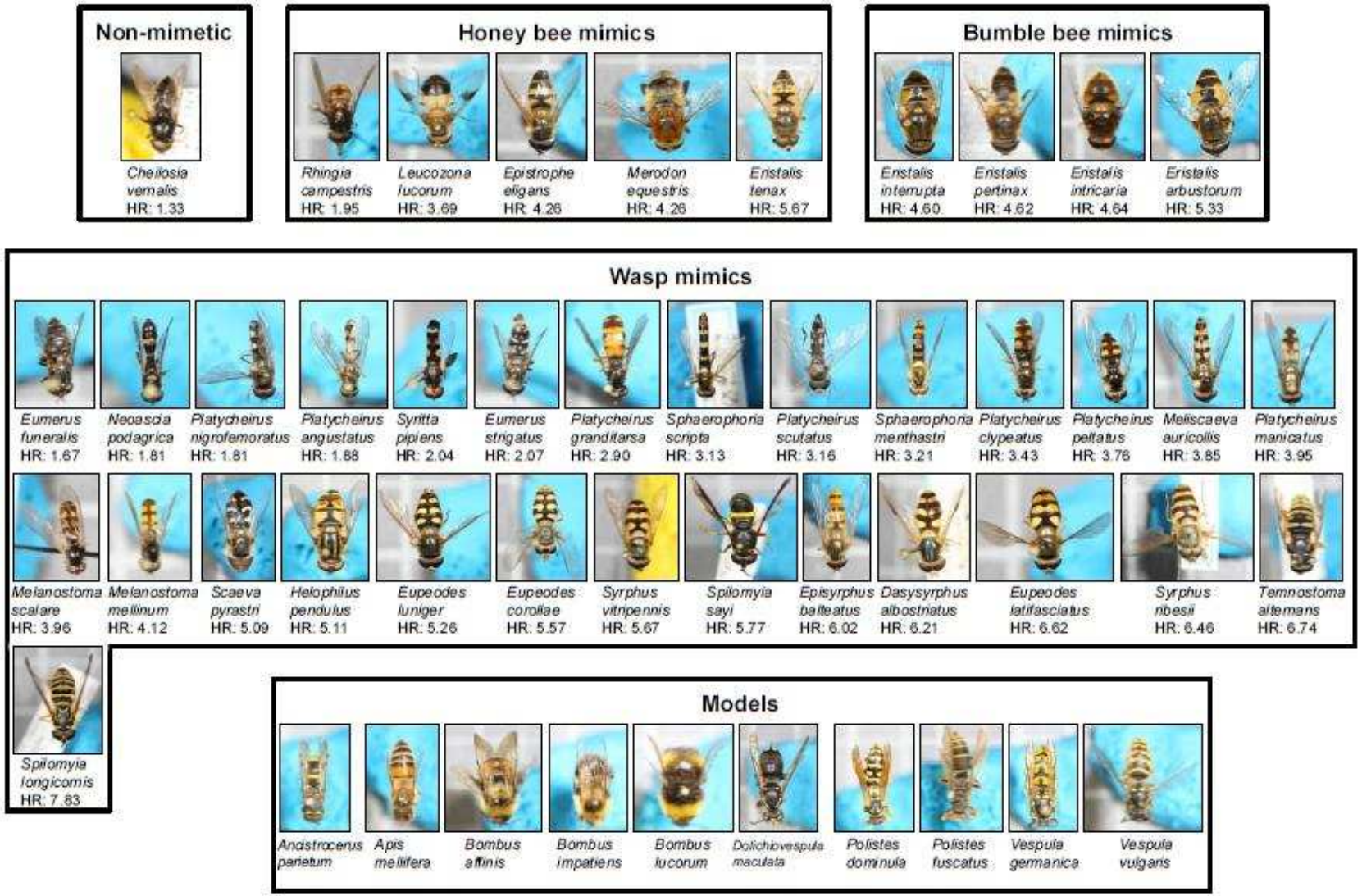

Figure S2 The relationship between the mimetic fidelities of 11 hover fly species assessed by pigeons trained to discriminate wasps from non-mimetic flies [1] and by humans [2]. Human rankings were obtained by asking human participants (n=25) to rank images of 11 syrphid species (presented at the same size) along with a non-mimetic fly and wasp (*Vespula* spp.) for their degree of similarity to a sample of 5 representative wasp (*Vespula* spp.) images. Species names: S.ri=*Syrphus ribesii*; T.ve=*Temnostoma vespiforme*; C.ca=*Chrysotoxum cautum*; H.pe=*Helophilus pendulus*; E.gr=*Epistrophe grossulariae*; X.pe=*Xanthogramma pedissequum*; C.bi=*Chrysotoxum bicinctum*; S.ve=*Sphecomyia vespiformis*; V.zo=*Volucella zonaria*; S.py=*Scaeva pyrastri*; I.gl=*Ichyrosyrphus glaucius*; Wasp=mixture of *Vespula vulgaris* and *Vespula rufa*; Fly=a mixture of Diptera species from the genera *Tabanus*, *Tachina*, *Sarcophaga* and *Scataphaga*. Pearson's product-moment correlation, r=0.854, df=11, p<0.001.

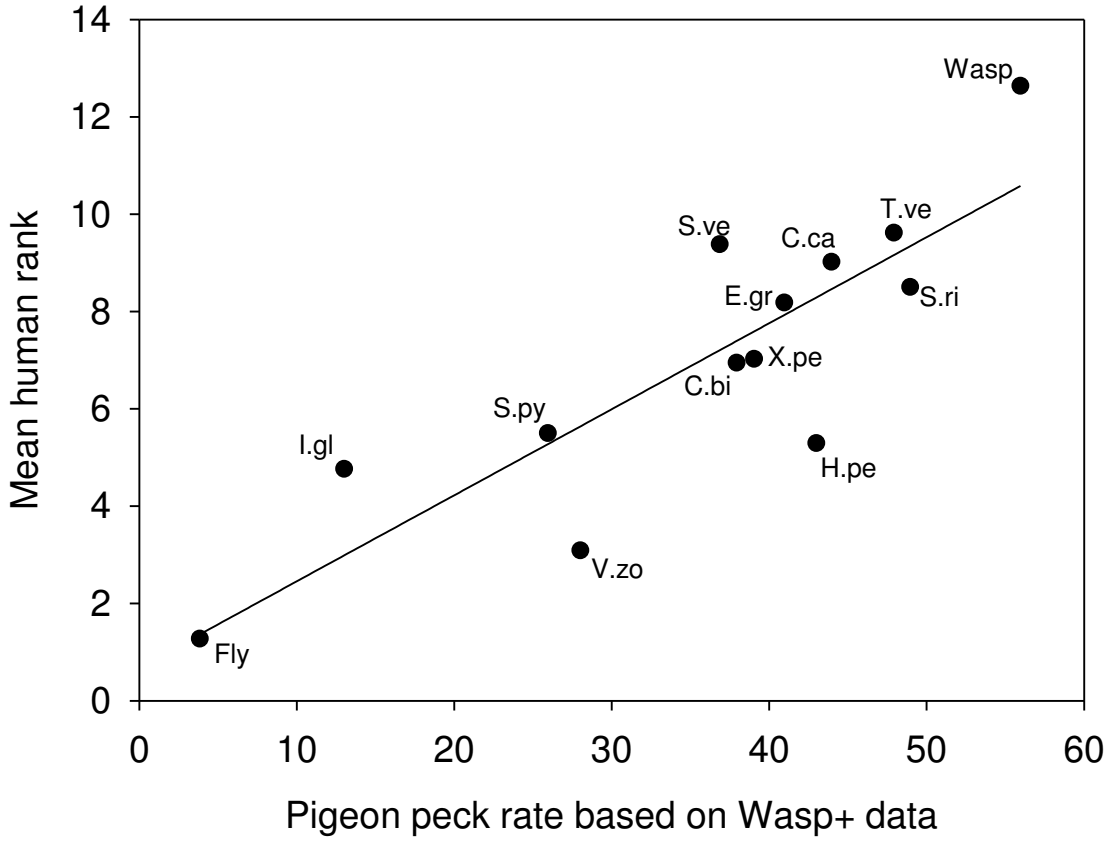

Figure S3 Relationships between relative abundance (logged in all plots apart from G) of hover fly (Diptera: Syrphidae) species recorded in 11 independent field studies and mimetic fidelity as measured by Mahalanobis distances. A=[3], B=[4], C=[5], D=[6], E=[7], F=[8], G=[9], H=[10], I=[11], J=[12], K=[13].

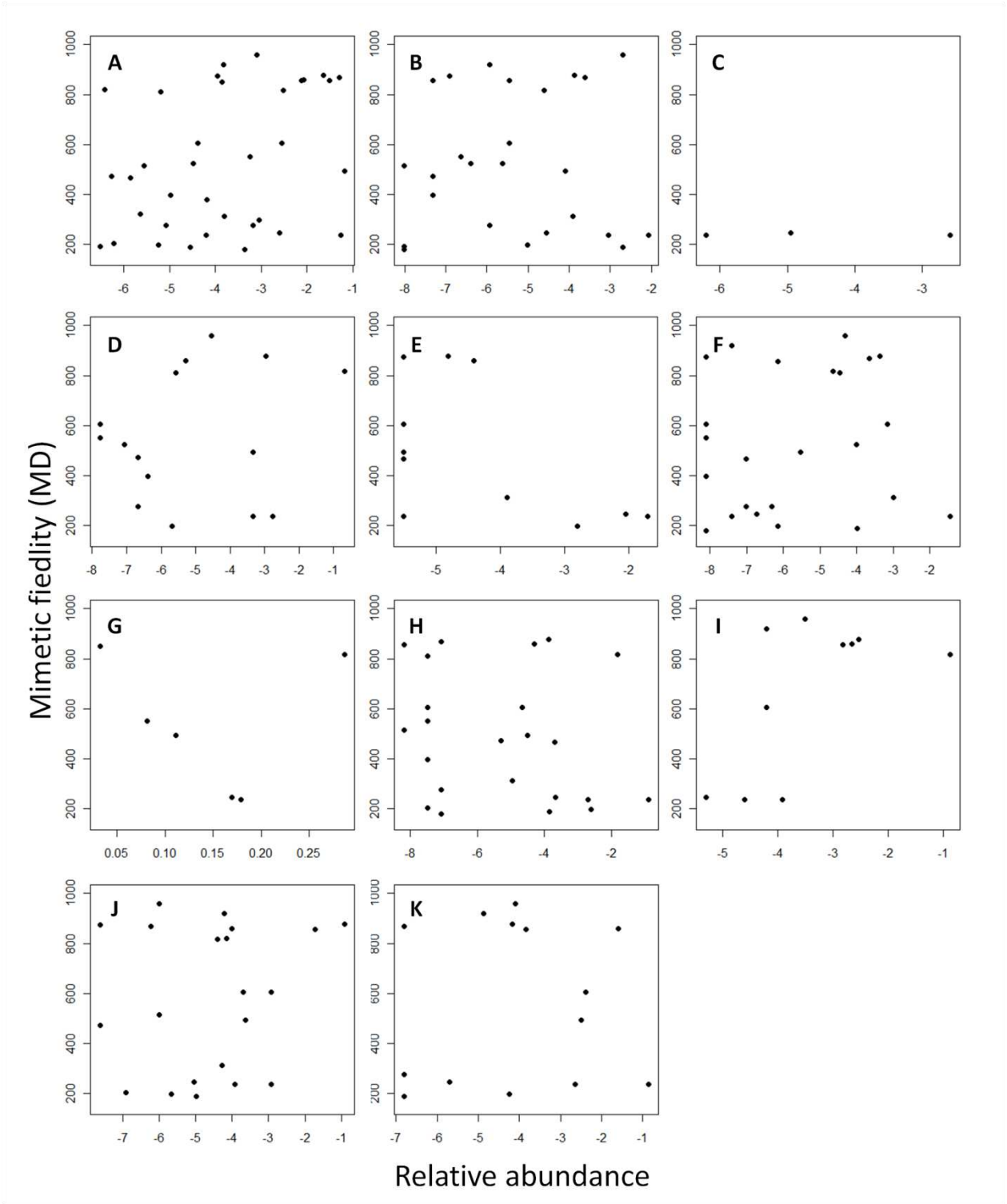

Figure S4 Relationships between relative abundance (logged in all plots apart from G) recorded in 11 independent field studies and mimetic fidelity as measured by human raters. Panels are as in **Figure S2**.

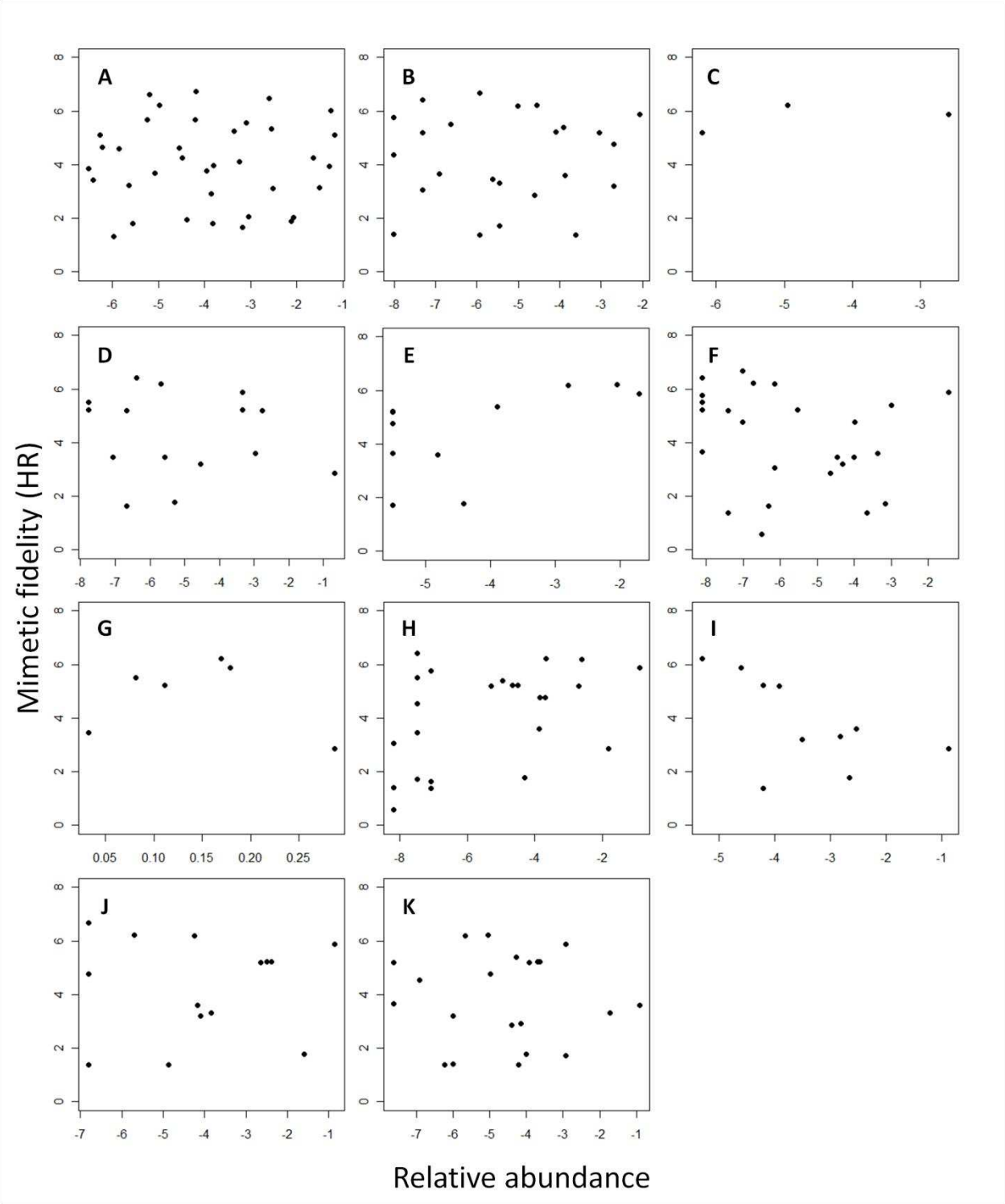

Figure S5 Relationships between relative abundance (logged in all plots apart from G) recorded in 11 independent field studies and body size. Panels are as in **Figure S2**.

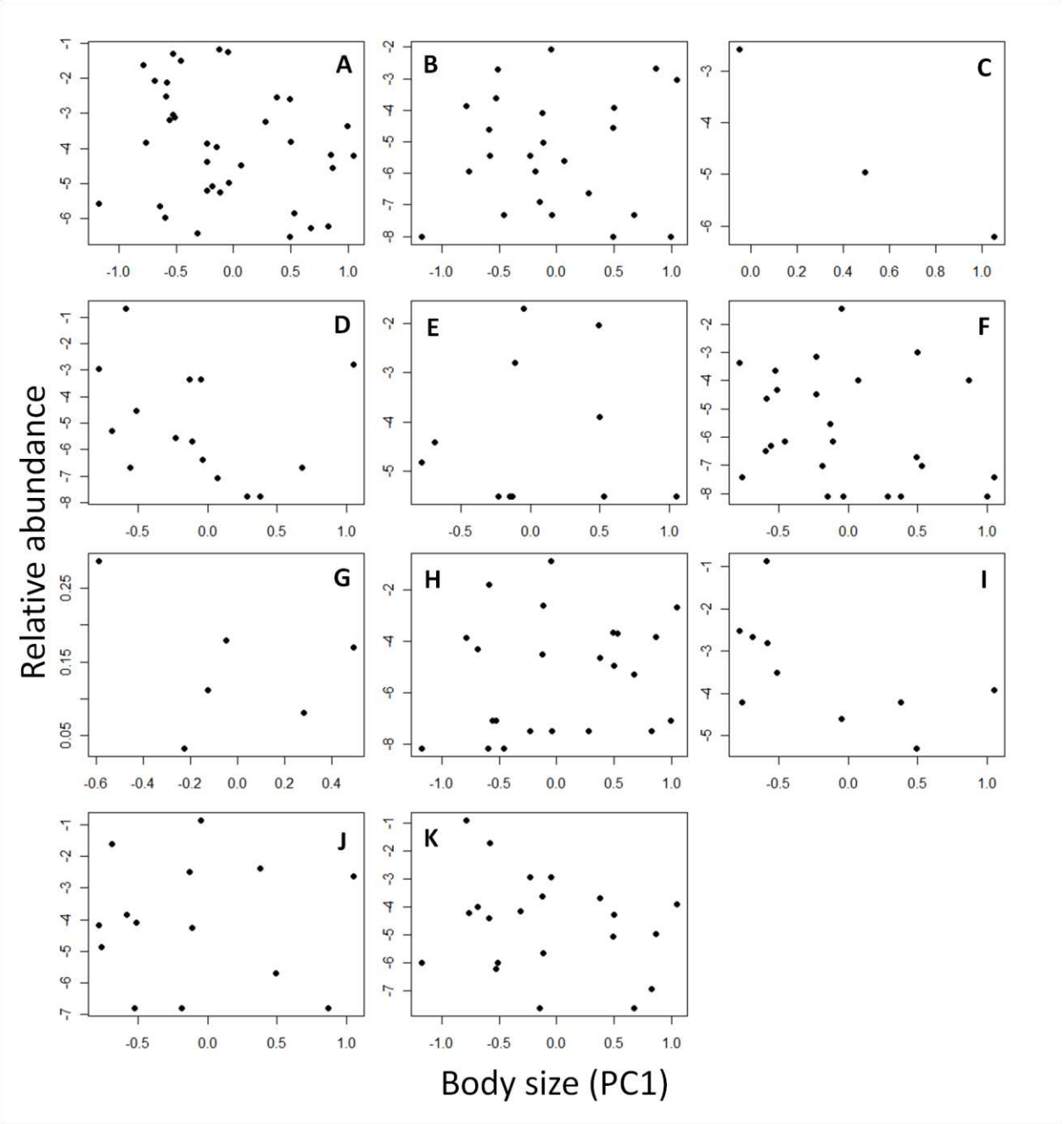

Figure S6 Phylogenetic relationships between 81 hover fly species (Diptera: Syphidae) used in the analysis for which COI genes have been sequenced. See text for details of tree construction methods. * indicates 31 species used in our analysis (see **Figure 3** in the main text) and codes following species names are individual specimen identification codes ("CNCD" = "Canadian National Collection Diptera", "JSS" = "Jeff Skevington Specimen"). See **Table S4** for details of specimens.

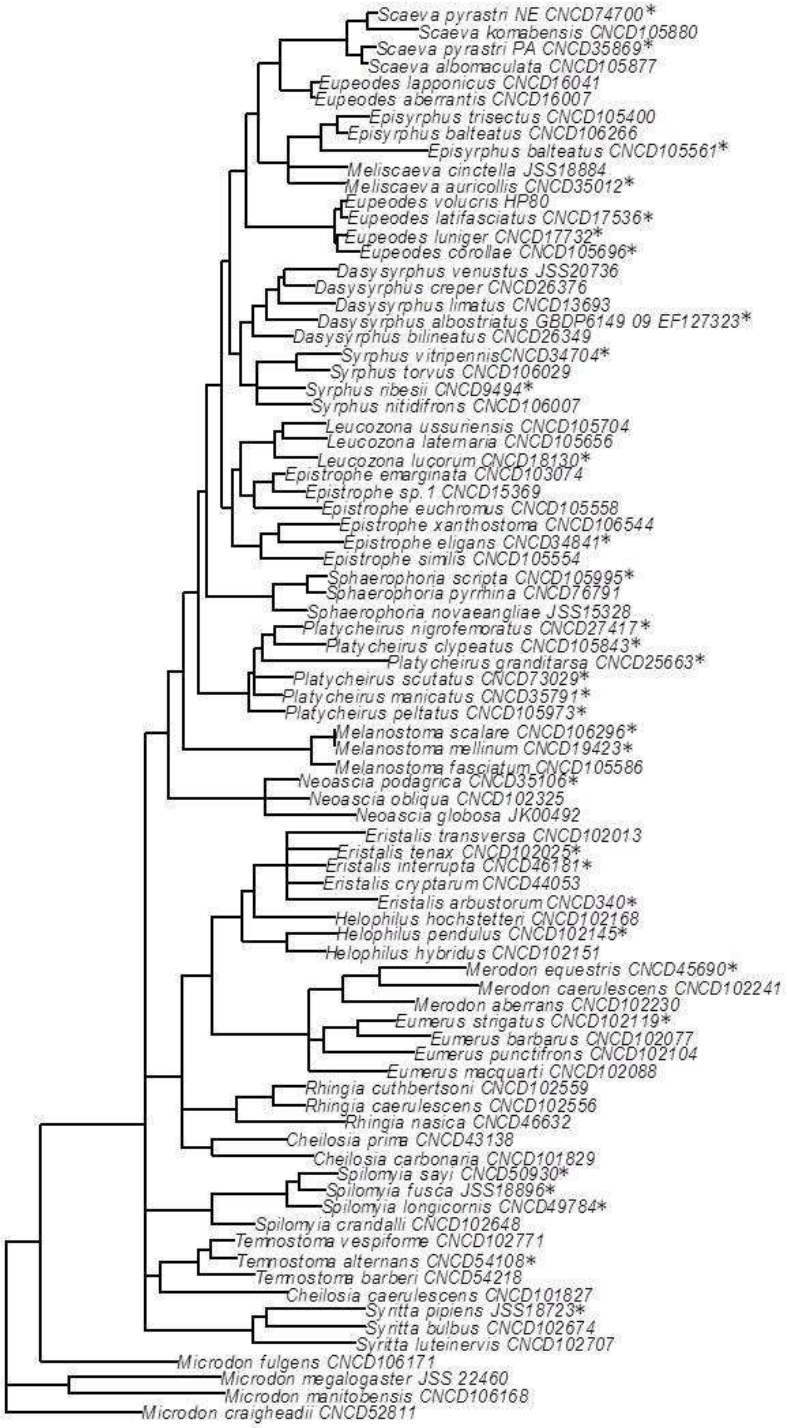

Table S1 Details of 11 independent studies that provide estimates of hover fly abundance.

Location	Season	Sampling method	No. specimens (no. species)	Reference
Finland, Western Russia, Estonia, Latvia, Lithuania	May to Sept, 1997 to 1999	Yellow traps (type Russell, pheromone trap).	246 (35)	[7]
England (31 arable fields)	3 weeks in June and July 2004	Window and water traps	1060 (28)	[9]
Germany (5 habitat types)	June and July, 2006	Sweep netting -100 m transects	829 (20)	[12]
Netherlands (16 stream beds)	Apr to mid Aug, 2002.	30 25x2m subplots. All syrphids seen in 5 min interval were caught. Sampled 3 times.	2017 (40)	[13]
Germany (32 grasslands)	Apr to Sept, 2004	6 transect walks. Syrphids in the 4m corridor ID'd in the field or caught.	3560 (75)	[10]
Poland	Apr to Sept, 2007.	500 net sweeps along 20 x 200m transects	200 (21)	[11]
France (woodland)	May 10- June 10 and Sept 13 to Oct 13, 2000	Malaise traps	3317 (100)	[8]
Spain (3 vegetation types)	May to Nov 2004; April to Sept 2005	Hand net, 2hr/month at each sampling site	2356 (72)	[6]
Belgium	Mar to Oct, 2002-2003.	Malaise, stump emergence, free hanging window traps	3020 (106)	[4]
Central Japan	May to Sept, 2005 and 2007	Malaise traps	990 (57)	[5]
England	Apr to Oct, 1979 - 1986	Malaise trap, one backyard	43359 (40)	[3]

Table S2 List of (a) Syrphidae and (b) Hymenoptera species included in the morphological analysis.

(a) Syrphidae

Subfamily	Tribe	Species		Included in phylogeny?	Abbreviation in Figure 1
Eristalinae	Eristalini	*Eristalis arbustorum*	Linnaeus	Yes	Ear
Eristalinae	Eristalini	*Eristalis interrupta*	Poda	Yes	Einte
Eristalinae	Eristalini	*Eristalis intricaria*	Linnaeus	No	Eintr
Eristalinae	Eristalini	*Eristalis pertinax*	Scopoli	No	Epe
Eristalinae	Eristalini	*Eristalis tenax*	Linnaeus	Yes	Ete
Eristalinae	Eristalini	*Eumerus funeralis*	Meigen	No	Efu
Eristalinae	Eristalini	*Eumerus strigatus*	Fallén	Yes	Est
Eristalinae	Eristalini	*Merodon equestris*	Fabricius	Yes	Meq
Eristalinae	Eristalini	*Helophilus pendulus*	Linnaeus	Yes	Hpe
Eristalinae	Eristalini	*Spilomyia longicornis*	Loew	Yes	Slo
Eristalinae	Eristalini	*Spilomyia sayi*	Goot	Yes	Ssa
Eristalinae	Eristalini	*Syritta pipiens*	Linnaeus	Yes	Spi
Eristalinae	Eristalini	*Temnostoma alternans*	Loew	Yes	Tal
Eristalinae	Eristalini	*Cheilosia vernalis*	Fallén	No	Cve
Eristalinae	Eristalini	*Rhingia campestris*	Meigen	No	Rca
Eristalinae	Brachyopini	*Neoascia podagrica*	Fabricius	Yes	Npo
Syrphinae	Bacchini	*Melanostoma mellinum*	Fabricius	Yes	Mme
Syrphinae	Bacchini	*Melanostoma scalare*	Fabricius	Yes	Msc
Syrphinae	Bacchini	*Platycheirus angustatus*	Zetterstedt	No	Pan
Syrphinae	Bacchini	*Platycheirus clypeatus*	Meigen	Yes	Pcl
Syrphinae	Bacchini	*Platycheirus granditarsa*	Forster	Yes	Pgr
Syrphinae	Bacchini	*Platycheirus manicatus*	Meigen	Yes	Pma
Syrphinae	Bacchini	*Platycheirus nigrofemoratus*	Kanervo	Yes	Pni
Syrphinae	Bacchini	*Platycheirus peltatus*	Meigen	Yes	Ppe
Syrphinae	Bacchini	*Platycheirus scutatus*	Meigen	Yes	Psc
Syrphinae	Syrphini	*Dasysyrphus albostriatus*	Fallén	Yes	Dal
Syrphinae	Syrphini	*Epistrophe eligans*	Harris	No	Eel
Syrphinae	Syrphini	*Episyrphus balteatus*	De Geer	Yes	Eba
Syrphinae	Syrphini	*Eupeodes corollae*	Fabricius	Yes	Eco
Syrphinae	Syrphini	*Eupeodes latifasciatus*	Macquart	Yes	Ela
Syrphinae	Syrphini	*Eupeodes luniger*	Meigen	Yes	Elu
Syrphinae	Syrphini	*Leucozona lucorum*	Linnaeus	Yes	Llu
Syrphinae	Syrphini	*Meliscaeva auricollis*	Meigen	Yes	Mau
Syrphinae	Syrphini	*Scaeva pyrastri*	Linnaeus	Yes	Spy
Syrphinae	Syrphini	*Sphaerophoria menthastri*	Linnaeus	Yes	Sme
Syrphinae	Syrphini	*Sphaerophoria scripta*	Linnaeus	Yes	Ssc
Syrphinae	Syrphini	*Syrphus ribesii*	Linnaeus	Yes	Sri
Syrphinae	Syrphini	*Syrphus vitripennis*	Meigen	Yes	Svi

(b) Hymenoptera

Family	Species		Abbreviation in Figure 1
Apidae	*Apis mellifera*	Linnaeus	Ame
Apidae	*Bombus affinis*	Cresson	Baf
Apidae	*Bombus impatiens*	Cresson	Bim
Apidae	*Bombus lucorum*	Linnaeus	Blu
Vespidae	*Ancistrocerus parietum*	Linnaeus	Apa
Vespidae	*Dolichovespula maculata*	Linnaeus	Dma
Vespidae	*Polistes dominula*	Christ	Pdo
Vespidae	*Polistes fuscatus*	Fabricius	Pfu
Vespidae	*Vespula germanica*	Fabricius	Vge
Vespidae	*Vespula vulgaris*	Linnaeus	Vvu

Table S3 Product moment **c**orrelation coefficients between the relative abundance of hover flies in 11 studies included in the meta-analysis (see **Table S1**). Values in bold (all positive) refer to statistically significant correlations in relative abundance ($P < 0.05$), letters refer to the individual studies.

	MW	**H**	**KL**	**Me**	**Mo**	**Ou**	**R**	**F**	**T**	**GO**
L	-0.162	0.538	-0.102	**0.599**	-0.459	**0.699**	-0.204	**0.526**	0.801	0.382
MW		0.458	-0.274	0.467	**0.998**	0.150	**0.907**	0.142	0.628	0.202
H			-0.060	**0.867**	-0.096	**0.949**	0.125	**0.772**	**0.981**	0.451
KL				**0.534**	0.070	0.153	-0.011	-0.015	0.933	0.353
Me					0.247	**0.849**	0.363	**0.667**	**0.969**	**0.459**
Mo						-0.086	**0.977**	-0.232	-0.249	-0.016
Ou							0.010	**0.605**	**0.980**	**0.464**
R								-0.006	0.147	0.116
F									**0.900**	0.380
T										0.993

L=[7], MW=[9], H=[12], KL=[13], Me=[10], Mo=[11], Ou=[8], R=[6], F=[4], T=[5], GO=[3]

Table S4 List of specimens used in the construction of the Syrphidae phylogeny (**Figure S5**) with their individual specimen codes (CNC = Canadian National Collection) and GenBank accession numbers.

Species	Author	GenBank # COI	Genbank # 28S	Unique # for COI
Cheilosia caerulescens	Meigen	JN991966		CNC DIPTERA 101827
Cheilosia carbonaria	Egger	JN991967		CNC DIPTERA 101829
Cheilosia prima	Hunter	JN991968		CNC DIPTERA 43138
Dasysyrphus albostriatus	Fallén	EF127323	EF127402	from [14]
Dasysyrphus bilineatus	Matsumura	JN991969		CNC DIPTERA 26349
Dasysyrphus creper	Snow	JN991970		CNC DIPTERA 26376
Dasysyrphus limatus	Hine	JN991971		CNC DIPTERA 13693
Dasysyrphus venustus	Meigen	JN991972		Jeff Skevington Specimen # 20736
Epistrophe (Epistrophe) eligans	Harris	JN991974		CNC DIPTERA 34841
Epistrophe (Epistrophella) emarginata	Harris	JN991975		CNC DIPTERA 103074
Epistrophe (Epistrophella) sp. 1		JN991973		CNC DIPTERA 15369
Epistrophe (Epistrophella) euchromus	Kowarz	JN991976		CNC DIPTERA 105558
Epistrophe similis	Doczkal & Schmid	JN991977		CNC DIPTERA 105554
Epistrophe (Epistrophe) xanthostoma	Williston	JN991978		CNC DIPTERA 106544
Episyrphus (Episyrphus) balteatus	De Geer	JN991980	EF127416	CNC DIPTERA 105561
Episyrphus (Episyrphus) balteatus	De Geer	JN991979		CNC DIPTERA 106266
Episyrphus (Episyrphus) trisectus	Loew	JN991981		CNC DIPTERA 105400
Eristalis (Eoseristalis) arbustorum	Linnaeus	JN991982		CNC DIPTERA 340
Eristalis (Eoseristalis) cryptarum	Fabricius	JN991983		CNC DIPTERA 44053
Eristalis (Eoseristalis) interrupta	Poda	JN991984		CNC DIPTERA 1833
Eristalis (Eristalis) tenax	Linnaeus	JN991985	AY261750	CNC DIPTERA 102025
Eristalis (Eoseristalis) transversa	Wiedemann	JN991986		CNC DIPTERA 102013
Eumerus barbarus	Coquebert	JN991987		CNC DIPTERA 102077
Eumerus macquarti	Ferguson	JN991988		CNC DIPTERA 102088
Eumerus punctifrons	Loew	JN991989		CNC DIPTERA 102104
Eumerus strigatus	Fallén	JN991990		CNC DIPTERA 102119
Eupeodes (Lapposyrphus) aberrantis	Curran	JN991991		CNC DIPTERA 16007
Eupeodes (Metasyrphus) corollae	Fabricius	JN991992	EU431467	CNC DIPTERA 105696
Eupeodes (Lapposyrphus) lapponicus	Zetterstedt	JN991993		CNC DIPTERA 16041
Eupeodes (Metasyrphus) latifasciatus	Macquart	JN991994		CNC DIPTERA 17536
Eupeodes (Metasyrphus) luniger	Meigen	JN991995		CNC DIPTERA 17732
Eupeodes (Eupeodes) volucris	Osten Sacken	JN991996		HP80
Helophilus (Pilinasica) hochstetteri	Nowicki	JN991997		CNC DIPTERA 102168
Helophilus (Helophilus) hybridus	Loew	JN991998		CNC DIPTERA 102151
Helophilus (Helophilus) pendulus	Linnaeus	JN991999	AY261751	CNC DIPTERA 102145
Leucozona (Ischyrosyrphus) laternaria	Muller	JN992000		CNC DIPTERA 105656

Leucozona (Leucozona) lucorum	Linnaeus	JN992001	EF501965	CNC DIPTERA 18130
Leucozona (Ischyrosyrphus) ussuriensis	Stackelberg	JN992002		CNC DIPTERA 105704
Melanostoma fasciatum	Macquart	JN992003		CNC DIPTERA 105586
Melanostoma mellinum	Linnaeus	JN992004		CNC DIPTERA 19423
Melanostoma scalare	Fabricius	JN992005	EF127417	CNC DIPTERA 106296
Meliscaeva auricollis	Meigen	JN992006	EF127423	CNC DIPTERA 35012
Meliscaeva cinctella	Zetterstedt	JN992007		Jeff Skevington Specimen # 18884
Merodon (Merodon) aberrans	Egger	JN992008		CNC DIPTERA 102230
Merodon (Merodon) equestris	Fabricius	JN992010	EU431455	CNC DIPTERA 45690
Merodon (Merodon) caerulescens	Loew	JN992009		CNC DIPTERA 102241
Microdon (Microdon) craigheadii	Walton	JN992011		CNC DIPTERA 52811
Microdon (Chymophila) fulgens	Wiedemann	JN992012		CNC DIPTERA 106171
Microdon (Microdon) manitobensis	Curran	JN992013		CNC DIPTERA 106168
Microdon (Microdon) megalogaster	Snow	JN992014		Jeff Skevington Specimen # 22460
Neoascia (Neoascia) globosa	Walker	JN992015		JK00492
Neoascia (Neoasciella) obliqua	Coe	JN992016		CNC DIPTERA 102325
Neoascia (Neoascia) podagrica	Fabricius	JN992017		CNC DIPTERA 35106
Platycheirus (Platycheirus) clypeatus	Meigen	JN992018		CNC DIPTERA 105843
Platycheirus (Pyrophaena) granditarsa	Forster	JN992019		CNC DIPTERA 4199
Platycheirus (Platycheirus) manicatus	Meigen	JN992020		CNC DIPTERA 35791
Platycheirus (Platycheirus) nigrofemoratus	Kanervo	JN992021	EF127432	CNC DIPTERA 27417
Platycheirus (Platycheirus) peltatus	Meigen	JN992022	AY261753	CNC DIPTERA 105973
Platycheirus (Platycheirus) scutatus	Meigen	JN992023		CNC DIPTERA 73029
Rhingia (Rhingia) caerulescens	Loew	JN992024		CNC DIPTERA 102556
Rhingia (Eorhingia) cuthbertsoni	Curran	JN992025		CNC DIPTERA 102559
Rhingia (Rhingia) nasica	Say	JN992026		CNC DIPTERA 46632
Scaeva albomaculata	Macquart	JN992027		CNC DIPTERA 105877
Scaeva komabensis	Matsumura	JN992028		CNC DIPTERA 105880
Scaeva pyrastri	Linnaeus	JN992029	EF127410	CNC DIPTERA 35869
Scaeva pyrastri	Linnaeus	JN992030	EF127410	CNC DIPTERA 74700
Sphaerophoria (Sphaerophoria) novaeangliae	Johnson	JN992031		Jeff Skevington Specimen # 15328
Sphaerophoria (Sphaerophoria) pyrrhina	Bigot	JN992032		CNC DIPTERA 76791
Sphaerophoria (Sphaerophoria) scripta	Linnaeus	JN992033	AY261755	CNC DIPTERA 105995
Spilomyia crandalli	Curran	JN992034		CNC DIPTERA 102648
Spilomyia fusca	Loew	JN992035		Jeff Skevington Specimen # 18896
Spilomyia longicornis	Loew	JN992036		CNC DIPTERA 49784
Spilomyia sayi	Goot	JN992037		CNC DIPTERA 50930
Syritta bulbus	Walker	JN992038		CNC DIPTERA 102674
Syritta luteinervis	de Meijere	JN992039		CNC DIPTERA 102707
Syritta pipiens	Linnaeus	JN992040	AY261713	Jeff Skevington Specimen # 18723
Syrphus (Syrphus) nitidifrons	Becker	JN992041		CNC DIPTERA 106007

Syrphus (Syrphus) ribesii	Linnaeus	JN992042		CNC DIPTERA 9494
Syrphus (Syrphus) torvus	Osten Sacken	JN992043		CNC DIPTERA 106029
Syrphus (Syrphus) vitripennis	Meigen	JN992044	AY261728	CNC DIPTERA 34704
Temnostoma alternans	Loew	JN992045		CNC DIPTERA 54108
Temnostoma barberi	Curran	JN992046		CNC DIPTERA 54218
Temnostoma vespiforme	Linnaeus	JN992047		CNC DIPTERA 102771

Supplementary Information A: Additional hypotheses to explain imperfect mimicry

Below is a list of some alternative theories for the evolution and maintenance of imperfect mimicry not covered in the main text. Note that these theories, like those in the main text, are not necessarily mutually exclusive.

Disequilibrium

Imperfect mimicry may potentially arise as a consequence of a temporary or permanent "breakdown" in mimicry. For instance, Sheppard [15] investigating the field distributions of mimetic African butterflies found that the proportion of individuals of a given species with a poor resemblance to the model was higher when mimics were relatively common. Likewise, Azmeh *et al*. [16] noted that the larvae of many hover fly mimics that are judged imperfect are aphidophagous and that these species may have increased dramatically in numbers following agricultural development. However in his review of imperfect mimicry in hover flies Gilbert [17] argued "I do not think there is any empirical or theoretical evidence for a non-equilibrial view of the evolution of mimetic colour patterns".

Multiple predators

A prey species would be expected to evolve increasing mimetic fidelity to a model that is noxious to a potential predator. However, if an additional predator is present that specialises on the model, mimetic perfection will be selected against due to increased predation from that specialist [18], resulting in an optimal phenotype that is highly but not perfectly faithful to the model. Like the multi-model hypothesis (main text) this mechanism is represents a specific realization of the constraint hypothesis, with counter-selection being imposed by predators species that do not find the model aversive.

Satyric mimicry

Howse and Allen [19] proposed that a phenotype that looked partly like a noxious model and partly like a palatable prey would confuse the predator allowing more time for the imperfect mimic to escape. There is currently no evidence for this phenomenon in hover flies [17] and one might argue that as such phenotypes become more common then predators would be less readily confused.

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