A comparative analysis of sex ratio investment parameters in ants

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Summary

1. Accurate estimates of female-to-male cost ratios are essential for testing theories about kin selection and worker control over sexual investments in ants. However, obtaining such estimates has proved to be notoriously difficult.

2. Comparative data on dry weight, energy content and respiration in ant sexuals were analysed across species, to explore biases following from the use of different female-to-male cost ratios.

3. Two groups of ants, those with claustral and independent colony foundation (without the help of workers; usually species with single-queen colonies) and those with non-claustral, dependent colony foundation (with the help of workers; generally species with multiple-queen colonies), showed consistent differences in weight and energetic cost ratios, with only a relatively small range of overlap.

4. The fat accumulation in females, relative to males, during maturation was a clear power function of sexual weight dimorphism when analysed across all ant species, but more like a constant fraction when ant species with independent and dependent colony founding were analysed separately.

5. Female-to-male respiration ratios were always lower than female-to-male dry weight ratios. The adult respiration ratio was a power function of adult sexual weight dimorphism but the pupal respiration ratio was found to be a constant fraction of the pupal dry weight ratio across ant species of both categories.

6. The across-species trends confirmed earlier species-specific findings. Cost ratios expressed as adult female-to-male dry weight ratios underestimate the relative energy content but overestimate the cost of respiration of females, relative to males.

7. A complete female-to-male cost ratio could be obtained for the Argentine ant, *Iridomyrmex humilis,* and a similar estimate was available for *Lasius niger* from a previous study. These estimates plus the less complete data for three other ant species agreed reasonably well with an earlier proposed 0·7 power-conversion factor, both for ants with independent and dependent colony founding.

Key-words: Colony foundation, energy content, respiration, sex allocation

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Introduction

The estimation of sex allocation in eusocial insects with progressive provisioning of offspring is problematic. In particular, the study of sex allocation in ants has suffered with difficulties in the proper estimation of investment by workers in the female and male sexuals (Trivers & Hare 1976; Nonacs 1986; Boomsma 1987; Crozier & Pamilo 1992). Using dry weight of mature gynes (prospective queens) and males (e.g. Trivers & Hare 1976) tends to result in underestimation of the relative investment in males (Boomsma 1989) and this

bias increases when energetic content is used instead of dry weight (Boomsma & Isaaks 1985; Crozier & Pamilo 1992). The major reason for such bias is that dry-weight and energy-content measures fail to take into account the costs of respiration during development from egg to maturity. These costs are higher for males than for females, and increasingly so with greater sexual dimorphism in body size. Based on data for the ant *Lasius niger,* and on general trends in the comparative data set used by Nonacs (1986), Boomsma (1989) hypothesized that in across-species comparisons such bias could be approximately cor-

rected by raising the female-to-male dry weight ratio to the 0·7 power. This assumes perfect proportionality between sexual size dimorphism on one hand and the factors affecting the female-to-male cost ratio, such as fat content and respiration rate, on the other hand. In another comparative study, Keller & Passera (1989) showed that the relative fat content of mature gynes is significantly higher for ant species with independent colony foundation (where queens depend only on their own body reserves until the first batch of off-spring-workers hatches) than for species with dependent colony foundation, where gynes start new colonies with the help of workers from existing colonies. Such differences are also associated with species-specific social organization, as independent colony foundation usually leads to monogynous (single-queen) colonies, whereas dependent colony foundation is typical for species with polygynous (multiple-queen) colonies (Keller 1991). These data, and the variable costs of respiration in three species of *Pogonomyrmex* ants (MacKay 1985), led to the statement by Crozier & Pamilo (1992) that 'considerable caution should be exercised in using such conversions'. A recent review by Helms (1994) further showed that the 0·7 power conversion cannot be unequivocally used in bees and wasps.

While in agreement with a general note of caution, it is also clear that we should distinguish between the use of conversions in across-species comparisons (e.g. Boomsma 1989; Pamilo 1990) and in single-species analyses. For across-species comparisons, it is important to have an investment parameter, which on average is unbiased. Thus, if the parameter used is not fully accurate, the cases for which it produces under-estimations should be balanced by opposite cases, where it produces overestimations. Here we end up with an unbiased estimate of the mean sex allocation across species, whereas the error variance around this estimate may only be of secondary concern. Such overall error variance becomes a problem, however, when we want to apply the general investment parameters to individual species. In such cases it is essential to have at least an approximate idea of the accuracy of a conversion before interpreting the data that result from its application. In a first attempt to quantify both mean trends and accuracy of investment parameters, this paper presents a quantitative analysis of the currently available data on sex-specific fat content, energy content and respiration in ants. The results are discussed with specific reference to inferences based on the 0·7 power conversion.

Materials and methods

Sources for the comparative data used in this study comprised our own data sets on dry weight, energy content and respiration in various ant species and similar data by others from the literature. The final column in the Appendix indicates which of these data

were partly or fully published before, and which are new. New data on fat contents mostly refer to males, sampled from populations where fat contents of gynes were analysed and published before (Keller & Passera 1989; Passera & Keller 1990). With regard to data on sex-specific respiration, a few references (Kneitz 1967; Schmidt 1968; Boomsma & Isaaks 1985, larval data) measured fresh weights instead of dry weights. As adult gyne-to-male fresh-weight ratios are consistently more male biased than similar dry-weight ratios (Nielsen, Skyberg & Peakin 1985a; Boomsma 1989; Crozier & Pamilo 1992), these data were either excluded from the analyses or combined with dry-weight data from other sources before analysis. Some other literature records on respiration (see Nielsen, Skyberg & Peakin 1985b for a review; Keller & Ross 1993) had to be excluded because data for males were lacking. In some cases (Schmidt 1968; Peakin, Nielsen & Skyberg 1989) data had to be inferred from a figure. Details about collection methods and laboratory techniques are given in the source papers listed in the Appendix. New respiration data were obtained for *Tetramorium caespitum* and *Iridomyrmex humilis* by using the micro-Wartburg technique described in Nielsen *et al.* (1985a) and Peakin *et al.* (1985). Only overall means of these new data are given here. Further details will be published elsewhere. The female and male ants for these analyses were collected at Mols, Denmark (*T. caespitum*), and Port Leucate, France (*I. humilis*).

Energy contents were estimated mostly from percentages of fat, assuming 1 mg fat to be equivalent to 39·3 J and 1 mg other tissue (proteins and carbohydrates) to be equivalent to 18·8 J (cf. Peakin 1972; also used in Keller & Passera 1989). For two *Lasius* and three *Pogonomyrmex* species both indirect and direct (calorimetric) estimates of energy-content ratios were available (Appendix), allowing a comparison of the two procedures. When we compared the direct estimates with the indirect ones, they were found to be equivalent (both expressed as functions of female-to-male dry weight, as described below, and tested for difference between adjusted means: ANCOVA, $F_{1,7} = 0.29$, NS). Hence the literature-derived conversions of 18·8 J mg^{-1} for protein/carbohydrates and 39·3 J mg^{-1} for fat are good approximations for ants.

Female-to-male ratios for fat content, energy and respiration were analysed for systematic biases using the average female-to-male dry-weight ratio as the independent variable. Two types of dry-weight ratios are used (see Appendix): ADWM is the maximal dry-weight ratio, which is found among sexuals in nuptial flight condition. This ratio was used for comparisons with fat content ratios, which are normally taken from mature sexuals. The other dry weight ratio (ADW) is based on a random sample of mature and immature sexuals. Most of the samples used in earlier analyses of comparative sex ratio data (Trivers & Hare 1976; Nonacs 1986; Boomsma 1989) were of this type and

the means for respiration rates used here refer to similar mixtures of mature and immature sexuals.

Trends are described by regression lines after taking the logarithms of both the dependent and the independent variable. Transformation is needed as female-to-male sex ratio data are always skewed to the right. Taking logarithms of such ratios not only produces normal distributions (Boomsma 1989) but also allows easily interpretable plots to be made (compared to the alternative of normalizing sex ratios by expressing them as arcsine transformed proportions). Using regression analysis to quantify slopes assumes that the error variance in the independent variable is small compared to the residual variance in the dependent variable. An earlier study showed that the error variance component in the across-species dry-weight ratio was only $c. 5\%$ (Boomsma 1989). Throughout our analyses we followed Keller & Passera (1989) and distinguished between species with independent and dependent colony foundation, respectively.

As some genera (e.g. *Lasius*) are overrepresented in the data set, it can be argued that regressions on the species level might be biased because of unequal phylogenetic relationships between the data points (Grafen 1989; Harvey & Pagel 1991). Therefore, analyses were repeated at the 'means per genus' level. As the latter results were very similar to the former, and because the proportion of total variance explained was usually very high, we refrained from further corrections for phylogenetic confounding.

Results

WEIGHT AND ENERGY CONTENT OF MATURE FEMALES AND MALES

Female-to-male energy ratios, as derived from fat contents, are plotted against specific dry-weight ratios in Fig. 1. The slope of the regression line in Fig. 1a (1·10) is significantly >1 ($t = 4.40$, $P < 0.001$), with 99·2% of the total variance in the energy ratio being explained. This indicates that there is a clear overall trend for energy-content ratios to increase more than proportionally with increasing sexual weight dimorphism at maturity (ADWM). Hence dry-weight estimates increasingly underestimate the energy-content ratio with increasing sexual size dimorphism across ants in nuptial flight condition. The intercept of this line (1·12) is also significantly >1 ($t = 2.93$, $P < 0.01$). When the regression is calculated from the geometric means per genus (keeping two separate means for those genera that have both claustral and non-claustral species), the slope (1·105; $t = 2.24$; $P < 0.05$) and intercept (1·128) remain virtually the same but the latter is no longer significant ($t = 1.82$, $P = 0.1$, $r^2 = 0.982$).

Claustral species have a much higher overall degree of sexual-weight dimorphism at maturity than non-claustral species. There is only a limited range of overlap between the two groups of species around
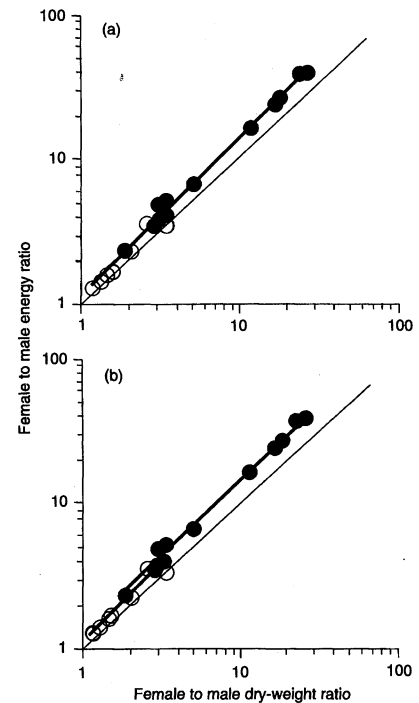

Fig. 1. Energy content ratio of females (gynes) and males in 20 ant species, 12 of which have claustral colony foundation (black dots) and eight of which have non-claustral colony foundation (open dots) (see Appendix for data). (a) The regression line fitted to the entire data set: $y = 1.120x^{1.100}$ ($r^2 = 0.997$). (b) The regressions for the claustral: $y = 1.235x^{1.064}$ ($r^2 = 0.997$) and non-claustral: $y = 1.117x^{1.033}$ ($r^2 = 0.889$) species, separately.

sexual-weight dimorphisms of 2–4. When the two categories of species are analysed separately (Fig. 1b), the slopes of the regression lines (1·06 and 1·03) are less significant or not significantly different from 1 ($t = 2.28$, $P < 0.05$ and $t = 0.32$, NS, for claustral and non-claustral species, respectively). The y-intercepts of the regression for claustral species (1·23) is significantly >1 ($t = 3.59$, $P < 0.01$) but the y-intercept for non-claustral species (1·12) is not ($t = 1.56$, $P > 0.1$). The percentages of variance in energy ratios explained by dry-weight ratios were 99·3% and 88·9%, respectively. When these regressions were calculated from the geometric means per genus, the slopes further decreased to 1·03 and 1·01, and the intercepts increased to 1·34 ($t = 2.69$, $P < 0.1$) and 1·14 ($t = 1.19$, NS) for claustral and non-claustral ant species, respectively. These results imply that for non-claustral species in nuptial flight condition the energy-content ratio is only marginally higher than the dry-weight ratio. For claustral species, however, the energy content ratio of sexually mature individuals appears to be 1·3–1·5 times as high as the dry-weight ratio and seems also largely (but not fully) independent of the specific degree of sexual-weight dimorphism (Fig. 1b; see also Discussion). The significantly positive y-intercept indicates that females have higher energy contents than males even if the sexes are equal in weight.

Female-to-male respiration ratios showed a pattern opposite to that found for energy-content ratios. Adult respiration ratios were analysed against the average female-to-male dry-weight ratio (ADW), such that the across-species trends represent the average cost of respiration during the adult maturation phase (Fig. 2a). Female-to-male respiration ratios for pupae and larvae were compared with the average pupal (PDW) and larval (LDW) dry-weight ratios (Fig. 2b). For claustral ants the adult respiration ratio clearly increases less than proportionally with increasing sexual-weight dimorphism (Fig. 2a). The slope of the regression line describing the overall trend across six species is 0·724. The difference from a slope of 1 is only marginally significant ($t=2\cdot16$, $P<0\cdot1$) but the regression explains 89% of the total variance in across-species respiration ratios. The intercept is 0·717 ($t=1\cdot47$, NS). When we calculated the regression from the geometric means of the three genera involved, the slope remained unchanged (0·717,
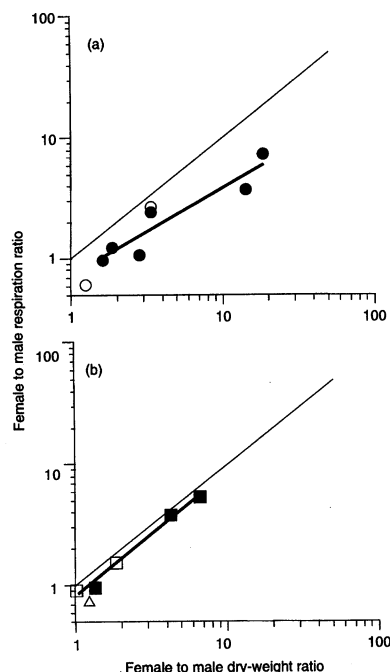

Fig. 2. (a) Respiration ratios of an average adult female and male for six ant species with claustral colony foundation (black dots) and two non-claustral species (open dots). Temperatures at which respiration rates were recorded are supposed to be a reasonable approximation of the average ambient temperatures experienced by these ant sexuals (20 °C for *Lasius* and *Tetramorium*, 25°C (average between the records for 20°C and 30 °C) for *Iridomyrmex humilis* and *Formica polyctena*, and 30 °C for *Pogonomyrmex* harvester ants). The fitted regression line applies to the data for claustral ants: $y=0\cdot717x^{0\cdot724}$ ($r^2=0\cdot889$). (b) Respiration ratios for pupae of three claustral (black squares) and two non-claustral species (open squares) plotted against pupal weight dimorphism. The larval respiration ratio for *Iridomyrmex humilis* (open triangle) is plotted against larval dry weight dimorphism. The plotted regression line refers to all pupal data: $y=0\cdot849x^{1\cdot014}$ ($r^2=0\cdot994$).

$r^2=0\cdot998$, intercept 0·715). As before, the difference between this slope and a slope of 1 is marginally significant ($t=8\cdot17$, $P\ll0\cdot1$). The two data points for non-claustral ants in Fig. 2a are somewhat more scattered. As the dry-weight ratio of the lowest point (*Formica polyctena*) was only available as ADWM estimate (see Appendix), the negative residual of this species could be somewhat inaccurate. The other point (*I. humilis*) is closer to the diagonal than any of the claustral ant species. Overall, however, these two data points seem to fit at least approximately to the pattern for claustral ant species. When these data points are included in the analysis, the regression (slope 0·769, intercept 0·688) explains 86·6% of the variation. Thus, as far as the cost of respiration is concerned, female-to-male cost ratios of adult ant sexuals tend to be generally underestimated when dry-weight ratios are applied, and this bias increases with increasing sexual-weight dimorphism.

The limited data available on respiration rates in immature developmental stages (Fig. 2b) indicate that pupal respiration ratios match their respective pupal dry-weight ratios much better than adult respiration ratios. Data are too limited to clarify any differences between claustral and non-claustral species. For all five species together, neither the slope of pupal respiration (1·01) nor the intercept (0·849) are significantly different from 1 ($t=0\cdot21$) and 0 ($t=2\cdot16$), respectively. The developmental pattern (cf. Appendix and Fig. 2a and 2b) in the three claustral species, *L. niger*, *Lasius flavus* and *T. caespitum* is very similar. Between eclosion and nuptial flight the female-to-male dry-weight ratio increases, whereas the respiration ratio remains virtually unchanged. The pattern in non-claustral ants is again more variable. In one species, *F. polyctena*, the adult female-to-male respiration ratio is much lower than the pupal respiration ratio, even though the sexual dimorphism increases. In the other species, *I. humilis*, the dry-weight ratio and respiration ratio increase almost proportionally, the latter increase being only slightly less than the former. The larval respiration ratio in *I. humilis* is, however, substantially lower than the larval dry-weight ratio (Fig. 2b).

Discussion

THE ACCURACY OF THE OVERALL TRENDS

The trends emerging from Figs 1 and 2 confirm several findings of earlier studies (Boomsma & Isaaks 1985; Nielsen *et al.* 1985a; Boomsma 1989; Keller & Passera 1989; Passera & Keller 1990), but also allow more general quantitative statements about the biases in different estimation procedures of sexual investment by ant workers. Dispersing gynes (prospective queens) of claustral ant species were known to be heavier and to have a higher fat/dry-weight ratio than gynes in non-claustral species (Keller & Passera 1989). The present data show that, in contrast to

gynes, males of claustral and non-claustral species have similar relative fat contents (Appendix). This results in female-to-male energy ratios being greater in claustral species as compared to non-claustral species (Fig. 1b). Considering all the ant species analysed (Fig. 1a), the relative accumulation of fat in queens increases with sexual-weight dimorphism but there is hardly any or no such increase when the claustral and non-claustral ants are kept separate (Fig. 1b). The slightly positive slope in claustral ants (1·06) may have been partly owing to the three lowest data points (*Pogonomyrmex* sexuals) being not fully comparable with the other data. These sexuals were not exclusively collected in the mature stage (i.e. directly before nuptial flight, MacKay 1985), such that the queens might not yet have completed the accumulation of fat reserves. Overall, the position of the lines in Fig. 1b indicates that the final, adult female-to-male energy-content ratio of claustral ant species is overestimated by about 40% when dry-weight ratios of adults in nuptial flight condition are used, whereas this overestimation is only *c.* 15% on average for non-claustral ant species.

A problem in evaluating the costs of respiration is that the data of the six species in Fig. 2 represent only very limited samples of the total developmental time of female and male sexuals. As shown by Nielsen *et al.* (1985a,b), respiration of queens is highly variable between eclosion and nuptial flight and the possibility remains that the averages for adults used in this review are rather inaccurate estimates of the overall mean. Another problem is that intermediate degrees of female-to-male sexual dimorphism (5–10) are not represented in the data set for adult sexuals, and that the fitted linear slope of Fig. 2a may prove to be an oversimplification when more data become available. Pupal respiration rates are less variable intraspecifically (Peakin *et al.* 1989) and are less biased towards males than adult respiration rates (Fig. 2b). However, all data on immature stages point in the same direction: specific respiration rates (μl O_2 mg^{-1} h^{-1}) in female pupae are always lower than in male pupae. Expressed as ratios, this difference amounts to about 0·97 for *F. polyctena,* 0·91 for *I. humilis* and *L. niger,* 0·85 for *L. flavus* and 0·74 for *T. caespitum* (Appendix). Sex-specific larval respiration rates per mg dry weight were only available for *I. humilis* and were even more biased towards males than pupal respiration ratios (Fig. 2b). Two other data sets on respiration ratios of immature stages seem to show the same trends but were not plotted in Fig. 2b as only data on fresh weight were available. In *F. polyctena,* prepupal respiration ratios are more male biased than pupal respiration ratios and in *L. niger,* larval respiration ratios are more male biased than pupal respiration ratios (Appendix). As discussed earlier by Boomsma (1989), female-to-male investment ratios based on adult fresh weight tend to produce less biased estimates than those based on dry weights. This is owing

to the fact that males have higher water contents than females (Boomsma & Isaaks 1985; Nielsen *et al.* 1985a; Crozier & Pamilo 1992), such that one bias partly compensates the other. However, as adding biases in opposite directions makes it more complicated to quantify total errors, the use of fresh-weight data cannot be recommended as a general solution for the study of sex allocation in ants.

Sex-specific respiration ratios thus show a trend opposite to the one observed for energy-content ratios: when female-to-male weight ratios increase, the sex-specific respiration ratio does not increase proportionally. As stated before, this is partly owing to the fact that the fat reserves in queens are metabolically inactive. This may explain the relatively unbiased adult respiration ratio in *I. humilis* but it cannot explain the biased adult respiration ratio in *F. polyctena,* unless the inferred female-to-male dry-weight ratio in this species was an overestimation (Appendix). However, there is also a direct effect of body size itself, such that large animals use on average less energy per unit weight for maintenance than small animals do. This issue is discussed in more detail by Peters (1983) and Keller & Passera (1989). The fact that the intercept in Fig. 2a is <1 could possibly be owing to the fact that adult males are generally more mobile and locomotory active than adult gynes in the period between eclosion and nuptial flight (J. J. Boomsma, personal observations).

The possible lack of accuracy in the estimates of the cost of respiration is not the result of the measurements themselves but owing to the fact that all costs have to be inferred by extrapolating laboratory data to field situations. Even if our estimates of the mean costs of respiration in the different developmental stages were fully accurate, we would still have only approximate ideas about the duration of the different stages, the appropriate individual activity and the relevant nest temperatures, and this would particularly affect the estimates for the mobile adult sexuals with their varying (in case of gynes) fat contents. Estimates for immature stages can, however, be rather accurate. The total energy expenditure of pupae of *I. humilis* as estimated from respiration rates, appeared to be in good agreement with the energy loss of tissue during the pupal stage (Table 1, see also section below).

HOW USEFUL IS THE 0·7 POWER CONVERSION OF DRY-WEIGHT RATIOS?

Evaluating the agreement of the present results with the general 0·7 power conversion proposed by Boomsma (1989) is a complicated matter. The data plotted in Figs 1 and 2 compare estimates of sex-specific rates of energy expenditure during different phases of development. Within-phase variability of these rates and a general lack of knowledge with regards to the duration and nest-temperatures of these phases, make it hard to arrive at precise inferences of

Table 1. Components of energy investment in an average gyne and male of the ant *Iridomyrmex humilis* at an ambient temperature of 25 °C. Total energy investment in the sexes was calculated as the sum of five (method 1) or four (method 2) different components. See text for details

	Development time (h)[1]	$\mu l\ O_2\ ind^{-1}\ h^{-1}$ [2]	$J\ \mu l^{-1}\ O_2$ [3]	Total energy (J)	
				Method 1	Method 2
Female (gyne)					
Full grown larva[4]				–	28·93
Callow[4]				14·45	–
Assimilation after eclosion[4,5]				11·45	11·45
Adult respiration	60	3·415	0·0201	4·12	4·12
Pupal respiration	600	1·100	0·0201	13·27	–
Larval respiration	624	0·46	0·0201	5·77	5·77
Total				49·05	50·27
Male					
Full grown larva[4]				–	14·54
Callow[4]				8·68	–
Assimilation after eclosion[4,5]				–	–
Adult respiration	60	1·270	0·0201	1·53	1·53
Pupal respiration	528	0·635	0·0201	6·74	–
Larval respiration	624	0·720	0·0201	9·03	9·03
Total				25·98	25·10

[1] Data from Benois (1973).
[2] See Appendix.
[3] Oxycaloric equivalent used earlier by Peakin (1972) and Boomsma & Isaaks (1985).
[4] From Table 1 in Passera & Keller (1987).
[5] Energy content at the time of mating minus the energy content of a callow.

the cumulative energy investments. On the other hand, the 0·7 power-conversion factor is itself an inference. It removes a positive correlation between the dry-weight sex investment ratio and sexual dimorphism across mostly monogynous ants, which otherwise could not be explained (Boomsma 1989). However, this conversion had no primary background in empirical data on energy expenditure, except that it fitted reasonably well to estimates for the ant *L. niger*, for which total energy investment in sexuals had been estimated (Boomsma & Isaaks 1985).

Our evaluation of the 0·7 power-conversion factor will be on two levels. First, we will use the rather complete data set on the non-claustral ant *I. humilis*, to derive a similar cumulative female-to-male energy investment ratio as was calculated earlier for the claustral ant species *L. niger* (Boomsma & Isaaks 1985). Second, we will graphically compare the different rates of sex-specific energy expenditure across species with the adult female-to-male dry weight ratio (ADW), which has been hypothesized to require the 0·7 power conversion to become unbiased.

Our data set for *I. humilis* contains both estimates on dry weight and adult energy content (Passera & Keller 1987) and data on sex-specific respiration rates in all three developmental stages (Appendix). When combined with data on specific developmental times (Benois 1973), these figures allow an estimate of the cumulative energy investment in individuals of both sexes throughout development. Investment is assumed to end when adults mate. Total energy

investment in an average gyne consists of the energy content of a callow adult, plus the extra energy assimilated between eclosion and nuptial flight, plus the energy used for respiration in the larval, pupal and adult stage until mating (method 1). Alternatively, one can start by taking the energy content of a full grown larva and omit the pupal respiration component, as the loss of energy in the pupal stage should be equivalent to the estimated cost of respiration during that stage (method 2). The energy investment in an average male contains the same components, except that there is no weight or energy increase after eclosion (Passera & Keller 1987), as is true for other ants as well (Peakin 1972; Boomsma & Isaaks 1985). The results of these calculations are given in Table 1.

Depending on what estimate for pupal respiration is used, the cumulative female-to-male energetic cost ratio for *I. humilis* comes out at 2·00 or 1·89 (1·94 on average). These estimates are much lower than the figures of 3·39 and 2·59 obtained for the dry-weight ratios ADW and ADWM, respectively. As it turns out, 1·94 is equivalent to $ADW^{0·54}$ and to $ADWM^{0·70}$, indicating that the hypothesized 0·7 power conversion is either correct or still too moderate for the non-claustral ant species *I. humilis*. An earlier study by Boomsma & Isaaks (1985) has produced a similar difference for the claustral ant *L. niger*. In this species, the cumulative energetic cost ratio was estimated to be 7·66, which is equivalent to $ADWM^{0·72}$ and to $ADW^{0·77}$ (Appendix). These values are at least not at variance with the overall 0·7 power conversion nor do

they suggest that fundamentally different corrections should apply to ant species with different degrees of sexual dimorphism and different modes of colony founding.

For three other ant species, *L. flavus, T. caespitum* (both claustral) and *F. polyctena* (non-claustral), available data on energy allocation are also rather good, but not complete enough to allow the estimation of cumulative energetic cost ratios, as developmental times and larval respiration are lacking. However, when we plot the known components of energy expenditure against adult dry-weight sexual dimorphism (ADW, the parameter mostly used to approximate cost ratios), we can evaluate to what extent patterns of bias are equal or different from those observed in the two species, *L. niger* and *I. humilis*, for which complete estimates are available. Such a plot is given in Fig. 3.

The main differences between Fig. 3 and Fig. 1 is that energy-content ratios are now plotted against average dry-weight (ADW) ratios instead of mature dry-weight (ADWM) ratios. Apparently, this has more effect at low sexual dimorphism (*Tetramorium*) than at high sexual dimorphism (*Lasius*), making the slope for claustral ants (0·85) <1. A similar trend seems to occur in the two non-claustral species of Fig. 3. The main difference between Fig. 3 and Fig. 2 is that respiration ratios for pupae and larvae are now plotted against the adult dry-weight (ADW) ratio, instead of their own (PDW) or (LDW) ratio as in Fig. 2b. Note, however, that this is precisely what one does, when using ADW as an estimate for the total female-to-male cost ratio when it is assumed that ADW is pro-
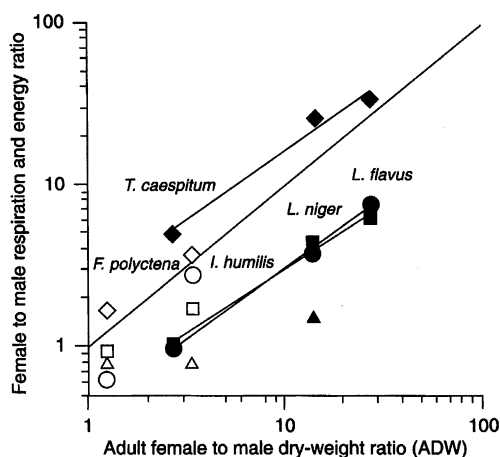
portional to some kind of weighted average of all different components of energy allocation towards the sexes. Plotting pupal respiration rates as in Fig. 3 produces a slope (0·78) <1 and not unlike the one found for adult respiration ratios (0·85 in Fig. 3 and 0·72 in Fig. 2a). As larvae of claustral and non-claustral species are unlikely to be very different, one could consider pooling these data. This would produce a slope of 0·32 and an intercept of 0·61 for larval respiration ratios in Fig. 3, corroborating the impression that overall weighted means of ratios of stage-specific investment will be considerably below the diagonal in Fig. 3.

Given the fact that we know that *L. niger* and *I. humilis* fit the overall 0·7 power conversion reasonably well, the pattern of Fig. 3 suggests that similar conclusions are likely to apply to other ant species as well. For female-to-male respiration ratios, there is no indication that the overall trend in Fig. 3 is different for claustral and non-claustral species. The only exception to this may be the adult respiration ratio in *I. humilis*, which is much closer to the diagonal than the other adult respiration ratios. A possible explanation for this could be that gynes of *I. humilis* are less energy constrained than gynes of most other ants. They mate in the nest without dispersing and can start to lay diploid eggs almost immediately after mating (Passera & Keller 1987). Continuously high metabolic rates and high fertility may thus be an advantage for queens in such species. The claustral ant species in Fig. 3 have a mating flight and a process of colony founding which is much more stressful and energy demanding. In such species, a relatively low initial oviposition rate is sufficient and a reduced metabolic rate may thus be an energy-saving adaptation during colony foundation. In this respect, a non-claustral species like *F. polyctena* could well be more similar to claustral ant species than to *I. humilis*, as *Formica* gynes generally disperse by flight at the time of mating. Many such queens have to seek adoption in a different colony from their natal one, which may also involve a stressful period where low metabolic rates are optimal.

The fact that gyne respiration rates may be higher in some ant species with dependent colony founding does not necessarily make gynes of such species more costly to produce, as the smaller increase in weight and fat content with dependent colony founding is associated with a shorter maturation period after eclosion. The average maturation period for gynes in species with dependent colony founding has been estimated to be 2–4 days, whereas a similar estimate for species with independent colony founding came out at 10 days (Passera & Keller 1992). In fact, the total relative weight increase of gynes in species with dependent colony founding is equivalent to about 25% of the relative weight increase of similar species with independent colony founding (L. Passera and L. Keller, unpublished data). This results not only in a smaller specific energy content of gynes in dependently founding species (Fig. 1) but also in a relative

Fig. 3. For five ant species for which relatively complete data were available, the various energy content ratios (diamonds) and respiration ratios (circles for adults, squares for pupae, triangles for larvae) are plotted against the adult dry weight (ADW) ratio, the parameter that is often used to represent all of these components of energy investment. Black symbols refer to claustral ant species, open symbols to non-claustral species. Regression lines were drawn for the claustral ant data only. Energy content ratios: $y = 2 \cdot 219 x^{0 \cdot 847}$ ($r^2 = 0 \cdot 947$). Adult respiration ratios: $y = 0 \cdot 416 x^{0 \cdot 848}$ ($r^2 = 0 \cdot 997$). Pupal respiration ratios: $y = 0 \cdot 479 x^{0 \cdot 782}$ ($r^2 = 0 \cdot 974$).

reduction of the cost of adult respiration, as fewer days are required to complete maturation.

The following hypothetical example may serve to illustrate the balancing effect of these two factors. Because data on energy content and respiration are available for all stages in the monogynous, claustral ant species *L. niger* (Boomsma & Isaaks 1985), it is possible to calculate the cost of producing a gyne that would stop its development at a quarter of the normal maturation process. Mature *L. niger* gynes normally reach an average dry weight of 15·45 mg, representing a cumulative energy investment of 689 J. Males at the time of nuptial flight have a dry weight of 0·93 mg, representing a cumulative investment of 90 J (Boomsma & Isaaks 1985). The cost of producing a gyne of a hypothetical *L. niger* species with dependent colony founding can be obtained by adding a quarter of the energy required for maturation (107·5 J) to the total energy required to produce a callow (259·3 J), which gives 366·8 J. Similarly, the dry weight of such a hypothetical queen can be obtained by adding a quarter of the dry-weight increase after eclosion (2·86 mg) to the weight of an average callow gyne (4 mg), giving 6·86 mg (see Boomsma & Isaaks 1985). In this example, the female-to-male dry-weight ratio for the hypothetical *L. niger* with dependent colony founding would be 7·38 and the female-to-male energetic cost ratio would be 4·08. The power conversion required to transfer this dry-weight ratio into the energetic cost ratio is almost exactly 0·7.

Overall, therefore, it seems that for ants the 0·7 power conversion produces estimates of female-to-male cost ratios which are on average similar to what the most detailed empirical studies on total energy expenditure can produce. Although the possibility exists that the empirical estimates and the 0·7 power conversion are both affected by another unknown biasing factor, the results of case studies so far suggest that the 0·7 power conversion is reasonably accurate as an average across species. As a consequence, overall means of sex allocation calculated after applying this conversion (Boomsma 1989; Pamilo 1990) are more likely to be correct than similar estimates based on uncorrected ADW cost ratios. However, the considerable scatter of adult respiration ratios (Fig. 2) and development times (e.g. Passera & Keller 1992), may still induce considerable errors when the 0·7 power conversion is applied in specific case studies (up to 20% in the case studies on *L. niger* and *I. humilis*). We agree, therefore, with Crozier & Pamilo (1992) that an uncritical use of this conversion is unwarranted and recommend that future studies on population-level sex allocation both give the uncorrected ADW sex-investment ratio and the 0·7 power-converted one. By doing so, it remains possible to evaluate to what extent the agreement (or lack thereof) of empirical results and theoretical expectations depends on possible errors in the estimation of the female-to-male cost ratio.

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Appendix.

Female(gyne)-to-male ratios of dry weight, energy content and respiration for ant species with claustral (c) and non-claustral (n) colony foundation. Adult dry-weight ratios (mg) are either based on maximal (mature) queen weight, around the time of nuptial flight (ADWM), or on average queen dry weight taken over the entire period of maturation from eclosion to nuptial flight (ADW). With two exceptions (note [1]), average weights of pupae and larvae are also given as dry weights (PDW and LDW, respectively). Energy content ratios were estimated either directly from bomb-calorimetric measurements (in which case both the total energy content of an average gyne and male and the ratio of these two are given) or indirectly from estimations of the sex-specific fat contents (assuming 1 mg fat to be equivalent to 39·3 J and 1 mg other tissue to be equivalent to 18·8 J), in which case both the specific fat contents of mature gynes and males and the inferred female-to-male energy ratio are given. For respiration, both the individual respiration rates (μl O_2 individual^{-1} h^{-1}) and their ratios are given. Sources indicate papers which have (partly or entirely) used the same data sets as applied for the current estimations (for fat content, most data for gynes have been published, whereas the new data for males come from samples from the same population).

	Colony foundation	Gyne	Male	Ratio	Sources
Camponotus ligniperda	c				
ADWM		89·5	7·6	11·78	Keller & Passera 1989
energy from fat %		0·43	0·03	16·76	new data
Camponotus planatus	n				
ADWM		2·8	0·82	3·41	Keller & Passera 1989
Energy from fat %		0·18	0·17	3·44	new data
Cataglyphis cursor	n				
ADWM		9·4	6·4	1·47	Passera & Keller 1990
Energy from fat %		0·29	0·18	1·62	new data
Formica gagates	c				
ADWM		15·0	4·5	3·33	Keller & Passera 1989
Energy from fat %		0·56	0·05	5·10	new data
Formica lugubris	n				
ADWM		10·2	6·7	1·52	Passera & Keller 1990
Energy from fat %		0·13	0·05	1·65	new data
Formica polyctena[1]	n				
ADWM[2]		10·21	8·19	1·25	Passera & Keller 1990
AFW		33·58	20·13	1·67	Kneitz 1967
Respiration 25 °C		44·77	73·56	0·61	Kneitz 1967
PFW		43·5	42·5	1·02	Schmidt 1968
Respiration 24·5 °C		11·02	11·88	0·93	Schmidt 1968
PPFW		49·67	54·76	0·91	Schmidt 1968
Respiration 16 °C		4·59	5·95	0·77	Schmidt 1968
Respiration 32 °C		20·08	24·45	0·82	Schmidt 1968

Formica truncorum	n				
ADWM (m)[3]		8·7	6·6	1·32	Sundström 1995
Energy from fat % (m)		0·16	0·07	1·44	Sundström 1995
ADWM (p)[3]		7·6	6·1	1·25	Sundström 1995
Energy from fat % (p)		0·15	0·10	1·30	Sundström 1995
Iridomyrmex humilis	n				
ADWM		1·08	0·42	2·59	Passera & Keller 1987
Energy from fat %		24·7	8·55	3·55	Passera & Keller 1987
ADW		1·12	0·33	3·39	new data
Respiration 20 °C		1·99	0·69	2·88	new data
Respiration 30 °C		4·84	1·85	2·61	new data
PDW		0·78	0·42	1·86	new data
Respiration 20 °C		0·69	0·42	1·63	new data
Respiration 30 °C		1·51	0·85	1·77	new data
LDW		0·41	0·33	1·24	new data
Respiration 20 °C		0·31	0·31	1·01	new data
Respiration 30 °C		0·61	1·13	0·54	new data
Lasius alienus	c				
ADWM		12·8	0·5	25·60	Keller & Passera 1989
Energy from fat %		0·54	0·05	38·64	new data
Lasius emarginatus	c				
ADWM		11·0	0·6	18·33	Keller & Passera 1989
Energy from fat %		0·55	0·09	26·72	new data
Lasius flavus	c				
ADWM		10·46	0·49	21·24	G. Peakin, unpublished data
Energy from fat %		0·62	0·06	33·49	G. Peakin, unpublished data
ADWM[4]		9·72	0·42	23·14	Nielsen *et al.* 1985a
Energy from fat %[4]		0·62	0·08	32·93	Peakin 1964
ADWM[4]		13·5	0·5	27·00	Keller & Passera 1989
Energy from fat %[4]		0·61	0·02	44·04	new data
ADW		8·94	0·32	27·94	Wright 1990, personal communication
Energy (J)		287·5	7·78	36·95	Wright 1990, personal communication
ADW		7·84	0·42	18·66	Nielsen *et al.* 1985a
Respiration 20 °C		6·88	0·94	7·32	Nielsen *et al.* 1985a
PDW[5]		3·65	0·51	7·20	new data
Respiration 20 °C		2·68	0·44	6·05	Peakin *et al.* 1989
Lasius niger	c				
ADWM		16·40	0·96	17·08	Keller & Passera 1989
Energy from fat %		0·51	0·07	24·71	new data
ADWM		15·45	0·93	16·61	Boomsma & Isaaks 1985
Energy (J)		424·9	16·9	25·1	Boomsma & Isaaks 1985
ADW		13·22	0·93	14·21	Boomsma & Isaaks 1985
Respiration 20 °C		5·18	1·38	3·75	Boomsma & Isaaks 1985
PDW		6·13	1·31	4·68	Boomsma & Isaaks 1985
Respiration 20 °C		4·27	1·00	4·27	Boomsma & Isaaks 1985
LFW[1]		8·63	2·22	3·89	Boomsma & Isaaks 1985
Respiration 20 °C		1·95	1·26	1·55	Boomsma & Isaaks 1985
Manica rubida	n				
ADWM		10·9	5·8	1·88	Keller & Passera 1989
Energy from fat %		0·43	0·19	2·29	new data
Myrmica rugulosa	n				
ADWM		2·0	1·0	2·0	Keller & Passera 1989
Energy from fat %		0·20	0·06	2·30	new data
Myrmica sulcinodis	n				
ADWM		1·5	1·27	1·18	Keller & Passera 1989
Energy from fat %		0·15	0·04	1·32	new data
Pogonomyrmex montanus	c				
ADW		6·48	3·48	1·86	MacKay 1985
Energy (J)		175·0	70·3	2·49	MacKay 1985
Energy from fat %		0·36	0·09	2·36	MacKay 1985
Respiration 30 °C		19·44	15·81	1·23	MacKay 1982
Pogonomyrmex subnitidus	c				
ADW		7·75	2·31	3·35	MacKay 1985
Energy (J)		204·6	44·8	4·57	MacKay 1985
Energy from fat %		0·28	0·08	4·03	MacKay 1985
Respiration 30 °C		14·96	6·13	2·44	MacKay 1982
Pogonomyrmex rugosus	c				
ADW		22·83	8·08	2·83	MacKay 1985
Energy (J)		668·9	180·2	3·71	MacKay 1985
Energy from fat %		0·315	0·10	3·44	MacKay 1985
Respiration 30 °C		30·82	28·28	1·09	MacKay 1982

Solenopsis invicta	c				
ADWM		8·24	2·68	3·07	McInnes 1994
Energy from fat %		0·482	0·209	3·82	McInnes 1994
Solenopsis geminata	c				
ADWM		10·31	2·01	5·13	McInnes & Tschinkel 1995
Energy from fat %		0·479	0·149	6·72	McInnes & Tschinkel 1995
Tetramorium caespitum	c				
ADWM		6·02	1·52	3·96	Peakin 1972
Energy from fat %		0·51	0·09	5·61	Peakin 1972
ADWM[6]		5·2	1·7	3·06	Keller & Passera 1989
Energy from fat %[6]		0·60	0·04	4·86	new data
ADW		3·20	1·99	1·61	new data
Respiration 20 °C		2·50	2·57	0·97	new data
PDW		3·10	2·28	1·36	new data
Respiration 20 °C		2·79	2·78	1·00	new data

[1] One of the few cases where fresh-weight data are given in the source papers for adults (AFW), pupae (PFW), prepupae (PPFW) or larvae (LFW).

[2] As no ADW estimate was available, the ADWM estimate was used in the analyses of Fig. 2a and Fig. 3.

[3] Abbreviations (m) and (p) refer to samples taken from monogynous and polygynous colonies, respectively. Only the (m) data were used in the statistical analyses.

[4] Data were excluded from the statistical analyses, because the dependent and independent variable were not measured from samples of the same population.

[5] Based on samples from other British populations (see Boomsma, Wright & Brouwer 1993).

[6] As only one record per species could be included in the analyses of Fig. 1, we chose this one, for reasons of consistency with the other Passera & Keller (1989) data.