

Research article

Male dimorphism in *Perdita portalis* (Hymenoptera, Andrenidae) has arisen from preexisting allometric patterns

B.N. Danforth¹ and C.A. Desjardins²

¹ Department of Entomology, Comstock Hall, Cornell University, Ithaca, NY 14853–0901, USA, e-mail: bnd1@cornell.edu

² Department of Entomology, University of Maryland, College Park, MD 20742, USA, e-mail: desjar@wam.umd.edu

Received 9 October 1997; revised 27 February 1998; accepted 13 March 1998.

Summary. Allometric scaling coefficients were quantified using principal components analysis for eight species of closely related *Perdita* bees. The coefficients were mapped onto a cladogram and male dimorphism in *P. portalis* was found to be the derived state, whereas polymorphism was ancestral. The phylogeny explained $87.4 \pm 1.1\%$ of the variation in male head allometry among taxa, indicating that the evolution of head allometry is highly congruent with the cladogram. These results were used to place *Perdita* male head allometry in the context of adaptive phenotypic plasticity. Wheeler's (1991) model for the evolution of discrete alternative castes in ants is applied to the morphometric data in *Perdita*. We argue that the developmental rules that govern the evolution of caste polymorphism in social insects can be applied to the evolution of alternative male mating tactics in other Hymenoptera.

Key words: Morphology, evolution, alternative male mating tactics, caste determination.

Introduction

Males of all species of insects exhibit continuous variation in many anatomical traits and many of these continuously variable traits are related to inter-male combat for access to females (Thornhill and Alcock, 1983; Andersson, 1994). Variation in male morphology and variation in male mating tactics may be coupled, such that males may adopt alternative mating tactics that are partially determined by morphology (conditional strategies; Gross, 1996). While alternative reproductive tactics are widespread in animals, they are rarely associated with discrete, non-overlapping alternative morphologies (male dimorphism). Males of only a few species of insects are known to exhibit discrete variation such that two, non-overlapping male phenotypes are present

in all populations. Such species are said to possess dimorphic males.

Within the order Hymenoptera, dimorphic males are known from several, distantly related families but the total number of species exhibiting dimorphism is small (Table 1). The discrete alternative morphologies have apparently arisen for differing reasons, and there is no single explanation for all cases of male dimorphism. In general, the discrete alternative morphs in parasitoid wasps (excluding the Agaonidae) are characterized by alternative forms of both males and females. The alternative morphs may be determined by environmental cues (the type of host tissues consumed during larval development [*Melittobia*; Schmieder, 1933], the type of host [*Trichogramma*; Salt, 1937], or the nutritional resources of the host [*Gelis*; Salt, 1952]), or have a genetic basis (*Cephalonomia*; Kearns, 1934). In some ants, there appear to be discrete morphs associated with fighting within the nest for access to females (fighter morph; also known as “ergatoid” males) or dispersing (flier morph). This is true of *Cardiocondyla* (see below) and *Hypoponera*. In *Formica*, on the other hand, there have been no direct observations of intra-nest male fighting. In *F. exsecta* (Fortelius et al., 1987), for example, there are two morphs: a small, dispersing, “micraner” form, and a larger, non-dispersing, “macraner” form. The “micraner” form is produced when colonies become crowded and resources limited and the “macraner” form is produced under low densities. The alternative male morphs in this species are thought to reflect alternating phases of dispersal and nest persistence.

The best studied species of male-dimorphic Hymenoptera include the fig wasps in the family Agaonidae (Herre et al., 1997), ants in the genus *Cardiocondyla* (Stuart et al., 1987a, b; Kinomura and Yamauchi, 1987; Yamauchi and Kawase, 1992; Heinze and Hölldobler, 1993; Heinze et al., 1993; Tsuji et al., 1994; Heinze and Trenkle, 1997), and communal bees in two different families: *Lasioglossum* (*Chilalictus*) *hemichalceum* (Halictidae; Kukuk and Schwarz,

Table 1. Examples of discrete male dimorphism in the order Hymenoptera. This list includes species in which there is evidence of two (or more) discrete alternative male morphologies expressed within the same species. While some of these examples include fighter: flier dimorphisms (in ants, bees, and fig wasps), many are insufficiently studied to know what selective factors have given rise to the alternative male morphs

Family	Genus species	Reference
Agaonidae	<i>Blastophaga</i> spp. <i>Philotrypesis caricae</i> <i>Philotrypesis pilosa</i> <i>Philotrypesis</i> spp.	Hamilton, 1979 Joseph, 1958 Murray, 1987 Grandi, 1930, 1959; Hamilton, 1979
Trichogrammatidae	<i>Trichogramma semblidis</i>	Salt, 1937
Eulophidae	<i>Melittobia chalybii</i>	Schmieder, 1933
Scelionidae	<i>Telenomus polymorphus</i>	Lima, 1944
Ichneumonidae	<i>Gelis corruptor</i>	Salt, 1952
Braconidae	<i>Psenobolus ficarius</i>	Ramirez and Marsh, 1996
Bethylidae	<i>Cephalonomia perpusilla</i> <i>C. gallicola</i> <i>Scleroderma domesticum</i> <i>Theocolax</i> spp.	Evans, 1963 Kearns, 1934 Kühne and Becker, 1974 Hamilton, 1979
Pompilidae	<i>Cryptocheilus</i> spp.	Day, 1984
Formicidae	<i>Cardiocondyla wroughtonii nuda</i> , and <i>emeryi</i> <i>Formica exsecta</i> <i>Formica sanguinea</i> <i>Formica naefi</i> <i>Hypoponera eduardi</i> <i>Hypoponera</i> spp <i>Hypoponera punctatissima</i>	Stuart et al., 1987 a, b; Kinomura and Yamauchi, 1987; Heinze and Hölldobler, 1993; Heinze et al., 1993; Heinze and Trenkle, 1997 Fortelius et al., 1987; Pamilo and Rosengren, 1984; Agosti and Hauschteck-Jungen, 1987 Fortelius et al., 1987 Kutter, 1957 Le Masne, 1956 Wilson, 1971; Kempf, 1962; Hamilton, 1979; Wheeler, 1937 Hamilton, 1979
Andrenidae	<i>Perdita mellea</i> <i>P. portalis</i>	Rozen, pers. comm. Rozen, 1970; Danforth, 1991a, b
Halictidae	<i>Lasioglossum hemichalceum</i>	Houston, 1970; Knerer and Schwartz, 1976, 1978; Kukuk and Schwarz, 1987, 1988
Apidae	<i>Nannotrigona postica</i>	Bego and Camargo, 1984

1988; as *L. [C.] erythrurum*) and *Perdita (Macroteropsis) portalis* (Andrenidae; Danforth, 1991a, b). Fig wasps can have fully winged males (the primitive condition), wingless males, and male dimorphism (with winged and wingless males in the same species). Genera with discrete male dimorphism include *Philotrypesis* (Hamilton, 1979; Murray, 1987), *Epichrysomalline*, and *Pseudidarnes* (Cook et al., 1997; Herre et al., 1997). In some genera (e.g. *Idarnes*), closely related species may be winged or wingless, a condition potentially derived from male dimorphism. In fig wasps and bees, one male morph is small, capable of flight, and tends to disperse early from the natal nest site. The other male morph is flightless (by virtue of reduced flight musculature or winglessness), and morphologically and behaviorally modified for fighting within an enclosed space such as the fig receptacle or the natal nest. In *Cardiocondyla*, flightless, fighter males are smaller (not larger) than winged males, but nevertheless fight within the nest. Morphological specializations in macrocephalic bees usually include a greatly expanded head capsule (carrying huge mandibular adductor muscles [Danforth, 1991b]), elongate mandibles, and reduced compound eyes. The flightless males are known to mate with female colony mates or females within the fig recep-

tacle. The macrocephalic males have been interpreted as guards in *L. (Chilalictus) hemichalceum* (Houston, 1970), but this seems unlikely given the frequency of intra-nest mating (Kukuk and Schwarz, 1988), and theoretical considerations associated with the evolution of male workers in the Hymenoptera (Bartz, 1982).

Male dimorphism is a remarkable evolutionary innovation. While numerous studies have documented morphological and behavioral differences between conspecific dimorphic males in the Hymenoptera, no study so far has attempted to trace the evolutionary origins of male dimorphism. Does male dimorphism arise from some preexisting morphological trait in the ancestor of dimorphic species or does it arise essentially *de-novo*? Based on studies of seven species closely related to the male dimorphic taxa, can we make predictions as to what traits predispose taxa to evolving male dimorphism? Do dimorphic taxa give rise to continuously variable, unimodal taxa (as suggested by West-Eberhard, 1989), or does dimorphism appear to be derived repeatedly from continuously variable, polymorphic ancestors?

The goal of this study was to identify the morphological or developmental attributes of species closely related to *P.*

portalis that could underlie the evolution of male dimorphism in that species. To do this we combined data on the morphometrics of seven species closely related to *P. portalis* with a well-resolved cladogram for these same species based on traits unrelated to male head allometry. Intra-specific scaling patterns were mapped onto the cladogram to reconstruct the history of evolutionary change in allometry. We then tested the hypothesis that scaling patterns are congruent with the cladogram's topology. The results of our study indicate that strong positive allometry in male head size precedes the evolution of male dimorphism and may provide the necessary, but not sufficient, basis for the evolution of male dimorphism in *P. portalis*.

The nesting biology (Danforth, 1991 a) and the differences between the two male morphs (Danforth, 1991 b) in *P. portalis* have been described elsewhere. In summary, *P. portalis* is a communal ground-nesting bee that occurs in mixed Chihuahuan desert-grassland habitats of southwestern Arizona and western New Mexico, south to central Mexico (Danforth, 1996). Up to 30 reproductively active females share a single nest but do not cooperate in any way in cell provisioning. Active nests contain a number of adult, large-headed males roughly equal to the number of adult females (Danforth, 1991b). While small-headed males disperse from their natal nests and mate primarily on flowers (*Sphaeralcea*; Malvaceae) with foraging females, large-headed males mate exclusively within their natal nest with female nestmates. Based on observations made in artificial subterranean nests, large-headed males fight to the death within nests and mate with females immediately prior to oviposition, as would be expected if sperm precedence was the rule in this species. Based on laboratory-reared larvae, small-headed males occur at a slightly higher frequency than the large-headed male (Danforth, unpublished), while the sex ratio is not significantly different from equality (Danforth, unpublished).

The nesting biology of other species included in this comparative study have been described elsewhere (*P. texana*: Barrows et al., 1979; Danforth and Neff, 1992; Neff and Danforth, 1992; *P. opuntiae*: Custer, 1928; Bennett and

Breed, 1985). In general, the female nesting habits of other species are similar to that of *P. portalis*; females nest communally with little interaction among nestmates. Interestingly, males of *P. texana*, while not dimorphic, do enter the nests of females, where mating may take place (Danforth and Neff, 1992).

Methods

Specimens of eight species of *Perdita* bees were obtained from institutions shown in Table 2. The institutional abbreviations used in the table are explained in the Acknowledgements. We included in the morphometric analysis all six described species of the subgenus *Macroteropsis* (*P. haplura*, *P. arcuata*, *P. magniceps*, *P. echinocacti*, *P. latior*, and *P. portalis*). *P. opuntiae* is representative of the subgenus *Cockerellula*, which is the sister group to *Macroteropsis*. *P. texana* is representative of the subgenus *Macrotera*, which is the sister group to *Macroteropsis* + *Cockerellula* (Danforth, 1996).

Four linear measurements were made using a binocular microscope equipped with an ocular micrometer. Measurements included one head measurement (intermandibular distance [IMD]) and three thoracic measurements (intertegular distance [ITD], forewing length [FWL], and hind tibia length [HTL]; Fig. 1). ITD has been shown to accurately estimate thoracic size in bees (Cane, 1987). Error estimates for each linear variable were made by re-taking 20 measurements and calculating their deviation from the original measurements. The differences were then divided by the original measurements and averaged to determine a percent error. Dry body weights for specimens of *P. texana* and *P. portalis* were obtained as described in Danforth, 1991 a. Weights were measured to the nearest 0.01 mg with a Mettler Toledo AG245 analytical balance.

Allometric relationships were calculated using major axis regression of the covariance matrix of the log-transformed data (LaBarbera, 1989). Jolicoeur's multivariate generalization of the simple bivariate allometric equation was used for the multivariate analysis (Jolicoeur, 1963 a, b; Shea, 1985). The elements of the first unit eigenvector of log-transformed variates, when the first principal component axis corresponds to overall size, represent allometric coefficients analogous to the simple allometric coefficient used in bivariate studies, α , in the equation $Y = bX^\alpha$. A null hypothesis was constructed using the equation $H_0 = 1/\sqrt{p}$, where p equals the number of variables (four in this case). Therefore, H_0 in this study equals 0.5 ($1/\sqrt{4}$). A modified Chi-squared test was used to test for statistically significant deviations from isometry, with $p-1$ degrees of freedom (Anderson, 1963 [in Jolicoeur, 1963 a]).

Table 2. Mean \pm coefficient of variation (sample size) for all measurements

Species	IMD	ITD	FWL	HTL	Loaning institutions
<i>arcuata</i>	1.457 \pm 0.114 (71)	0.975 \pm 0.069 (71)	3.315 \pm 0.043 (71)	1.069 \pm 0.062 (71)	KU
<i>echinocacti</i>	1.484 \pm 0.129 (60)	1.006 \pm 0.074 (60)	3.275 \pm 0.055 (60)	1.091 \pm 0.052 (60)	UCR
<i>haplura</i>	1.536 \pm 0.076 (10)	1.055 \pm 0.038 (10)	3.192 \pm 0.034 (10)	1.115 \pm 0.032 (10)	UCR,UCB, KU, CAS, CTMI
<i>latior</i>	1.624 \pm 0.123 (56)	1.156 \pm 0.069 (56)	3.284 \pm 0.050 (56)	1.160 \pm 0.051 (56)	UCR
<i>magniceps</i>	1.304 \pm 0.125 (52)	0.996 \pm 0.057 (52)	2.939 \pm 0.039 (52)	1.044 \pm 0.047 (52)	
<i>opuntiae</i>	1.557 \pm 0.088 (19)	1.113 \pm 0.061 (19)	3.524 \pm 0.039 (19)	1.353 \pm 0.059 (19)	UCR
<i>portalis</i> (small)	1.141 \pm 0.080 (52)	0.915 \pm 0.073 (50)	2.822 \pm 0.043 (49)	0.883 \pm 0.059 (52)	
<i>portalis</i> (large)	1.571 \pm 0.031 (47)	0.882 \pm 0.043 (47)	2.476 \pm 0.024 (39)	0.861 \pm 0.032 (46)	
<i>texana</i>	2.652 \pm 0.128 (108)	1.534 \pm 0.070 (108)	5.136 \pm 0.055 (108)	1.712 \pm 0.054 (108)	KU

IMD = intermandibular distance, ITD = intertegular distance, FWL = forewing length, HTL = hind tibia length.

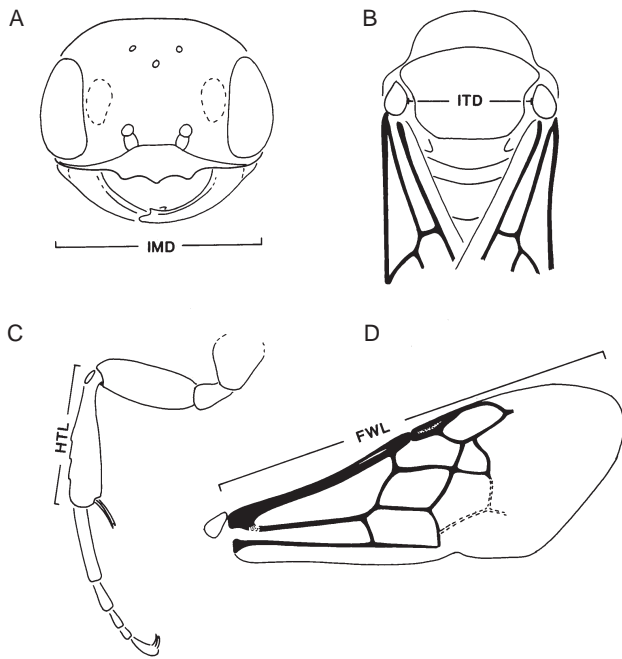


Figure 1. Morphological measurements are shown on *Perdita portalis* (small-headed morph). (A) Anterior view head, IMD = intermandibular distance; (B) dorsal view mesosoma, ITD = intertegular distance; (C) hind tibia, HTL = hind tibia length; (D) forewing, FWL = forewing length

The multivariate approach is used in place of the simple bivariate model of allometry because it can simultaneously determine the allometric relationship among all variables. An accurate measure of body size would be nearly impossible to determine with a single linear measurement.

Character mapping was done in MacClade using a discrete, ordered trace (Maddison and Maddison, 1992). The range of coefficients was divided into 10 equal sub-ranges which were each assigned a discrete variable. The variables were then mapped on the cladogram using parsimony.

The Cheverud et al. (1985) phylogenetic autocorrelation method was used to estimate the amount of trait variation due to phylogenetic and specific components (see also Harvey and Pagel, 1991; Christman

et al., 1997). A **W** matrix was constructed that was congruent with the cladogram (Fig. 7), using the deepest node between two species to estimate relatedness between those species. The program was written in Matlab, and a p value was calculated based on $m = 1000$ points. An error was found in equation 20 of Cheverud et al. (1985), in which the σ^4 outside the brackets should read σ^{-4} (McLeod, pers. comm.).

Results

The measurements are summarized in Table 2 and are listed as the mean \pm coefficient of variation (sample size). There were two obvious scaling patterns observed among the eight species included in this study. One, which we will refer to as “polymorphism,” involves continuous variation in quantitative traits with no discrete morphs apparent in any single trait. *P. texana* is a typical polymorphic species in that there is continuous variation in male head size and shape over a broad range of head sizes (Fig. 2A) and there is a single, linear relationship between head size and dry body weight (Fig. 3A). Polymorphism applies to all species included in this study except for *P. portalis*. *P. portalis* clearly exhibits discrete “dimorphism” in that for at least one variable (IMD) there are two discrete and non-overlapping phenotypes (Fig. 2B). Small-headed males (shaded) fall below the standardized mean of zero, large-headed males (black) fall above the standardized mean of zero, and there are no males with head sizes between a standardized IMD of 0.0 and 0.1. When log IMD is regressed on the log of dry body weight two discrete morphs are apparent which follow different allometric scaling patterns (Fig. 3B).

The scaling coefficients for IMD are used to quantitatively compare allometric scaling patterns among species. Previous studies (Danforth and Neff, 1992) have shown that IMD presents an accurate picture of overall head size, and is an important morphometric measure because it appears to be related to male fighting ability and reproductive success. The magnitude of the IMD scaling coefficient can be taken as a reflection of the relative trade-off between investment in head size and investment in overall, non-head body size.

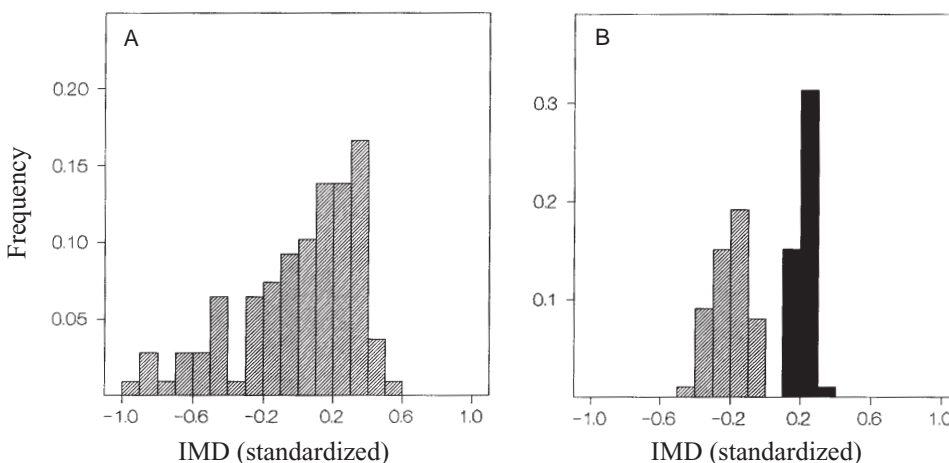


Figure 2. Head size (as measured by intermandibular distance [IMD]) distributions in male (A) *Perdita texana* (n=108) and (B) *Perdita portalis* (n=99). *P. texana* is termed polymorphic because the distribution of head sizes is continuous and unimodal. *P. portalis* is termed dimorphic because there are two discrete alternative morphs: small-headed males (shaded) and small-headed males (black). Measurements were standardized to a mean of 0.0 by subtracting the mean from all values

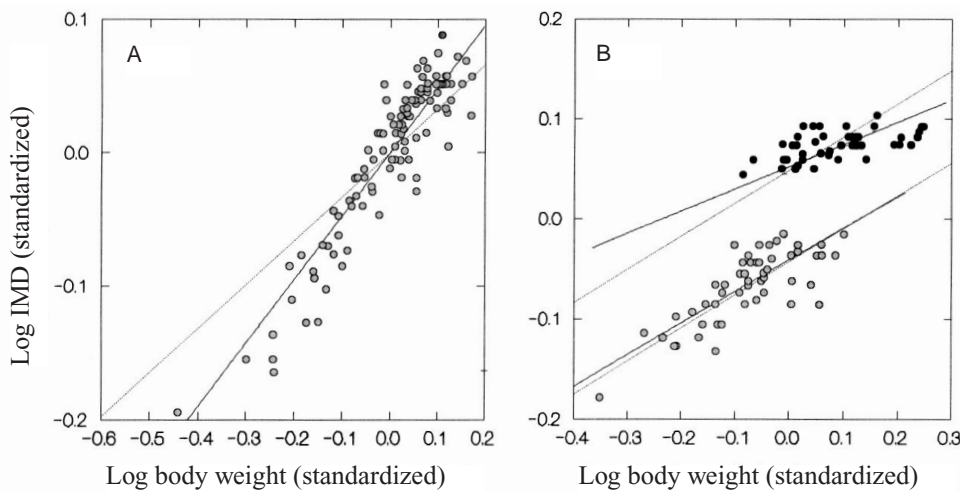


Figure 3. Regression of standardized log IMD on the standardized log of adult dry body weight in (A) *Perdita texana* (n=108) and (B) *Perdita portalis* (n=99). Regression lines are indicated by solid lines and the null hypothesis of isometry is indicated by dashed lines

Table 3. Allometric scaling coefficients for all measurements and Chi-squared values for the first unit eigenvectors are shown

Species	IMD	ITD	FWL	HTL	Chi-square
<i>arcuata</i>	0.785	0.419	0.258	0.377	239
<i>echinocacti</i>	0.814	0.440	0.273	0.263	165
<i>haplura</i>	0.833	0.346	0.296	0.315	29
<i>laticornis</i>	0.798	0.425	0.301	0.303	329
<i>magniceps</i>	0.864	0.344	0.225	0.290	181
<i>opuntiae</i>	0.703	0.471	0.292	0.446	115
<i>portalis</i> (small)	0.629	0.554	0.324	0.439	160
<i>portalis</i> (large)	0.538	0.830	-0.006	0.146	40
<i>portalis</i> (overall)	0.953	-0.015	-0.300	-0.008	311
<i>texana</i>	0.814	0.393	0.313	0.291	897

IMD = intermandibular distance, ITD = intertegular distance, FWL = forewing length, HTL = hind tibia length. The degrees of freedom = 3 in all cases ($p - 1$).

The scaling coefficients and Chi-squared values for all measurements are shown in Table 3. Chi-squared values and degrees of freedom are also listed. The large-headed *P. portalis* had the lowest scaling coefficient (0.54). The small-headed *P. portalis* and *P. opuntiae* had the next lowest scaling coefficients equaling 0.629 and 0.703, respectively. *P. arcuata*, *P. laticornis*, *P. echinocacti*, *P. texana*, *P. haplura*, and *P. magniceps* all had increasingly high scaling coefficients

Table 4. The eigen values of the first and second principal component axes expressed as percent variation explained by each axis

Species	PCA1	PCA2
<i>arcuata</i>	88.1	5.8
<i>echinocacti</i>	85.0	8.1
<i>haplura</i>	86.6	6.1
<i>laticornis</i>	92.1	5.8
<i>magniceps</i>	89.1	6.4
<i>opuntiae</i>	96.1	3.1
<i>portalis</i> (small)	91.7	4.8
<i>portalis</i> (large)	55.8	22.8
<i>texana</i>	93.5	3.2

equaling 0.785, 0.798, 0.814, 0.833, and 0.864, respectively. All coefficients were significantly different from isometry ($p < 0.01$). The scaling coefficients are depicted graphically in Figure 4. The horizontal line depicts the null hypothesis of isometry (scaling coefficient = 0.5). Bars above the line indicate positive allometry, while bars below the line indicate negative allometry. A histogram showing the range and magnitude of the IMD scaling coefficient is depicted in Figure 5. The overall value for *P. portalis* is clearly separated from the rest of the species examined.

The percent variation explained by the first two principal component axes is shown in Table 4. The first axis explains over 85% of the variance in all species except for *P. portalis* and the first axis corresponds to overall size in all species except *P. portalis*. In *P. portalis* the first axis represents a contrast term between head size and body size (Table 3 and Fig. 6) and therefore represents the dimorphism. Notice in Figure 6 the limited variance shown in the large-headed males as compared to the small-headed males. Error estimates for measurements ranged from 0.46% (IMD) to 1.42% (FWL), demonstrating that measurement error is not a significant source of variability in this study.

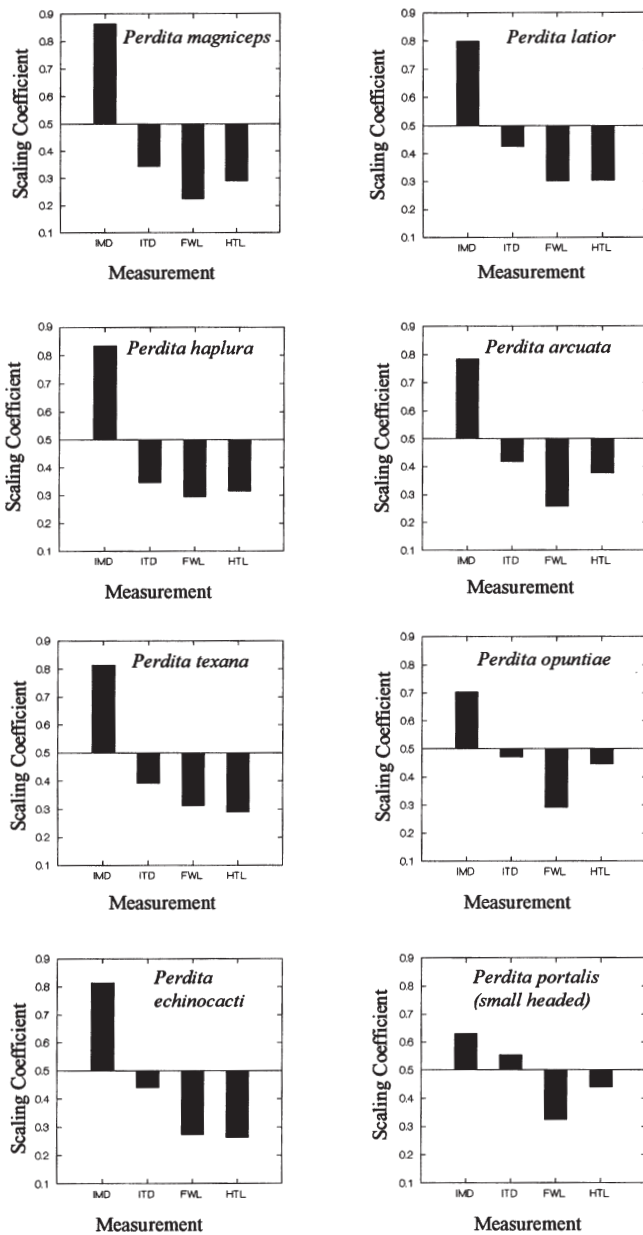


Figure 4. Graphical representations of allometric scaling coefficients shown in Table 3. The horizontal lines show isometry (0.5). Bars above the line indicate positive allometry, whereas bars below the line indicate negative allometry

Scaling coefficients are shown mapped onto the cladogram in Figure 7. The primitive condition for these three subgenera of *Perdita* is hypothesized to be a scaling coefficient around that of *P. texana* (0.814). In *P. opuntiae*, there is a large decrease in the scaling coefficient to 0.703. The primitive condition for the subgenus *Macroteropsis* is hypothesized to be around that of *P. texana* or slightly higher, and these coefficients are exhibited in *P. echinocacti*, *P. latior*, and *P. haplura*. *P. magniceps* and *P. arcuata* exhibit a small increase and decrease in allometry, respectively. *P. portalis* exhibits a drastic increase in allometry (reflecting the evolu-

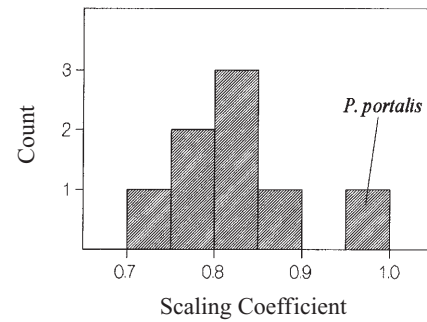


Figure 5. Histogram showing the allometric scaling coefficient for IMD for each species. *P. portalis* is a distinct outlier

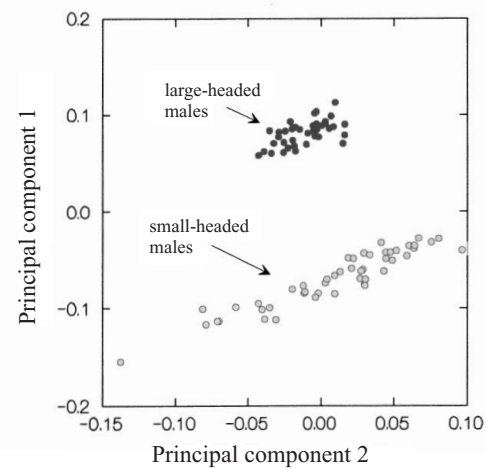


Figure 6. Plot of PCA1 and PCA2 scores from principal component analysis of *Perdita portalis*. Large and small-headed males fall into two discrete groups

tion of male head size dimorphism) relative to its sister species, *P. haplura*, and all other members of the subgenus *Macroteropsis*.

According to the Cheverud et al. (1985) phylogenetic autocorrelation method, $87.4 \pm 1.1\%$ (mean \pm standard error; $t = 78.04^{**}$) of the variation in IMD scaling is explained by the phylogeny. The remaining variation, 12.6%, is therefore due to specific variation.

Discussion

Evolution of allometric scaling patterns – what factors influence the magnitude of IMD scaling?

Based on comparisons among species in the magnitude of IMD scaling coefficients (Table 3, Fig. 4), there is considerable variation in head allometry among the species of *Perdita* included in this study. We do not consider this variability as random; indeed the significant association between allo-

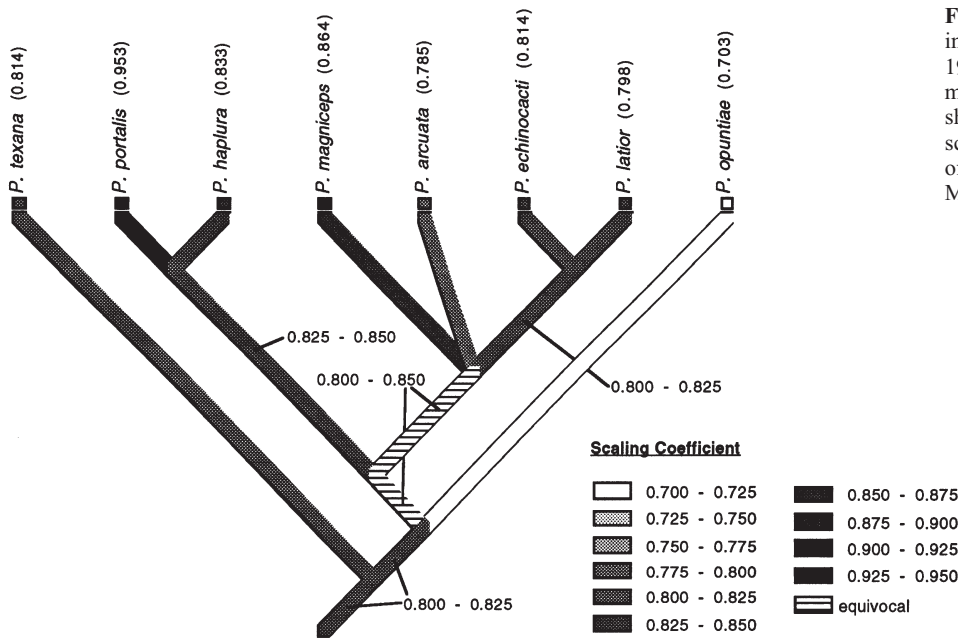


Figure 7. Cladogram for species of *Perdita* included in this study (based on Danforth, 1996) with allometric scaling coefficients mapped on. Numerical ranges of branch shading are shown in the legend. Ranges of scaling coefficients for the internal branches of the cladogram (as determined by the MacClade trace) are shown on the cladogram

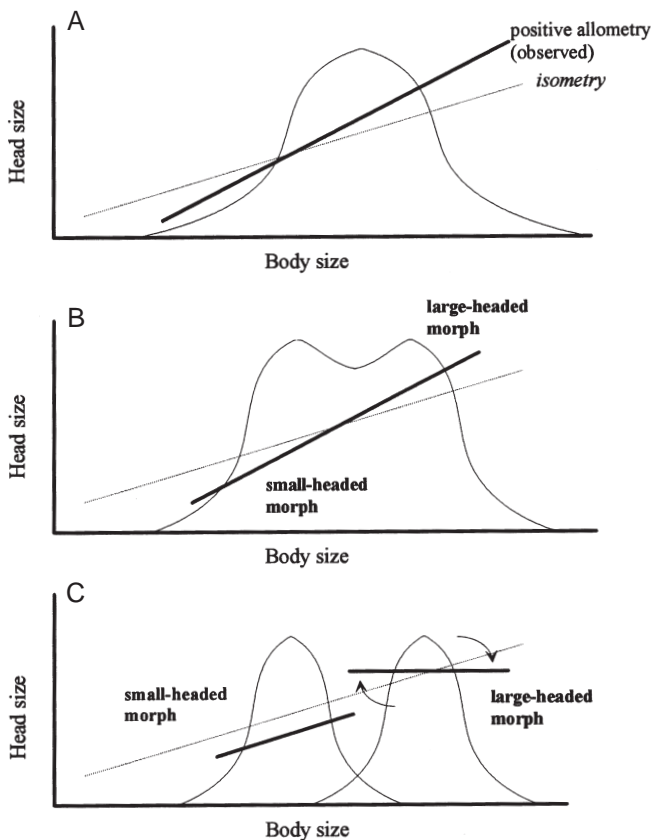


Figure 8. Model for evolution of dimorphism based on Wheeler (1991) and morphometric data presented herein. (A) Primitive condition is for males to show positive head allometry with a unimodal distribution of body sizes. (B) Through disruptive selection, males of intermediate body size may be partially or completely eliminated. (C) Once developmentally decoupled through the addition of new critical size for pupation, the two male morphs would be free to vary independently in the allometric relationship between head size and body size

metric scaling coefficients and the phylogeny suggests that allometric patterns are evolving along specific trajectories. Allometric scaling coefficients have recently been shown to respond to selection in beetles (Emlen, 1994, 1996, 1997) and we suspect that head allometry in *Perdita* may be shaped by selection as well. Previous studies of *P. texana* have shown that larger headed males have a distinct reproductive advantage in both male-male competition for receptive females on flowers and in their ability to grasp females and initiate copulation (Danforth and Neff, 1992). The sample of males found in copula on flowers had significantly larger heads than a random sample of males. Also, males with larger heads were found to exclude smaller males from flowers by direct competition. The morphometric analysis supports this theory by demonstrating that larger males invested more heavily in structures involved in grasping and fighting. In an anthophorid bee, *Centris pallida*, larger males were shown to almost always defeat smaller males in competition for mates (Alcock et al., 1977).

Following West-Eberhard (1989) and Travis (1994), we view head allometry in *Perdita* as an example of adaptive phenotypic plasticity. By phenotypic plasticity we mean that a single genotype is capable of producing a range of phenotypes in response to variation in some environmental variable. In the case of mass-provisioned bees, male body size (and hence head size) is primarily determined by the amount of food (pollen and nectar) provided by the mother (Visscher and Danforth, 1997) and intra-specific allometry provides the mechanism by which head size (and hence fighting ability) is determined. We presume that, while the slope of the allometric curve relating head size to body size is under selection and presumably heritable (as in dung beetles [Emlen, 1996]), the actual position that any male occupies along the curve is determined environmentally (by the amount of food consumed during development). We have no

direct evidence that dimorphism in *P. portalis* is *not* genetic, but all evidence so far suggest that head size in both polymorphic and dimorphic species is determined by overall size alone. Large- and small-headed males are significantly different in body weight both as larvae and as adults (Danforth, unpublished), and genetic polymorphisms are rarely the basis of alternative reproductive phenotypes (Gross, 1996).

What environmental factors would be likely to alter intraspecific scaling coefficients in these bees? We know from previous studies that head size is an important factor in determining mating success in direct male:male combat on flowers (see above; Danforth and Neff, 1992). We suspect that increased female density, either on flowers or within nests, leads to elevated levels of male combat. Hence, relative male head size may be highly influenced by female density and its effect on the intensity of male:male combat. In fact, we suspect that the variation in the magnitude of the IMD scaling coefficient observed in this study may arise from interspecific differences in female density. In species with, on average, low female densities one would expect low allometric coefficients relating head size to body size. Most males would be expected to invest in thoracic size (indirect flight musculature) and mobility in order to locate widely distributed females on flowers. If direct male:male interactions on flowers are rare, then investment in expanded head size would confer little advantage to larger males. In species with high female densities, or highly heterogeneous female densities (with some localities showing high female densities and other localities showing low female densities), high intraspecific allometry would be expected such that males invest disproportionately more in morphological traits associated with fighting (head size and associated mandibular muscle size; Danforth, 1991 b). We have no direct evidence of a relationship between female density and male allometry, but the hypothesis could be tested by relating female density among populations with the population-specific allometric scaling patterns in males.

The origin of male dimorphism via Wheeler's (1991) model: a hypothesis

Discrete male dimorphism in *P. portalis* clearly has its origins in the strong positive allometric trends observed in closely related polymorphic species. All of the members of the subgenera *Macrotera*, *Cockerellula*, *Macroteropsis* and *Macroterella* have positive head allometry in males (Danforth, pers. obs.), and all of the species included in this study show significant deviation from isometry (Table 3).

Male dimorphism in *P. portalis*, and in other Hymenoptera, bears a striking resemblance to discrete differences among castes in social insects. In social ants, for example, workers (females) may assume from two to three discrete phenotypes in roughly 15% of the species and discrete worker castes have evolved in eight different lineages (Hölldobler and Wilson, 1990). Wilson (1953) hypothesized that the discrete polymorphism arose from continuously variable, intraspecific allometry, and he differentiated among various allometric patterns, including monomorphism (isometry),

monophasic allometry (polymorphism, in our terminology), diphasic allometry, triphasic allometry, and complete dimorphism (equivalent to what we term dimorphism). The proximate mechanism of caste determination involves differences in juvenile hormone (JH) titer during a critical period in larval development, and JH titer itself is affected by differences in larval nutrition (Nijhout and Wheeler, 1982; Wheeler and Nijhout, 1984; Nijhout, 1994). Wheeler (1991) combined experimental data on caste determination with comparative data on the morphometrics of caste in ants to develop a model for the evolution of discrete morphological castes in ants. According to her model, discrete castes evolve by a two-step process: (1) reprogramming of critical size at metamorphosis, and (2) reprogramming of growth parameters (allometries). The transition from monophasic allometry to complete dimorphism involves the addition of a new critical size to the plesiomorphic developmental system. With two critical sizes, genetically identical larvae can assume two discrete phenotypes. Once two separate critical sizes are attained, reprogramming of the individual growth parameter (allometry) within each caste takes place. (See Jeanne et al. [1995] for an example in epiponine wasps that is inconsistent with this model of caste origins.) Using Wheeler's model (1991) and morphometric data presented in this paper, we outline a hypothesis for the origin of male dimorphism in *P. portalis*.

We assume that the ancestor of *P. portalis* and *P. haplura* was a species with continuously variable males, but with strong positive allometry in head size. This is supported by the fact that all species included in this study showed significant positive head allometry (Fig. 8A). Larger males in this species would have had disproportionately large heads in relation to their bodies while small males would have had disproportionately small heads. We presume also that, as in ants, a single critical size exists, which is partially determined by larval nutrition.

In the early stages of the evolution of dimorphism, males of intermediate size may have been at a selective disadvantage relative to males of either large or small body size. This could arise if two discrete alternative mating opportunities were available to males. At low female densities (on flowers, for example), small males may have a reproductive advantage while at very high female densities (within nests in a communal bee), large, aggressive males may have an advantage. Their large heads and associated structures give them a clear advantage in male-male fighting and the grasping of females to initiate copulation (Danforth, 1991 b). If the extremes of the body size distribution possess distinct advantages, and intermediate sized males are inferior in relation to either extreme, then disruptive selection would be expected to eliminate the males of intermediate body size. Elimination of males of intermediate body sizes (Fig. 8B) in combination with positive allometry in head size would tend to produce males of discretely different head sizes, even if the body size distributions were broadly overlapping. The higher the ancestral scaling coefficient, the more distinct the alternative male "morphs" following elimination of intermediate body sizes.

In mass-provisioning bees, disruptive selection could act through female provisioning decisions. If intermediate-sized males were at a selective disadvantage, females tending to produce males of either small or large body size would themselves have higher fitness. In fact, one might expect female provisioning decisions to change rapidly in response to variation in male fitness. With selection favoring males at either end of the size spectrum and females tending to produce either large or small males, one might expect the evolution of an additional critical size for metamorphosis, as hypothesized by Wheeler's (1991) model. With two distinct critical sizes, large- and small-headed males would metamorphose at different body weights. Wheeler's model should apply equally well to mass-provisioned Hymenoptera like ground-nesting bees, as it does to progressively-provisioned ant larvae.

In the derived condition, which is present in *P. portalis*, the ancestral allometry is either lost or reduced (Fig. 8C). Once the small- and large-headed morphs are decoupled from each other by the intercalation of a second critical size, selection can act separately on both morphs. The negative slope and extremely low variation in large-headed *P. portalis* males (Table 2 and Fig. 6) suggest that developmental or ecological constraints may place an upper limit on head size. A common pattern observed in plots of head size on body size in ant castes is that, while the overall relationship of head size is positively allometric, the slopes of one or more of the line segments for individual castes are negatively allometric or isometric (Wheeler, 1991). This relationship results in the maintenance of a relatively constant size for a body part, such as the head, across the range of body sizes within a caste. In the evolution of dimorphic castes, then, growth parameters may continue to evolve to enhance caste function after initial evolution of dimorphism.

Our results have some bearing on a hypothesis proposed by West-Eberhard (1989). She argued that discrete, alternative, intra-specific phenotypes may provide the material basis for the evolution of species-level differences. One prediction of her hypothesis is that dimorphic species should tend to give rise to continuously variable, polymorphic species. Our results indicate that the reverse trend has taken place in *Perdita*; male dimorphism has arisen from a unimodal, continuously variable ancestor. This is also true in the *Lasioglossum* subgenus *Chilalictus*, in which one dimorphic species (*L. (C.) hemichalceum*) has arisen from within a group of 32 polymorphic species (Walker, 1996, Table 4). It remains to be seen if male dimorphism is itself an evolutionary dead end.

Allometric patterns have often been viewed as evolutionary constraints acting on organisms. Gould (1966), for example, viewed the giant antlers of male Irish elk as a maladapted consequence of fixed inter-specific allometric scaling coefficients. We see no evidence of a relationship between body size and the degree of head allometry, so there does not appear to be strong inter-specific allometry acting in these bees. Two of the species with the highest scaling coefficients, *P. texana* and *P. magniceps*, are at either end of the range of body sizes (as estimated by ITD; Table 2). The results of this study therefore support the view that intra-

specific allometric scaling patterns are evolutionarily labile and most likely under selection arising from the frequency and predictability of male: male combat.

Acknowledgements

We are extremely grateful to Ian Mcleod, who programmed the phylogenetic autocorrelation method into Matlab. We are also grateful to Lars Hedin, Paul Sherman, John Ascher, Mike Engel, and one anonymous reviewer for helpful comments on an earlier draft of this paper. The following institutions generously loaned specimens for this study: University of California at Riverside (UCR), University of California at Berkeley (UCB), University of Kansas (KU), the California Academy of Sciences (CAS), and the Central Texas Melittological Institute (CTMI). This study was funded in part by a USA National Science Foundation Research Grant in Systematic Biology (DEB-9508647) to BND and in part by a Cornell University Undergraduate Research Grant to CAD.

References

- Agosti, D. and E. Hauschteck-Jungen, 1987. Polymorphism of males in *Formica exsecta* Nyl. (Hym.: Formicidae). *Insectes soc.* 34: 280–290.
- Alcock, J., C.E. Jones and S. L. Buchmann, 1977. Male mating strategies in the bee *Centris pallida* Fox (Hymenoptera: Anthrophoridae). *Amer. Nat.* 111: 145–155.
- Anderson, T.W., 1963. Asymptotic theory for principle component analysis. *Ann. Math and Statistics* 34: 122–148.
- Andersson, M.B., 1994. *Sexual Selection*. Princeton University Press, Princeton.
- Barrows, E.M., M.R. Chabot, C.D. Michener and T.P. Snyder, 1979. Foraging and mating behavior in *Perdita texana* (Hymenoptera: Andrenidae). *J. Kansas Entomol. Soc.* 49: 275–279.
- Bartz, S.H., 1982. On the evolution of male workers in the Hymenoptera. *Behav. Ecol. Sociobiol.* 11: 223–228.
- Bego, L.R. and C.A. Camargo, 1984. On the occurrence of giant males in *Nannotrigona (Scaptotrigona) postica* Latreille (Hymenoptera, Apidae, Meliponinae). *Bolm. Zool., Univ. S. Paulo* 8: 11–16.
- Bennett, B. and M.D. Breed, 1985. The nesting biology, mating behavior and foraging ecology of *Perdita opuntiae* (Hymenoptera: Andrenidae). *J. Kansas Entomol. Soc.* 58: 185–194.
- Cane, J.H., 1987. Estimation of bee size using intertegular span (Apoidea). *J. Kansas Entomol. Soc.* 60: 145–147.
- Cheverud, J.M., M.W. Dow and W. Leutenegger, 1985. The quantitative assessment of phylogenetic constraints in comparative analyses: sexual dimorphism in body weight among primates. *Evol.* 39: 1335–1351.
- Christman, M.C., R.W. Jernigan and D. Culver, 1997. A comparison of two models for estimating phylogenetic effect on trait variation. *Evol.* 51: 262–266.
- Cook, J.M., S.G. Compton, E.A. Herre and S.A. West, 1997. Alternative mating tactics and extreme male dimorphism in fig wasps. *Proc. Royal Soc. London Ser. B* 264: 747–754.
- Custer, C.P., 1928. The bee that works stone: *Perdita opuntiae* Cockerell. *Psyche* 35: 67–84.
- Danforth, B.N., 1991a. Female foraging and intranest behavior of a communal bee, *Perdita portalis* Timberlake (Hymenoptera: Andrenidae). *Ann. Entomol. Soc. Am.* 84: 537–548.
- Danforth, B.N., 1991b. The morphology and behavior of dimorphic males in *Perdita portalis* (Hymenoptera: Andrenidae). *Behav. Ecol. Sociobiol.* 29: 235–247.
- Danforth, B.N., 1996. Phylogenetic analysis and taxonomic revision of the *Perdita* subgenera *Macrotera*, *Macroteropsis*, *Macroterella*, and *Cockerellula* (Hymenoptera: Andrenidae). *Kansas Sci. Bull.* 55: 635–692.

- Danforth, B.N. and J.L. Neff, 1992. Male polymorphism and polyethism in *Perdita texana* (Hymenoptera: Andrenidae). *Ann. Entomol. Soc. Am.* 85: 616–626.
- Day, M.C., 1984. Male polymorphism in some Old World species of *Cryptocheilus* Panzer (Hymenoptera: Pompilidae). *Zool. J. Linn. Soc.* 79: 83–101.
- Emlen, D.J., 1994. Environmental control of horn length dimorphism in the beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). *Proc. Royal Soc. Lond., B* 256: 131–136.
- Emlen, D.J., 1996. Artificial selection on horn length-body size allometry in the horned beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). *Evol.* 50: 1219–1230.
- Emlen, D.J., 1997. Diet alters male horn allometry in the beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). *Proc. Royal Soc. Lond., B* 264: 567–574.
- Evans, H.E., 1963. A new species of *Cephalonomia* exhibiting an unusually complex polymorphism (Hymenoptera: Bethyilidae). *Psyche* 70: 151–163.
- Fortelius, W., P. Pamilo, R. Rosengren and L. Sundström, 1987. Male size dimorphism and alternative reproductive tactics in *Formica exsecta* ants (Hymenoptera, Formicidae). *Ann. Zoologici Fennici* 24: 45–54.
- Gould, S.J., 1966. Allometry and size in ontogeny and phylogeny. *Biol. Rev.* 41: 587–640.
- Grandi, G., 1930. Monografia del genero *Philotypesis* Forst. *Boll. Lab. Ent. R. Istituto Superiore Agrario Bologna* 3: 1–181.
- Grandi, G., 1959. The problems of “morphological adaptation” in insects. *Smith. Misc. Coll.* 137: 203–230.
- Gross, M.R., 1996. Alternative reproductive strategies and tactics: diversity within sexes. *Trends Ecol. Evol.* 11: 92–98.
- Hamilton, W.D., 1979. Wingless and fighting males in fig wasps and other insects. In: *Sexual Selection and Reproductive Competition in Insects* (M.S. Blum and N.A. Blum, Eds.), Academic Press, New York. pp. 167–220.
- Harvey, P.H. and M.D. Pagel, 1991. *The Comparative Method in Evolutionary Biology*. Oxford University Press, Oxford. pp. vii+239.
- Heinze, J. and B. Hölldobler, 1993. Fighting for a harem of queens: physiology of reproduction in *Cardiocondyla* male ants. *Proc. Natl. Acad. Sci.* 90: 8412–8414.
- Heinze, J., K. Kuehnholz, K. Schilder and B. Hölldobler, 1993. Behavior of ergatoid males in the ant *Cardiocondyla nuda*. *Insectes soc.* 40: 273–282.
- Heinze, J. and S. Trenkle, 1997. Male polymorphism and gynandromorphs in the ant *Cardiocondyla emeryi*. *Naturwissenschaften* 84: 129–131.
- Herre, E.A., S.A. West, J.M. Cook, S.G. Compton and F. Kjellberg, 1997. Fig wasps: pollinators and parasites, sex ratio adjustment and male polymorphism, population structure and its consequences. In: *The Evolution of Mating Systems in Insects and Arachnids* (J. Choe and B.J. Crespi, Eds.), Cambridge University Press, Cambridge. pp. 226–239.
- Hölldobler, B. and E.O. Wilson, 1990. *The Ants*. Harvard University Press, Cambridge. pp. 732.
- Houston, T.F., 1970. Discovery of an apparent male soldier caste in a nest of a halictine bee (Hymenoptera: Halictidae) with notes on the nest. *Aust. J. Zool.* 18: 345–351.
- Jeanne, R.L., C.A. Graf and B.S. Yandell, 1995. Non-size-based morphological castes in a social insect. *Naturwissenschaften* 82: 296–298.
- Jolicoeur, P., 1963 a. The multivariate generalization of the allometry equation. *Biometrics* 19: 497–499.
- Jolicoeur, P., 1963 b. The degree of general robustness in *Martes americana*. *Growth* 27: 1–27.
- Joseph, K.J., 1958. Recherches sur les chalcidiens *Blastophaga psenes* (L.) et *Philotrypesis caricae* (L.) du figuier *Ficus carica* (L.). *Ann. Sci. Nat.* 20: 197–260.
- Kearns, C.W., 1934. Method of wing inheritance in *Cephalonomia gallicola* Ashmead (Bethyilidae: Hymenoptera). *Ann. Entomol. Soc. Am.* 27: 533–541.
- Kempf, W.W., 1962. Retoques à classificação das formigas neotropicais do gênero *Heteroponera* Mayr (Hymenoptera: Formicidae). *Papéis Avulsos Dept. Zool. São Paulo* 15: 29–47.
- Kinomura, K. and K. Yamauchi, 1987. Fighting and mating behaviors of dimorphic males in the ant *Cardiocondyla wroughtonii*. *J. Ethol.* 5: 75–81.
- Knerer, G. and M. Schwarz, 1976. Halictine social evolution: the Australian enigma. *Science* 194: 445–448.
- Knerer, G. and M. Schwarz, 1978. Beobachtungen an Australischen Furchenbienen (Hymenoptera; Halictinae). *Zool. Anz.* 200: 321–333.
- Kühne, H. and G. Becker, 1974. Zur Biologie und Ökologie von *Scleroderma domesticum* Latreille (Bethyilidae, Hymenoptera), einem Parasiten holzzerstörender Insektenlarven. *Z. ang. Ent.* 76: 78–303.
- Kukuk, P.F. and M. Schwarz, 1987. Intranest behavior of the communal sweat bee *Lasioglossum (Chilalictus) erythrurum* (Hymenoptera: Halictidae). *J. Kansas Entomol. Soc.* 60: 58–64.
- Kukuk, P.F. and M. Schwartz, 1988. Macrocephalic male bees as functional reproductives and probable guards. *Pan-Pac. Entomol.* 64: 131–137.
- Kutter, H., 1957. Zur Kenntnis schweizerischer Coptoformicarten (Hym. Form.), 2. Mitteilung. *Mitt. Schweiz. Entomol. Ges.* 30: 1–24.
- LaBarbera, M., 1989. Analyzing body size as a factor in ecology and evolution. *Ann. Rev. Ecol. Syst.* 20: 97–117.
- Le Masne, G., 1956. La signification des reproducteurs aptères chez la fourmi *Ponera eduardi* Forel. *Insectes soc.* 3: 239–259.
- Lima, A. da Costa, 1944. Quarta contribuicao ao conhecimento da biologia do *Telenomus polymorphus* n. sp. (Hymenoptera: Scelio-nidae). *Anais Acad. Brasileira Ciencias* 15: 211–227.
- Maddison, W.P. and D.R. Maddison, 1992. MacClade version 3: *Analysis of Phylogeny and Character Evolution*. Sinauer, Sunderland, Mass. xi+398.
- Murray, M.G., 1987. The closed environment of the fig receptacle and its influence on male conflict in the Old World fig wasp, *Philotrypesis pilosa*. *Anim. Behav.* 35: 488–506.
- Neff, J.L. and B.N. Danforth, 1992. The nesting and foraging behavior of *Perdita texana* (Cresson) (Hymenoptera: Andrenidae). *J. Kansas Entomol. Soc.* 64: 394–405.
- Nijhout, H.F., 1994. *Insect Hormones*. Princeton University Press, Princeton, NJ. xi+267.
- Nijhout, H.F. and D.E. Wheeler, 1982. Juvenile Hormone and the physiological basis of insect polymorphisms. *Quart. Rev. Biol.* 57: 109–133.
- Pamilo, P. and R. Rosengren, 1983. Evolution of nesting strategies of ants: genetic evidence from different population types of *Formica* ants. *Biol. J. Linn. Soc.* 21: 331–348.
- Ramirez, W.B. and P.M. Marsh, 1996. A review of the genus *Psenobolus* (Hymenoptera: Braconidae) from Costa Rica, an inquiline fig wasp with brachypterous males, with descriptions of two new species. *J. Hym. Res.* 5: 64–72.
- Rozen, J.G. 1970. Department of Entomology Report 102. *Ann. Rept. Am. Mus. Nat. History* 102: 4–5.
- Salt, G., 1937. The egg parasite of *Sialis lutaria*: a study of the influence of the host upon a dimorphic parasite. *Parasitology* 29: 539–553.
- Salt, G., 1952. Trimorphism in the ichneumonid parasite *Gelis corruptor*. *Quart. Journ. Microscr. Sci.* 93: 453–474.
- Schmieder, R.G., 1933. The polymorphic forms of *Melittobia chalybii* Ashmead and the determining factors involved in their production (Hymenoptera: Chalcidoidea, Eulophidae). *Biol. Bull.* 65: 338–354.
- Shea, B.T., 1985. Bivariate and multivariate growth allometry: statistical and biological considerations. *J. Zool., Series A* 206: 367–390.
- Stuart, R.J., A. Francoeur and R. Loiselle, 1987a. Fighting males in the ant genus *Cardiocondyla*. In: *Chemistry and Biology of Social Insects (Proceedings of the Tenth International Congress of the International Union for the Study of Social Insects, Munich, 1986)* (J. Eder and H. Rembold, Eds.), Peperny, Munich. pp. 551–552.

- Stuart, R.J., A. Francoeur and R. Loiselle, 1987b. Lethal fighting among dimorphic males of the ant, *Cardiocondyla wroughtonii*. *Naturwissenschaften* 74: 548–549.
- Thornhill, R. and J. Alcock, 1983. *The Evolution of Insect Mating Systems*. Harvard University Press, Cambridge, Mass. ix+547.
- Travis, J., 1994. Evaluating the adaptive role of morphological plasticity. In: *Ecological Morphology* (P.C. Wainwright and S.M. Reilly, Eds.), University of Chicago Press, Chicago. pp. 99–122.
- Tsuji, N., K. Yamauchi and N. Yamamura, 1994. A mathematical model for wing dimorphism in male *Cardiocondyla* ants. *J. Ethol.* 12: 19–24.
- Visscher, P.K. and B.N. Danforth, 1997. Biology of *Calliopsis pugionis* (Hymenoptera: Andrenidae): nesting, foraging, and investment sex ratio. *Ann. Entomol. Soc. Am.* 86: 822–832.
- Walker, K., 1996. Revision of the Australian native bee subgenus *Lasioglossum* (*Chilalictus*) (Hymenoptera: Halictidae). *Mem. Mus. Victoria* 55: 1–423.
- West-Eberhard, M.J., 1989. Phenotypic plasticity and the origins of diversity. *Ann. Rev. Ecol. Syst.* 20: 249–278.
- Wheeler, W.M., 1937. *Mosaics and Other Anomalies Among Ants*. Harvard University Press, Cambridge, Mass. pp. iii+95.
- Wheeler, D.E., 1991. The developmental basis of worker caste polymorphism in ants. *Amer. Nat.* 138: 1218–1238.
- Wheeler, D.E. and H.F. Nijhout, 1984. Soldier determination in the ant *Pheidole bicarinata*: inhibition of adult soldiers. *J. Insect Physiol.* 30: 127–135.
- Wilson, E.O., 1953. The origin and evolution of polymorphism in ants. *Quart. Rev. Biol.* 28: 136–156.
- Yamauchi, K. and N. Kawase, 1992. Pheromonal manipulation of workers by a fighting male to kill his rival males in the ant *Cardiocondyla wroughtonii*. *Naturwissenschaften* 79: 274–276.