

Allometry of Workers of the Fire Ant, *Solenopsis invicta*

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Abstract

The relationship between worker body size and the shape of their body parts was explored in the polymorphic ant, *Solenopsis invicta*. The data consisted of 20 measurements of body parts as well as sums of some of these measurements. Size-free shape variables were created by taking the ratios of relevant measures. After log-transformation, these ratios were regressed against the logarithm of total body length, or against the log of the size of the parent part. Slopes of zero indicated that shape did not change with size, and non-zero slopes signaled a size-related change of shape. Across the range of worker sizes, the head length retained a constant proportion to body length, but relative headwidth increased such that head shape changed from a barrel-profile to a somewhat heart-shaped profile. Antennae became relatively smaller, with the club contributing more to this decline than the other parts. The alinotum became relatively shorter and higher (more humped), and the gaster increased in both relative width and length, and therefore in volume. All three pairs of legs were isometric to body length. The component parts of the legs, with one exception, were isometric to their own total leg length. The body of *S. invicta* is therefore dominated by mostly modest allometries, giving large workers a somewhat different shape than small ones. None of these size-shape relationships was different for different colonies. The functional meaning of these shape changes is unknown, but that does not stop us from speculating.

Keywords: allometry, isometry, morphometry, shape, worker size, caste, polymorphism, size-shape relationships, relative growth, morphology

Abbreviation:

HL	head length
BL	body length
HW1	width across the eyes
HW2	width above the eyes
HW3	width below the eyes

Introduction

The most obvious differences among related organisms are often differences in the shape and size of their bodies, or parts of their bodies. Shape and size often vary together, but shapes can be described in a size-free manner as ratios of selected dimensions. These alternative shapes are the products of differences in the relative growth rates of their dimensions. Such changes in relative growth are a major mode through which homologous structures change shape in the course of evolution; body regions become relatively larger or smaller, appendages relatively longer or shorter and parts become rounder, flatter, more elongate and so on. This process exerts its effect from the microscopic to the macroscopic, during the growth and maturation of an individual organism, and during the evolution of populations.

In most species, variability of such processes results in

normal variation of body size and shape, but among a number of species of ants, selection for large differences in growth and relative growth has produced a worker caste that is greatly variable in both body size and shape. This phenomenon is referred to as worker polymorphism and is present in about 15% of ant genera (Hölldobler and Wilson, 1990; Oster and Wilson, 1978; Wilson, 1953).

Worker polymorphism contrasts with the condition of the worker caste in the great majority of ant species. In these, the worker caste shows only normal, modest variation of size, essentially not different from the body-size variation expected of any insect species. In the extremes of polymorphism, the largest workers may weigh hundreds of times as much as the smallest (Hölldobler and Wilson, 1990; Oster and Wilson, 1978). Because insects do not grow as adults, and ant workers are adults, the larvae of some workers of polymorphic species must grow faster than others, or they grow for longer periods, or both. Wheeler (1991) showed that in the dimorphic

Pheidole and the polymorphic *Solenopsis*, major workers result from the reprogramming of the critical size for initiating metamorphosis.

Great size variability among workers may or may not be accompanied by differences in the shapes of body parts. If certain dimensions grow at different rates than others, then the relevant parts of larger workers will be shaped differently than those of smaller workers. This type of growth is called allometric growth. When the dimensions grow at the same rate, shape does not change, and the parts are said to grow isometrically. Among polymorphic ants, the head is often the most conspicuous target of allometric growth, with larger workers often having disproportionately large heads, as compared to smaller workers. Examples abound, and can be found in many studies (e.g., (Baroni Urbani, 1976; Baroni Urbani and Kutter, 1979; Fernández et al., 1994; Franks, 1985; Franks and Norris, 1987; Hölldobler and Wilson, 1990; Maavara, 1983; Meunier et al., 1999; Retana and Cerdá, 1994; Wilson, 1953).

The major analytical methods that have been applied to size/shape relationships are simple and multiple regression (Wilson, 1985a; Dinizfilho, 1994), principal components analysis (Diniz Filho et al., 1994), polynomial regression (Baroni Urbani, 1976) and Cartesian coordinate transformations (Franks and Norris, 1987). In some polymorphic species, the slopes of regressions change across the range of worker body size, creating a more complex relationship between size and shape. Such size-shape relationships are referred to as multi-phasic (Wilson, 1985a), with up to three and four distinct phases having been reported (Franks, 1985; Wilson, 1985a). There is even a claim of five phases (Baroni Urbani and Kutter, 1979). The phases have often been interpreted as distinct physical castes because they result from different size-shape relationships. On the basis of comparative studies, Wilson (1953) proposed how these different polymorphisms and physical castes evolved.

Table 1. The basic measurements of *Solenopsis invicta* and their combinations.

Abbreviation	Dimension (mm)
AL	alinotum length
AH	alinotum height
HL	head length
HW1	headwidth across the eyes
HW2	headwidth above the eyes, ca. 75% of the distance from the clypeus to the apex of the head
HW3	headwidth below the eyes, ca. 25% of the distance from the clypeus to the head apex
ML	Mandible length
MW	Mandible width at base
FL*	flagellum length, minus club length
SC	scape length
CL	club length
AN	Antennal length= FL (with club) + SC
GL	length of the first gaster segment
GW	width of the first gaster segment
FE (1,2,3)	Femur length
TB (1,2,3)	Tibia length
TA (1,2,3)	Tarsus length
LG (1, 2, 3)	Total leg length= FE + TB + TA
PL (1,2)	Petiole length, segments 1, 2
PH (1,2)	Petiole height, segments 1, 2
BL	Total body length= HL + AL + PL1 + PL2 + GL (excludes gaster segments>1).

Whereas most authors have simply viewed allometries as the outcomes of growth of parts at different rates, Nijhout and Wheeler (1996) argued that the situation in holometabolous insects is fundamentally different. In these, adult structures grow mostly from imaginal discs in the last larval instar during preparation for metamorphosis, undergoing eversion and cell rearrangement during the prepupal and pupal stages. Because these stages do not feed, the resources for imaginal disc growth come from fixed metabolic stores or body tissues. The imaginal discs must therefore compete for these fixed resources, and an increased rate of growth in one disc must be compensated by decreased growth of another. Their model also accommodates reprogramming of the critical size at metamorphosis and of the growth parameters, and can produce most of the allometric patterns observed among ant workers.

Studies of polymorphic ants do not commonly report relationships among more than two or three measurements. Most commonly measured are the head width, head length and alinotum length, and more rarely, leg length and other body dimensions (Franks, 1985) (Klotz et al., 1992; Maavara, 1983). Studies often report only measures that relate to specific functional hypotheses, and ignore other measurements. The literature therefore contains few comprehensive studies of the size/shape relationships of all major body parts, although all body parts are subject to natural selection for size/shape changes. It therefore seemed profitable to carry out a more complete and complex allometric analysis of a selected ant species to look for more subtle changes of body shape. A prime candidate for such an analysis is the much-studied fire ant, *Solenopsis invicta*. This exotic species has become one of the best-known ants, and a vast literature on its biology, physiology, ecology and morphology exists (Porter, 1993). Headwidth is widely and routinely used to classify the workers of this polymorphic species by size. Headwidth was reported to be isometric with body weight (Porter and Tschinkel, 1985), although Wilson (1978) reported *S. invicta* to be “weakly allometric”. Our analysis found that a number of significant shape changes occur across a range of worker sizes.

Materials and Methods

Sampling and measurements

Fire ant workers were haphazardly collected by aspirator from field colonies in Tallahassee, Florida, killed by freezing and then oven-dried at 50° C. From these samples, workers of large and small size were sampled preferentially to increase the power of the subsequent regressions and to decrease the confidence limits around the parameter estimates. Individual dry weight of each worker was taken on a Cahn Microbalance, with a sensitivity of 0.01 mg. Workers were then dissected and manipulated into positions that allowed the clearest 2-dimensional view of the body parts of interest, and digitally photographed using a Javelin JE12HMV camera at 50 x magnification. Image-Pro Plus 4.0 software was used to record the set of measurements described in Table 1. To avoid the telescoping-segments problem, we measured the length and width of only the first gaster segment. Headwidth across the eyes was of the head contour and did not include the bulge of the eyes. The measurements in Table 1 made up the data for the detailed morphometric analysis, and all came from a single colony. Individuals from an additional 3 colonies were similarly collected

Line No.	Dimension 1 (x-axis)	Dimension 2 (y-axis)	Log slope	t-value	d.f.	p-value	R ²
1	BL	HL/BL	-0.013	-0.98	48	n.s.	---
2	BL	HW1/BL	0.15	6.49	48	<0.0001	45%
3	BL	HW2/BL	0.27	9.68	48	<0.0001	65%
4	BL	HW3/BL	0.058	1.87	50	n. s.	---
5	BL	HW1/HW3	0.096	4.93	50	<0.0001	31%
6	BL	HW2/HW3	0.20	7.43	50	<0.0001	52%
7	HL	HW2/HL	0.35	11.6	49	<0.0001	72%
8	BL	HW2/HL	0.33	13.2	49	<0.0001	78%
9	BL	ML/HW2	-0.16	-2.83	21	<0.01	24%
10	BL	ML/HW3	0.032	0.61	21	n.s.	---
11	BL	ANT/BL	-0.30	-16.1	48	<0.0001	84%
12	AN	SC/AN	0.027	0.91	48	n.s.	---
13	AN	FL/AN	-0.017	-0.77	48	n.s.	---
14	AN	CL/AN	-0.17	-3.46	48	<0.005	18%
15	BL	SC/BL	-0.27	-10.8	49	<0.0001	70%
16	BL	FL*/BL	-0.26	-3.72	50	<0.0005	20%
17	BL	CL/BL	-0.43	-10.9	50	<0.0001	70%
18	BL	LG1/BL	-0.034	-1.77	124	n.s.	---
19	BL	LG2/BL	-0.016	-.82	124	n. s.	---
20	BL	LG3/BL	-0.015	-0.49	124	n.s.	---
21	L3	FE3/LG3	-0.071	-2.85	48	<0.01	13%
22	L3	TB3/LG3	0.049	1.58	47	n.s.	---
23	L3	TA3/LG3	0.04	1.56	49	n.s.	---
24	BL	HL/BL	-0.013	-0.97	123	n.s.	---
25	BL	AL/BL	-0.06	-3.56	123	<0.001	8.5%
26	BL	GL/BL	0.17	8.06	125	<0.0001	34%
27	BL	AH/BL	0.14	2.51	125	<0.05	4%
28	GL	GW/GL	1.17	2.54	50	<0.05	10%
29	BL	GW/BL	0.31	11.6	48	<0.0001	73%
30	BL	AH/AL	0.21	3.97	125	<0.0005	11%

Table 2. Regression parameters for the major morphometric comparisons of *Solenopsis invicta*. All variables were regressed as logarithms of ratios in the form $\log y = b+a[\log(x/y)]$. Slopes that are significantly different from zero indicate that the ratio (size-free shape) changes with the size of the whole body or body part. Abbreviations as in Table 1.

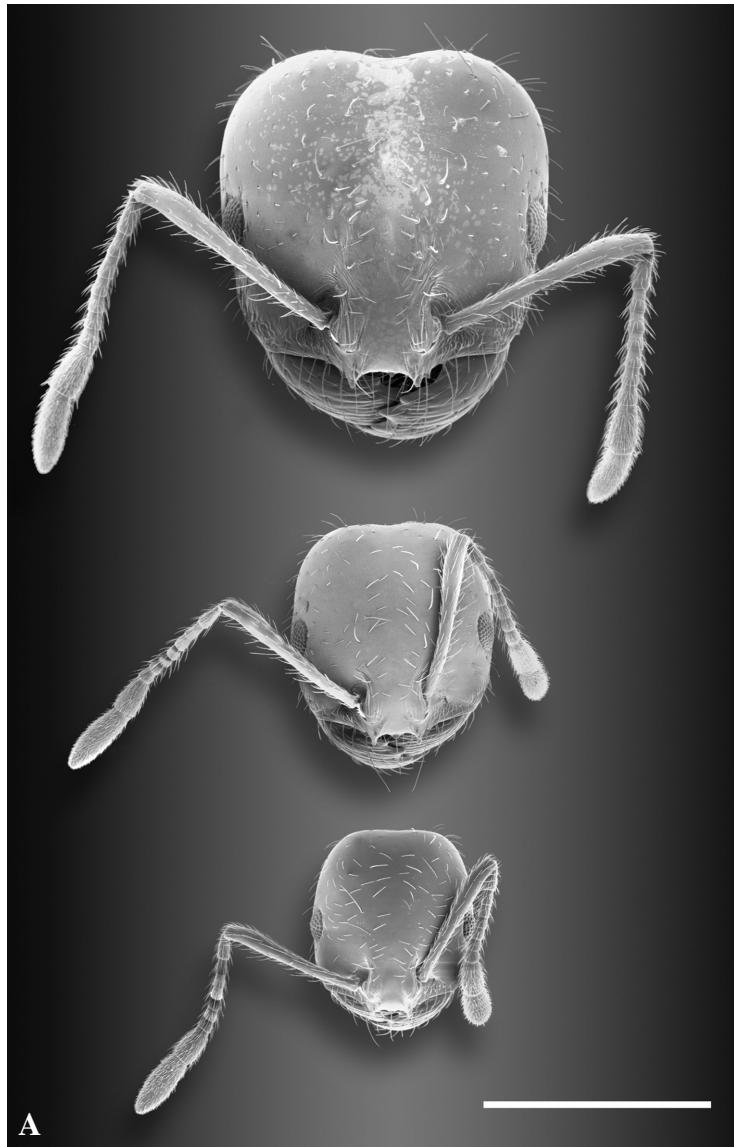
and prepared, but a smaller set of measurements was made on these workers. These data were used to determine if the allometric constants differed among colonies. When the same measurements were made on both sets, both were included in the detailed morphometric analysis.

Data Analysis

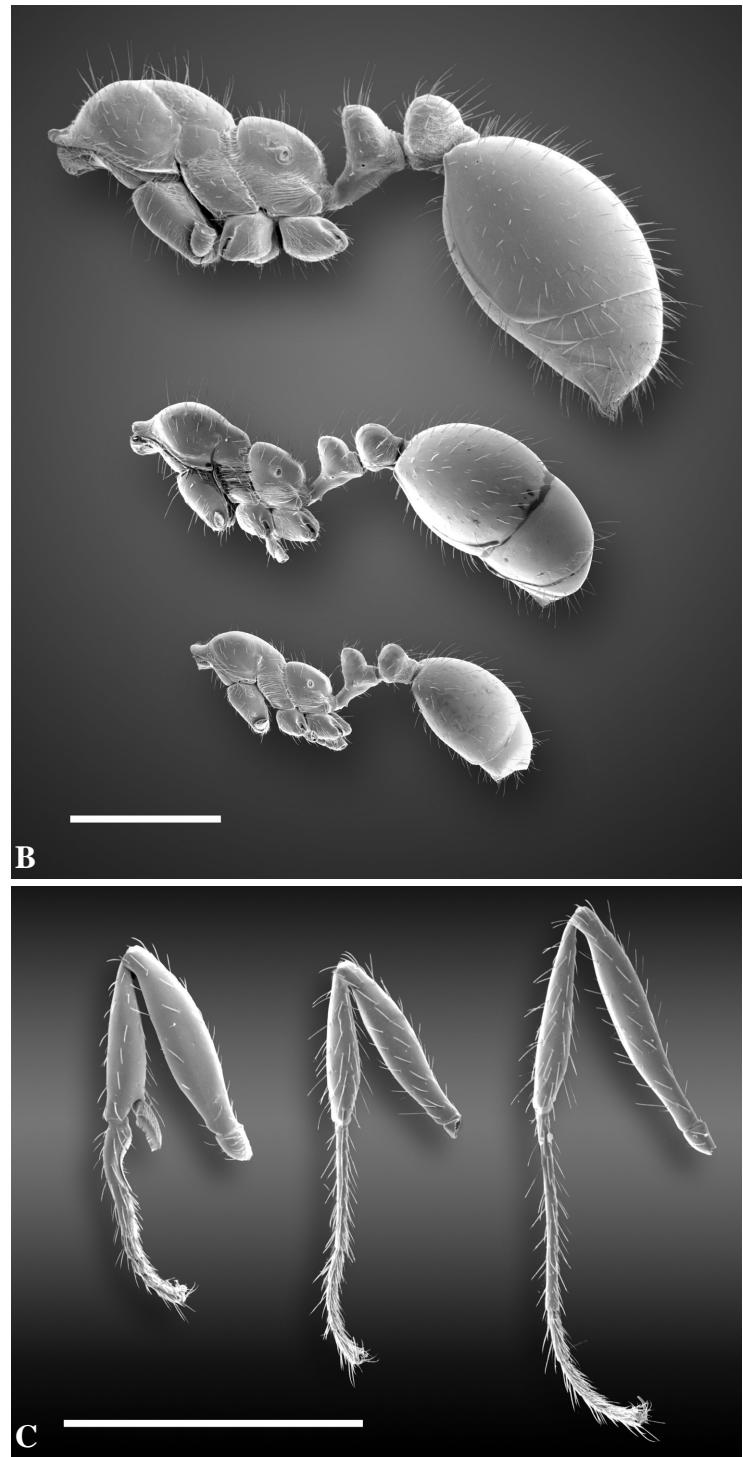
The basic question that we sought to answer was how does each body part grow, relative to the body as a whole and relative to other relevant body parts? One must therefore have an estimate of the whole body size, but each of the commonly used estimates has both strengths and drawbacks. Body dry weight, especially of arthropods, may vary without much change in body dimensions, reducing the predictive power of body weight for dimensions and vice versa. On the other hand, body weight has the advantage that it can be easily and precisely measured. For the exoskeletons of arthropods, body length as the sum of the major body regions would

appear to be a good measure of body size, and is easily interpreted. However, the telescoping of abdominal segments in insects adds uncertainty to this measure of whole body size. Consequently, the first gastral segment was used as a proxy for gaster length. For ease of interpretation, we used only body length as an estimate of whole body size.

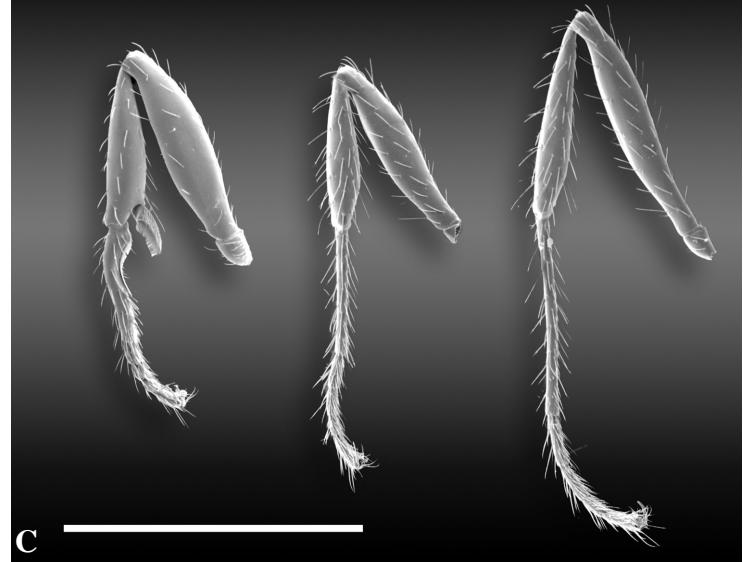
Relative changes of size were estimated by regressing the logarithms of dimensions against one another, or against the estimate of whole body size. When the size of parts changes at the same rate, the slope of these regressions equals 1.0 (Zar, 1999). A slope not significantly different from 1.0 indicates that growth is isometric. A slope significantly less than 1.0 indicates a negative allometry, and more than 1.0 a positive allometry. Excepting the intercolony comparison, rather than test each of our slopes against 1.0, we created a size-free estimate of shape from the logarithm of the ratio of two dimensions, and then regressed these log-ratios against the logarithm of the whole body size (Mosiman and James, 1979). A



A



B



C

Figure 1A (above). Frontal view of the heads of small, medium and large workers of *Solenopsis invicta*. **B (right).** Lateral view of the trunk and gasters of small, medium and large workers. **C (right).** Proleg (left), mesoleg (middle) and metaleg (right) of a small worker. Scale bar is 1 mm in all three figures.

slope not significantly different from zero (*t*-test) indicated that the shape did not change with body size (i.e., was isometric with body size), whereas a non-zero slope indicated that it did (i.e., was allometric). From the very large set of possible ratios, we chose a set that seemed most biologically meaningful, that is, that described shapes of functional body parts, or their size relative to other functional parts. The statistics for these regressions are presented in Table 2. For those who wish to test other ratios, the raw measurements are presented in Appendix I.

In the intercolony comparison, differences in allometric coefficients among the colonies were verified using *t*-tests (Bonferroni-adjusted for multiple comparisons, $p = 0.0167$). Power analyses of these tests were conducted using MINITAB (version 12).

Results

Scanning electron micrographs of the heads, bodies and

legs of small, medium and large workers of *S. invicta* are shown in Fig. 1A-C. Most of the trends described below can be seen by comparing these images.

Whole body size estimate

Total morphological length was computed for each worker by adding head length, alinotum length, length of petiole segments 1 and 2, and gaster segment 1 length. These values ranged from 2.65 to 6.16 mm. The largest workers we measured were therefore somewhat more than twice the whole body length of the smallest (a 20-fold weight range). These values are not an exact or complete estimate of the dorsal silhouette of a worker ant because the head is not carried with mandibles projecting forward, and only the first

gaster segment was included in the estimate. The most posterior segments were excluded because they telescope and are thus not a fixed dimension.

Growth-related shape changes of the head

As worker ants grow to larger sizes, the shape of the head changes. This is because head length (HL) grows at the same rate as whole body length (BL)(Table 2, line 1), whereas two of the three head width measurements grow 10 and 20% more rapidly (Fig. 1A, Fig. 2). A doubling of body length is thus associated with a 2.2-fold increase in width across the eyes (HW1), a 2.4-fold increase in the width above the eyes (HW2) and a 2-fold, isometric increase in the width below the eyes (HW3). The ratio of HW1 and HW2 to BL thus increases as body length increases, whereas the ratio of HW3 to BL does not (Table 2, lines 2, 3, 4 respectively).

The relation of these head widths to each other at various body sizes can be visualized by plotting the ratio of HW1 and HW2 to HW3 against the body length (Fig. 3; Table 2, lines 5, 6). In small workers, headwidth above the eyes (HW2) is about equal to that below (HW3), so that their ratio is approximately 1.0. The width across the eyes (HW1) is larger than either other measure, so that this ratio averages about 1.07 in the smallest workers. As body size increases, HW2 increases faster than HW1, so that in large workers, their ratios to HW3 average 1.12 and 1.14, respectively, that is, they have both become proportionally larger than HW3 but almost equal to each other. These changes are visible in frontal views of fire ant heads—as head size increases, the head outline changes from barrel-shaped to heart-shaped, with the top of the head relatively wider than the bottom (Figs. 1A, 3).

HW is coupled somewhat more tightly to head length than to body length. Body length accounts for 65% of the variation in HW2/BL, but 78% of the variation in HW2/HL (Table 2, lines 3, 7, 8).

The mandibular length is approximately isometric with the headwidth below the eyes (HW3), i.e., close to the mouthparts (Table

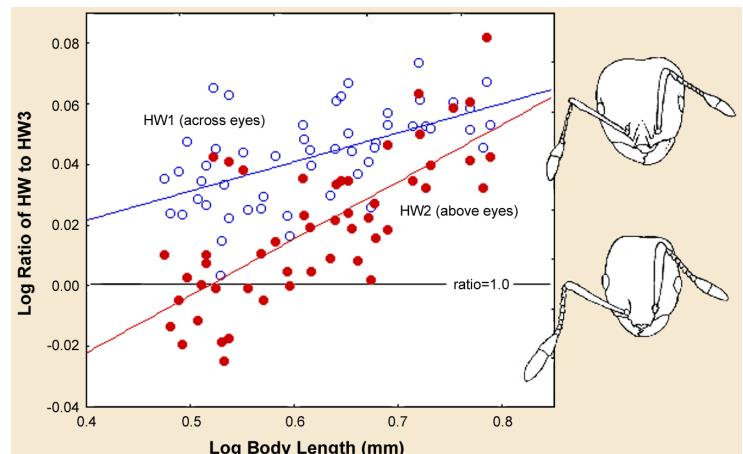


Figure 3. Size-related change in shape of the frontal view of the head of *Solenopsis invicta*, plotted as the log ratio of the two allometric headwidths (HW1, HW2) to the isometric one (HW3) vs. the log of the body length. Headwidths 1, 2 and 3 are across the eyes, above the eyes and below the eyes, respectively (see Table 1). The outline drawings to the right are of a large worker (top, 1.2 mm mean headwidth) and small worker (bottom, 0.6 mm headwidth) scaled to the same size.

2, line 10), but grows more slowly than the headwidth above the eyes (HW2), most distant from the mouthparts (Table 2, line 9). The headwidth below the eyes (HW3) is isometric with body length (Table 2, line 4), making the mandible length also isometric with body length. The head shape thus changes with body size, but the relative size of the mandibles to the body does not.

Growth-related changes in antennal ratios

The total antennal length (the sum of the scape and flagellum (including the club)) grows much more slowly than total body length. Doubling body length results in only a 60% increase in antennal length (Table 1, line 11). Relative antennal length thus decreases by 20% as body length doubles. The three antennal parts do not share equally in this relative size change. Relative to total body length the club decreases significantly more rapidly than the remaining flagellum (i.e. minus the club) and the scape (Fig. 4; Table 2, lines 15, 16, 17). As a result, relative size of the antennal parts to each other also changes with growth: the club makes up a smaller proportion of larger antennae than of small ones (Fig. 4; Table 2, lines 12, 13, 14). Doubling antennal length increases the club by only 1.8-fold. Its relative size therefore decreases by 10% as antennal length doubles. Both the scape and the flagellum grow at approximately the same rate as the entire antenna. Fig. 5 shows an antenna from a large worker scaled to the same scape length as that of a small worker. The smaller relative size of the club in the large worker can readily be seen, as can the (unmeasured) reduction of caliber.

Growth-related changes in the legs

All three pairs of legs are isometric with body length, retaining a constant proportion to it (Table 1, lines 18, 19, 20). Doubling the body length is accompanied by a doubling in the length of all three pairs of legs. Because all legs are isometric to body length, they are also isometric to each other. However, they are not all the same length: as a percent of the sum of all three leg-lengths, the prothoracic legs make up 29 % of the total, the mesothoracic 31

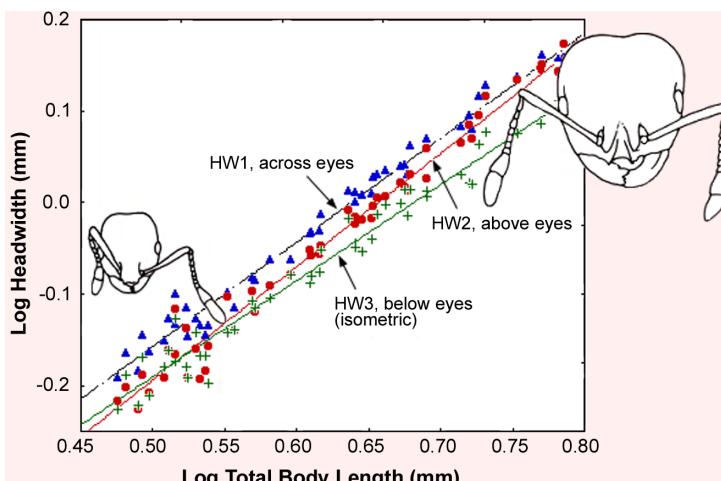


Figure 2. Three headwidths plotted against body length of *Solenopsis invicta*. Headwidth becomes increasingly allometric from the clypeal region to the vertex. The slopes of the regressions are 1.05 (isometric) below the eyes (HW3), 1.14 across the eyes (HW1) and 1.24 above the eyes (HW2). Head shape thus changes as body (and head) size increase, as can be seen in the scale drawings of a small worker head (left) and a large one (right).

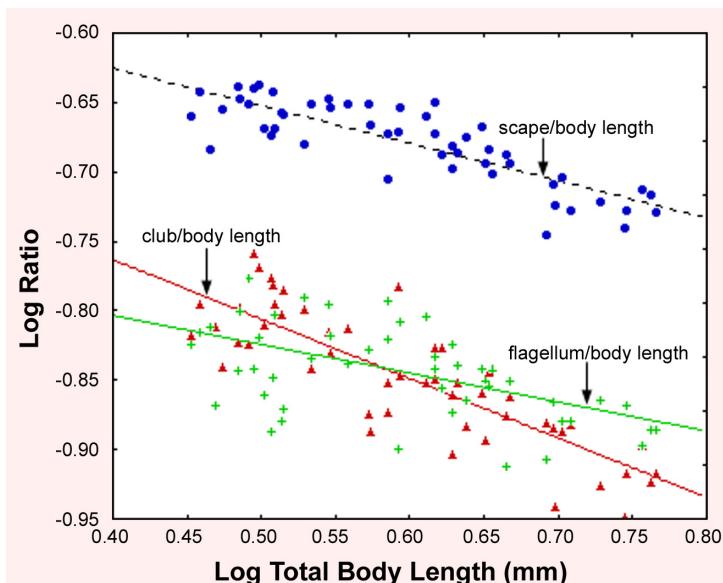


Figure 4. Size-related changes of shape in the antennal parts of *Solenopsis invicta*, shown in relation to total body length. All antennal parts become relatively shorter as body size increases, but the club does so at a higher rate.

% and the metathoracic 40%. The first two pairs of legs are nearly the same length, and the third pair is considerably longer (Fig. 1C). These relationships do not change with body size.

The proportion of each leg made up by the femur, tibia and tarsus changes differently for the three pairs of legs (Fig. 1C). In the prothoracic leg, each of the three parts is essentially isometric with the entire leg length. No matter what the prothoracic leg length, the femur makes up 40% of its length, the tibia 27 % and the tarsus 33%. In the mesothoracic leg, the parts are also isometric with the whole, but the femur and the tarsus each make up 38% of the whole, while the tibia makes up the remaining 24%. In the metathoracic leg, the femur is negatively allometric to the length of the whole leg, the tarsus is isometric and the tibia is positively allometric, although not significantly so. Doubling the length of the metaleg is accompanied by a 1.9 -fold increase in the femur, a 2-fold increase in the tarsus and a 2.1 -fold increase in the tarsus (Table 2, lines 22, 23, 24). The femur and tarsus make up about 3% less and more, respectively, of the entire metaleg as this doubles in length. These reciprocal internal changes conserve the isometry of the leg to body length.

Growth related changes in major body sections

Body length is composed of the sum of the lengths of the head, alinotum, petiole 1, petiole 2 and the gaster. As worker body size increases, some of these grow faster than others, changing in their proportion of total body length (Fig. 7). The head length grows isometrically to the body, so that as the body length doubles, head length also doubles (Table 2, line 24). Alinotum length is slightly negatively allometric with total body length, increasing by 1.9-fold with a doubling of body length (Table 2, line 25). It therefore makes up 36% of total length in small workers and 34% in large ones. Both petiole segments increase in length at lower rates than the whole body, increasing by a factor 1.86 and 1.82, respectively, as the body length doubles (statistics not shown). They form only 11 and 7% of total body length at the largest body size, 1-2% less than

at the smallest size. Gaster length (first segment only) increases by a factor of 2.3 as total body length doubles (Table 2, line 26). It therefore composes 20% of total length in small workers and 23% in large ones. The changes in the proportion of length that is gaster and alinotum are therefore about equal and opposite.

In addition to the proportion of total body length, one must consider growth-related shape changes of each major body segment. Head shape has been covered above, showing the greatest shape changes (Figs. 2 and 3). Alinotum height grows more rapidly than its length (2.2-fold with a body length doubling; Table 2, lines 25, 27), such that the ratio of height/length changes from 0.27 in small workers to 0.32 in large ones (Table 2, line 30). As a result, large workers have a distinctly more humped, robust alinotum than small workers, as is visible in Figs. 1 and 6. In Fig. 6, the image of the alinotum of a small worker is superimposed over the silhouette of a large worker scaled to the same length, making the shape differences apparent. Neither petiole segment shows any change in shape as body size changes (length and height are isometric). Gaster width grows slightly more rapidly than length, increasing 2.15-fold with a doubling of gaster length (Table 2, line 28). In small ants, gaster width is 96% of its length, whereas in large ones, it is 106%. As body length doubles, gaster width increases 2.5-fold, contrasting with the 2.2-fold increase of gaster length (Table 2, lines 26, 29). If gaster dimensions had merely doubled with body length (ie., had been isometric), the increase in gaster volume would have been 8-fold. The actual increase was about 13-fold, or 63% greater than isometric. Gaster volume of large workers is therefore proportionally almost two-thirds greater than that of small ones.

Intercolony shape differences

There were no significant differences between colonies for any of the measured allometric coefficients (Figure 7). Since group sample sizes were identical ($N=25$), the power of a comparison varied with the magnitude of the standard error for each measurement. For moderate effect sizes (0.08 difference between coefficients) most t-tests had a small (>0.10) probability of making a Type II error. However, comparisons of the thorax length measure

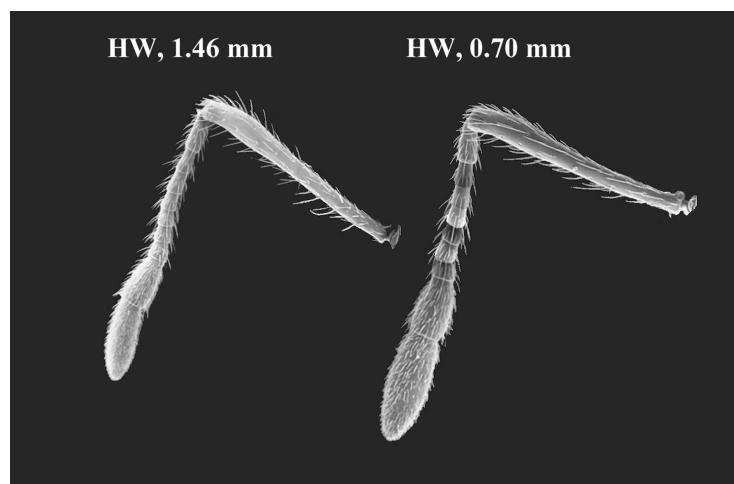


Figure 5. Antennae of a small worker of *Solenopsis invicta* (right), and a large one of about twice the headwidth (left), scaled to the same absolute length of the scape. The antennal size does not double with head size, and the club is relatively smaller in the large antenna.

were considerably less powerful (>0.24 probability of making a Type II error).

Discussion

The power of regression analysis of body measures is very high. In most cases, variation in body length explained 91 to 99% of the variation in the size of the focal part. As a result, even small shape changes could be detected. It follows that when the data showed isometry, this conclusion was very strong. Nevertheless, only the head length, the most ventral headwidth, the mandibles and the legs were actually isometric with total body length. Most other parts showed substantial allometry to the body as a whole, some positive, and some negative. Allometry was especially strong in the head. The change in head shape with size is easily seen, as is the relative size of the antenna and the club (Figs. 1A, 5). The shape of the alinotum was also conspicuously different in large and small workers (Fig. 6). Less conspicuous but probably not less important, the gaster is relatively larger in larger workers.

The subparts of a tagma may have different relationships to the whole body and to their parent tagma. Thus, although the total antennal length was strongly allometric to body length, the flagellum (without the club) and scape were isometric to the total antennal length. The club contributed disproportionately to the decline of the relative size of the antenna in relation to body length. Similarly, one of the headwidths was isometric to the body length but allometric to the other two headwidths. Although all legs were isometric to body length, and all parts of legs 1 and 2 were isometric to the length of their respective legs, femur 3 was allometric to the length of leg 3.

Among ant species, polymorphism is always associated with division of labor, with some (often loose) degree of matching between worker size and particular types of tasks (Hölldobler and Wilson, 1990). However, the functional meaning of the shape changes is mostly unknown, although it invites speculation. The relative increase of head size, especially dorsally, may be associated with changes in the mandibular muscles. A muscle that increases in size isometrically is expected to become relatively weaker (Calder, 1984). Perhaps allometric increases in mandibular muscles maintain a constant relationship between strength and size. The absolute

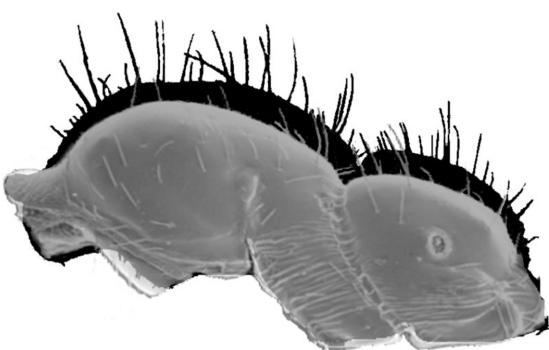


Fig. 6. Alinotum of a small worker of *Solenopsis invicta* (in grey-scale) superimposed on the silhouette (black) of a large worker scaled to the same alinotum length. The more humped shape of the larger worker alinotum is visible, as are several smaller shape differences.

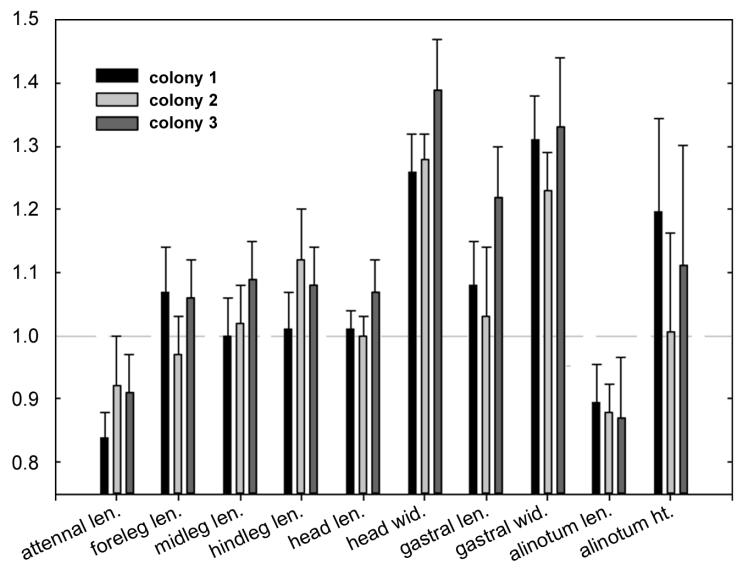


Figure 7. Intercolony differences in the allometric constants for three randomly chosen colonies of *Solenopsis invicta*. There were no significant differences among colonies in any of the parameters.

strength would, of course, increase with size in any case. Interestingly, mandible length is isometric to body length. Similar principles may apply to the change in alinotum shape, with the relatively more humped alinotum of large workers accommodating a larger mass of muscle to conserve relative strength.

Isometry between leg length and body length suggests that, to the extent that maximum running speed depends upon leg length, running speed ought to increase isometrically to body size. In army ants, leg length is associated with running speed (Franks 1985). However, in three species of *Pogonomyrmex*, running speed did not increase with body size (Morehead and Feener, 1998), suggesting that the functional consequences of morphological differences are often difficult to predict.

A relatively larger gaster suggests a relatively greater maximum crop volume, which in turn suggests a greater crop-storage of food. Glancey et al. (1973) claimed that large workers stored oil for long periods, but experimental flaws and the work of Howard and Tschinkel (1981), Wilson (1978), Ricks and Vinson (1972) cast doubt on this claim. Howard and Tschinkel (1981) found that whereas large workers do not imbibe more liquid food on a per weight basis than small ones, they do retain it longer. Although this lends some support to the food storage function of large workers, the evidence does not clearly link worker function with relative gaster size, and by proxy, crop size. Perhaps the meaning of the increased relative gaster size of large workers lies in the ability to accommodate relatively greater fat stores, as large workers are reported to do (Tschinkel, 1993).

Fig. 8 shows that the body is a mosaic of negative and positive allometry and isometry. Relative growth does not appear to be patterned as a gradient along the body axis. The negatively allometric antennae are attached to the positively allometric head, and the isometric legs to the mixed allometric alinotum. Our findings are more readily interpretable under the competition model of Nijhout and Wheeler (Nijhout and Wheeler, 1996; Emlen, 2000b). Most of the imaginal disc growth that produces the adult body in

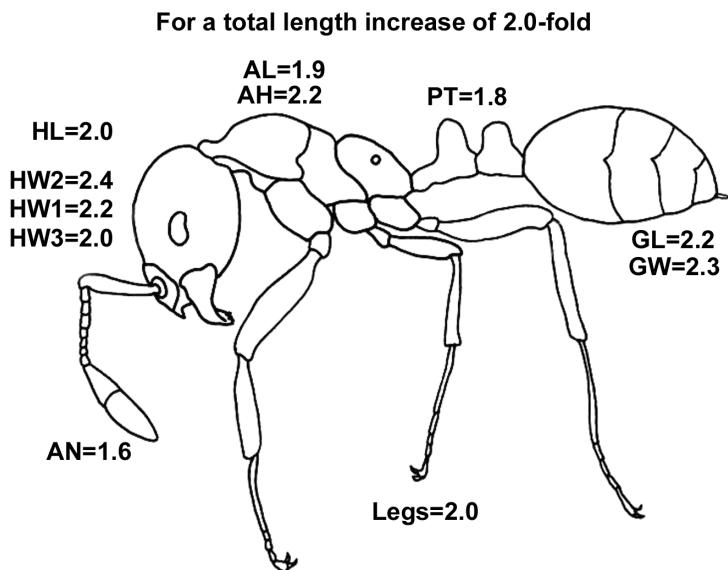


Figure 8. Side view of a fire ant worker of *Solenopsis invicta* summarizing the size increase of each body part for a doubling of total body length. A value of 2.0 indicates isometry, less than 2.0 negative allometry and greater than 2.0, positive allometry.

ants takes place during metamorphosis, after the larvae have stopped feeding. The imaginal discs therefore compete for fixed resources, and increased growth rate of one must be compensated by decreased growth by another. Which particular discs grow at the expense of which others cannot be determined without experimental analysis. In dung beetles, growth of the exaggerated male horns exerts a negative influence on the growth of nearby structures—horns on the front of the head reduce antennal size, those on the center of the head reduce eye size and those on the thorax reduce wing size (Emlen 2000a,b, 2001). This influence wanes with physical distance. Clear indications of inter-disc competition are weak in *S. invicta*, perhaps because allometries are weak and their costs are low. The negative allometry of the antennae is difficult to explain in this manner because the antennae are attached to a head region that is isometric.

Nijhout and Wheeler's model deals only with overall disc growth, but it is apparent that the several dimensions of an imaginal disc need not grow at the same rate. In contrast to competition among discs of *S. invicta*, resource competition within discs of some appendages seems quite clear—the third leg is isometric with the body, but the proportion made up by the femur, tibia and tarsus changes with leg (and body) size, suggesting that within-disc competition among leg segments may occur. Similarly, the negative allometry of the antenna is disproportionately the result of negative club allometry. In the development of legs in *Drosophila*, Abu-Shaar and Mann (1998) showed that mutually antagonistic interactions among several developmental genes within the leg disc convert an initial gradient of gene activity into discrete domains, each of which corresponds to a leg segment. Differences in such antagonistic interactions might change the relative sizes of the domains, and thus the segments, within an appendage, as seen in the antenna and metathoracic leg of *S. invicta*. In *Drosophila*, much of the change in shape of the leg disc during evagination results from cell rearrangement and changes in cell shapes, rather than cell division or growth (Fristrom, 1976). The within-disc growth rate

differences that lead to the changes in head shape (Fig. 1) are of a gradient, rather than a discrete nature. Perhaps such gradients are the origin of the constraints on the evolution of head shapes described by Franks and Norris (1987).

The great range of body size in *S. invicta* arises from reprogramming the critical size for initiating metamorphosis; workers of less than 0.75 mm headwidth are minors, all others are majors. The worker population thus consists of two subpopulations, a majority of minor workers having a small mean size and low variability, and a minority of major workers with a greater mean size and much larger variability. Together, these subpopulations overlap slightly to form the familiar right-skewed size distribution. The imaginal discs in majors can grow much more because they are in a larger body that has more resources. Greater growth magnifies the allometric differences intrinsic in the growth constants of the imaginal discs. However, unlike the situation in dimorphic ants, the smallest majors overlap with the largest minors, and the growth constants of their discs seem to be identical, with no signs of multiphasic regressions. In addition, no clear signs of large compensatory effects or damped growth at extreme sizes are apparent. The mild allometries of *S. invicta* probably do not exact such costs.

Lack of variation of the regression parameters among colonies is perplexing. If the size/shape relationship is to be subject to natural selection, there must be variation of the parameters among colonies. In the Australian ant, *Camponotus consobrinus*, different families of workers within polygyne colonies differ significantly in their proportion of soldiers and in their allometric growth trajectories (Fraser et al., 2000). Variation between colonies disappeared after adjustment for within-colony family variation, suggesting that much of the variation in polymorphism may be of genetic origin (although environmental influences were not completely ruled out). It is possible that such inter-colony variation would appear in our data if more colonies were sampled, or that the observed variation is sufficient for natural selection to get a grip on. It is also possible that North American *S. invicta* is relatively invariant as a result of a loss of genetic diversity through the founder-effect bottleneck that occurred during transit from South America (Ross et al., 1987). The lack of variation is especially odd because colonies vary significantly in so many other biologically important characteristics, including physiological, behavioral and physical traits.

All colonies we studied were mature and contained the full range of worker sizes. By contrast, newly founded colonies contain only very small, monomorphic workers called minims or nanitics. Polymorphism appears and increases as colonies grow (Nowbahari et al., 2000; Tschinkel, 1988; Wilson 1983, 1985b). In *S. invicta*, it results from an increasing proportion of major workers (see above). Major workers develop when a certain size threshold is surpassed in an early larval instar and the critical size for pupation is programmed upward (Wheeler, 1990, 1991). All workers of greater than about 0.75 mm headwidth are majors. During the first half-year of colony life, the mean size of both minors and majors increases, but thereafter, polymorphism increases only because the proportion of major workers continues to climb as an ever larger proportion of early-instar larvae exceed the threshold size for reprogramming. However, this mechanism addresses only the final worker size. The question of how the allometries described in this

paper appear and develop during colony growth is mostly open. Do the allometric constants gradually take on their mature values (those described in this paper) as colonies grow, or do they have their final values when the first majors are produced? In other words, do individual worker growth rules change with colony size, or is worker shape a function only of worker size, not colony size? The answer is relevant to interpreting the functional meaning of size/shape relationships in social insects. In *Cataglyphis niger*, the characteristic allometry is only established at colony maturity (Nowbahari et al., 2000). Few comparable studies exist.

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Appendix I. The raw measurements of *S. invicta* body parts. See text for details.

Worker No.	WT	SCAPE	FLAGEL	CLUB	FEMUR	TIBIA	TARSUS	FEMUR_2	TIBIA_2	TARSUS_2	FEMUR_3	TIBIA_3	TARSUS_3	HD_LEN GT
1	.480	.808	1.081	.556	.886	.624	.713	.935	.619	.943	1.148	.750	1.398	1.003
2	.410	.727	1.014	.536	.772	.545	.739	.789	.533	.813	.982	.647	1.190	.901
3	.350	.692	1.024	.516	.788	.518	.441	.785	.577	.470	.955	.693	.644	.800
4	.600	.716	.994	.545	.808	.573	.633	.837	.545	.840	.893	.683	1.383	.899
5	.440	.705	1.083	.536	.876	.618	.681	1.042	.675	1.325	1.030	.716	1.294	.879
6	.330	.790	.854	.455	.928	.619	1.150	.701	.531	.655	.735	.479	.655	.770
7	.430	.807	.835	.485	.768	.562	.671	.783	.490	1.103	.986	.639	1.223	1.223
8	.620	.817	1.122	.541	.979	.647	.547	.961	.644	.975	1.154	.743	1.404	1.029
9	.830	.906	1.204	.572	1.082	.706	.867	1.048	.714	1.099	1.279	.915	1.639	1.202
10	.320	.734	.989	.533	.820	.501	.695	.813	.534	.831	1.026	.559	1.287	.872
11	.390	.763	.991	.491	.859	.573	.658	.841	.560	.841	1.055	.692	1.224	.968
12	.530	.835	1.056	.500	.937	.552	.823	.922	.620	.917	1.128	.782	1.383	.982
13	.820	.880	1.193	.585	1.039	.663	.868	1.059	.670	1.036	1.073	.874	1.418	1.062
14	.460	.741	.962	.537	.838	.559	.714	.825	.547	.878	1.003	.625	1.102	.897
15	.280	.689	.972	.487	.795	.540	.684	.888	.494	.815	.944	.625	1.280	.833
16	.380	.780	1.055	.520	.909	.576	.811	.890	.554	.962	1.030	.738	1.295	.929
17	.740	.789	1.099	.536	.933	.616	.761	.906	.644	.940	1.122	.751	1.380	.965
18	.270	.693	.983	.464	.798	.549	.692	.796	.536	.823	.981	.659	.659	.835
19	.240	.655	.901	.461	.701	.525	.608	.732	.460	.781	.869	.585	1.088	.794
20	.290	.700	.895	.458	.733	.506	.575	.748	.512	.750	.896	.647	1.142	.813
21	.250	.605	.903	.452	.676	.465	.627	.668	.486	.723	.817	.587	1.054	.751
22	.640	.927	1.212	.616	1.155	.672	.953	.924	.697	.990	1.224	.853	1.524	1.116
23	.580	.835	1.139	.646	.926	.691	.823	.960	.609	.996	1.138	.813	1.402	1.047
24	.370	.717	.977	.536	.536	.561	.681	.796	.556	.817	1.003	.658	1.250	.848
25	.310	.681	.952	.537	.755	.510	.643	.768	.509	.782	.903	.661	1.179	.821
26	1.320	.998	1.320	.655	1.222	.872	.941	1.241	.879	1.315	1.464	1.093	1.868	1.323
27	1.530	.974	1.329	.650	1.231	.822	.866	1.152	.887	1.222	1.411	1.021	1.853	1.385
28	.860	.919	1.162	.569	1.075	.735	.850	1.011	.727	1.104	1.291	.905	1.634	1.130
29	1.060	.948	1.181	.615	1.113	.798	.887	1.055	.770	1.106	1.378	.910	1.674	1.147
30	.660	.886	1.167	.531	1.046	.733	.842	1.056	.703	1.084	1.267	.880	1.591	1.091
31	2.210	1.109	1.442	.690	1.365	.967	1.174	1.390	.897	1.267	1.505	1.080	2.011	1.471
32	2.150	1.106	1.447	.723	1.280	.929	1.038	1.306	.945	1.241	1.533	1.155	1.928	1.461
33	1.680	1.018	1.366	.635	1.165	.879	1.029	1.181	.844	1.256	1.501	1.042	1.894	1.372
34	2.000	1.041	1.427	.674	1.308	.916	.957	1.328	.917	1.246	1.516	1.045	1.915	1.402
35	1.780	1.010	1.120	.625	1.195	.911	1.008	1.172	.852	1.268	1.465	1.049	1.814	1.407
36	.970	.943	1.308	.571	1.099	.808	.938	1.152	.783	1.190	.986	.798	1.799	1.232
37	.570	.760	1.136	.515	.924	.594	.884	.885	.664	.960	1.148	.777	1.494	1.013
38	.220	.659	.956	.429	.733	.455	.622	.723	.443	.746	.846	.608	1.099	.780
39	.130	.681	.929	.491	.795	.467	.664	.728	.510	.774	.901	.631	1.165	.849
40	.680	.860	1.207	.624	1.009	.652	.878	1.007	.727	1.018	1.196	.847	1.518	1.091
41	.450	.620	.855	.431	.684	.476	.577	.671	.448	.700	.847	.548	1.084	.745
42	.230	.718	.944	.514	.795	.456	.690	.715	.523	.771	.937	.650	1.154	.805
43	.990	.883	1.256	.647	1.084	.821	.952	1.195	.777	1.171	1.198	.987	1.662	1.238
44	1.260	.956	1.344	.670	1.199	.877	1.024	1.206	.884	1.202	1.414	1.013	1.855	1.314
45	.900	.941	1.295	.638	1.114	.802	.933	1.145	.746	1.119	1.343	.924	1.712	1.210
46	.560	.855	1.158	.587	1.023	.676	.828	1.033	.704	1.056	1.257	.849	1.514	1.078
47	.800	.958	1.255	.615	1.062	.721	.966	1.116	.765	1.102	1.301	.960	1.638	1.174
48	.880	.899	1.299	.651	1.166	.754	.977	1.161	.839	1.120	1.374	.968	1.756	1.235
49	1.620	1.089	1.464	.705	1.313	.912	1.066	1.295	.901	1.102	1.536	1.080	1.821	1.413
50	.690	.882	1.224	.604	.990	.712	.877	1.006	.708	1.085	1.215	.960	1.576	1.126
51	.510	.871	1.167	.557	1.035	.688	.821	1.002	.664	.988	1.189	.843	1.540	1.035
52	.720	.932	1.276	.645	1.059	.743	.906	1.098	.712	1.090	1.291	.920	1.572	1.174
53	.760	.894	1.215	.574	1.035	.724	.785	1.054	.686	1.037	1.256	.854	1.545	1.094

Continued on next page.

Appendix I continued from page 10.

HD_WID_1	HD_WIT_2	HD_WIT_3	GASTR_L	GAST_WI_D	PET_1_L	PET_2_L	PET_1_H	PET_2_H_T	ALI_LENGTH	ALI_HT	LEG_1	LEG_2	LEG_3
.866	.812	.785	.778	.822	.441	.277	.328	.303	1.115	.248	2.223	2.496	3.295
.768	.729	.661	.655	.727	.385	.232	.300	.264	.983	.232	2.056	2.135	2.820
.734	.641	.680	.731	.734	.439	.237	.249	.256	1.020	.243	1.747	1.833	2.292
.795	.765	.748	.733	.758	.397	.264	.305	.282	.835	.272	2.014	2.223	2.959
.798	.788	.721	.831	.786	.404	.281	.307	.281	.986	.268	2.175	3.041	3.040
.716	.649	.679	.680	.710	.382	.241	.285	.254	.875	.265	2.698	1.887	1.870
.715	.685	.678	.767	.751	.389	.364	.276	.259	1.003	.290	2.001	2.375	2.848
.924	.887	.818	.936	.887	.430	.267	.344	.322	1.189	.301	2.173	2.581	3.301
1.098	1.038	1.034	1.116	.983	.504	.306	.366	.384	1.353	.371	2.655	2.861	3.834
.746	.691	.721	.753	.708	.409	.247	.286	.282	.938	.230	2.016	2.177	2.871
.768	.724	.725	.747	.743	.405	.295	.311	.294	1.004	.241	2.089	2.242	2.970
.866	.835	.835	.886	.848	.452	.292	.331	.308	1.128	.313	2.313	2.458	3.294
1.000	.947	.902	1.051	.993	.439	.340	.382	.362	1.248	.391	2.571	2.765	3.364
.741	.716	.702									2.111	2.250	2.730
.745	.688	.688	.661	.665	.357	.224	.291	.271	.988	.278	2.019	2.197	2.849
.821	.759	.768	.824	.827	.424	.242	.310	.341	1.103	.361	2.296	2.406	3.063
.828	.800	.781	.839	.849	.401	.237	.329	.294	1.069	.281	2.310	2.491	3.253
.735	.683	.671	.700	.676	.399	.223	.281	.265	.946	.294	2.039	2.155	2.299
.685	.628	.648	.680	.670	.399	.153	.272	.237	.851	.232	1.834	1.972	2.541
.705	.643	.661	.720	.661	.349	.224	.267	.256	.943	.314	1.814	2.009	2.685
.655	.594	.601	.637	.633	.395	.227	.227	.237	.910	.245	1.767	1.877	2.459
1.027	.964	.893	1.020	.985	.442	.299	.380	.359	1.266	.307	2.779	2.611	3.600
.930	.877	.839	.945	.930	.439	.316	.362	.321	1.170	.299	2.440	2.565	3.352
.733	.696	.634	.788	.745	.404	.245	.296	.265	.987	.238	1.779	2.168	2.910
.672	.591	.667	.757	.717	.430	.243	.291	.264	.959	.228	1.907	2.059	2.743
1.305	1.245	1.156	1.312	1.292	.505	.361	.475	.422	1.547	.456	3.034	3.435	4.425
1.245	1.215	1.051	1.182	1.302	.653	.286	.471	.434	1.476	.464	2.919	3.261	4.284
1.084	1.014	.996	1.061	1.081	.530	.304	.425	.370	1.322	.301	2.661	2.842	3.830
1.149	1.061	1.017	1.094	1.140	.633	.269	.433	.390	1.482	.405	2.798	2.931	3.962
1.066	.990	.915	1.106	1.054	.471	.263	.403	.365	1.321	.336	2.620	2.843	3.739
1.442	1.491	1.236	1.457	1.546	.729	.359	.538	.592	1.767	.545	3.505	3.553	4.596
1.435	1.391	1.293	1.387	1.619	.654	.379	.554	.532	1.832	.535	3.246	3.492	4.616
1.369	1.364	1.192	1.363	1.490	.532	.390	.527	.496	1.700	.512	3.072	3.281	4.438
1.449	1.414	1.286	1.331	1.605	.700	.386	.545	.513	1.749	.651	3.180	3.491	4.476
1.394	1.401	1.219	1.344	1.525	.665	.383	.530	.501	1.755	.537	3.114	3.292	4.329
1.204	1.174	1.046	1.237	1.177	.630	.375	.426	.428	1.518	.426	2.845	3.124	4.161
.929	.877	.832	.926	.918	.437	.284	.355	.325	1.193	.330	2.402	2.509	3.419
.688	.620	.616	.712	.641	.341	.236	.251	.240	.906	.255	1.809	1.912	2.554
.715	.643	.644	.693	.703	.461	.243	.268	.232	.931	.252	1.927	2.011	2.697
1.020	.957	.884	1.044	.981	.482	.309	.376	.344	1.261	.303	2.538	2.752	3.562
.644	.607	.594	.701	.631	.301	.224	.237	.234	.863	.226	1.737	1.820	2.479
.716	.654	.681	.762	.695	.471	.251	.268	.260	.977	.245	1.941	2.010	2.741
1.213	1.163	1.074	1.270	1.208	.597	.369	.446	.409	1.443	.414	2.858	3.142	3.847
1.345	1.308	1.194	1.295	1.350	.566	.365	.505	.437	1.565	.434	3.100	3.292	4.282
1.175	1.147	1.031	1.167	1.207	.530	.351	.415	.414	1.392	.397	2.849	3.010	3.979
1.022	.962	.911	1.041	.994	.528	.337	.344	.349	1.275	.237	2.527	2.792	3.620
1.095	1.049	.997	1.157	1.109	.479	.294	.422	.379	1.352	.322	2.750	2.983	3.900
1.153	1.072	1.035	1.018	1.222	.573	.331	.439	.397	1.369	.353	2.897	3.120	4.098
1.408	1.373	1.246	1.494	1.566	.740	.423	.560	.499	1.767	.531	3.291	3.298	4.437
1.074	1.013	.970	.989	1.075	.553	.317	.368	.355	1.305	.303	2.579	2.799	3.751
.971	.896	.887	.946	.927	.445	.290	.364	.346	1.205	.281	2.544	2.654	3.572
1.073	1.028	.966	1.124	1.060	.519	.333	.383	.377	1.359	.314	2.707	2.900	3.783
1.030	.982	.962	.942	1.023	.429	.319	.390	.368	1.301	.285	2.544	2.778	3.655