# The economy of the shape of limbed animals

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**Abstract.** A simple, high-level wire-minimization model appears to drive the relationship between animal limb number and body-to-limb proportion in some animals across at least seven phyla: annelids, arthropods, cnidarians, echinoderms, molluscs, tardigrades and vertebrates. Given an animal's body-to-limb proportion, the model enables one to estimate the animal's number of limbs, and vice versa. Informally, the model states that a limbed animal's large-scale morphology is set so as to maximize its number of limbs subject to the constraint that there is not a more economical shape which reaches out to the same places. A consequence of animals conforming to the model is that their large-scale morphology is "minimally wired." Just as wire minimization is important in artificial information processing devices, it is hypothesized that one reason why animals' large-scale morphologies conform to a save-wire principle is to minimize the system-wide information processing times.

## 1 Introduction

Wire minimization is important in the engineering of computers and other artificial information processing devices, and has spurred within graph theory the development of appropriate algorithms for determining economical wiring layouts (Graham and Hell 1985; Hwang et al. 1992; Sherwani 1995). Wire minimization is important for such artificial devices for at least three reasons. A first and most obvious reason is that using less wire per device means saving money on purchasing wire. A second reason is that less wire per device means that a device of any given size can be made more powerful, e.g. by fitting more silicon chips into the

device. A third reason is that, all things being equal, a device made with less wire will have shorter propagation delays between its components, and thus the device will process information more quickly.

Each of these three reasons to save wire in artificial devices has an analogous reason in the context of biological information processing systems. The idea that wire or volume optimization principles apply in biology is not new. Such principles have been found to apply well to the morphology of organisms at many levels of anatomy: arteries and veins (Kamiya and Togawa 1972; Zamir 1976; Woldenberg and Horsfield 1983; Schreiner and Buxbaum 1993; Changizi and Cherniak 2000), tree branches and roots (Cherniak 1992; Cherniak et al. 1999), dendrites and axons (Cherniak 1992; Cherniak et al. 1999), and large-scale organization of nervous systems (Durbin and Mitchison 1990; Mitchison 1991, 1992; Ruppin et al. 1993; Cherniak 1994, 1995; Van Essen 1997; Changizi 2000). Save-wire principles have not been studied at the level of entire organism shape, however. There are at least three reasons for an organism's large-scale morphology to be optimal (i.e. to use the minimum amount of tissue), and the reasons are analogous to those mentioned above for artificial information processing devices. First, all things equal, an animal whose shape requires using less body material will be better off because it has less body material to maintain. Second, a more optimal large-scale morphology means that, for any given size, the animal can be "more powerful" because more energy can be devoted to other adaptive components, e.g. thicker scales. Finally, all things being equal, an animal with a more optimally-wired large-scale morphology will have lower propagation delays between its parts and thus process information more quickly and react to the environment more successfully.

In this paper I focus on the large-scale morphology of limbed animals only, and I concentrate specifically on only one salient aspect: the "body-limb structure," by which I mean the animal's number of limbs and its body-to-limb proportion. I show that a principle of the rough form – "have as many limbs as possible subject to

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the constraint that the resulting shape cannot be made more wire-minimal" – entails a particular relationship between an animal's number of limbs and its body-to-limb proportion, and that limbed animals across seven phyla conform to the predicted relationship despite the wide diversity of limb functions. These animals' large-scale morphologies thus appear to be driven, in part, by a wire-minimization principle (and, in part, by a need-limbs-for-reaching principle). Note that the model can only be expected to be a "zeroth order" approximation, as there are surely many competing evolutionary pressures on the large-scale morphology besides economy of wiring. The model should be considered in the same light as models for allometric scaling laws (Schmidt-Nielson 1984), where the aim is not to make accurate predictions, but instead, to capture underlying biological principles. Here we will be interested in how the number of limbs scales as the body becomes larger compared to the limbs, and we will capture principles underlying the body-limb structure of limbed animals.

## 2 The model

In this section I develop the model, which consists of two assumptions, or principles; I call the model the "Max-MST" (maximum degree minimal spanning tree) model. Some preliminary definitions must be introduced first.

A *network* consists of nodes, and wires (or edges) may be connected between them. Nodes can usually be viewed as points and wires as lines drawn between nodes. A limbed animal is modeled here as a type of network called a "body-limb network." In what sense is a limbed animal a network? First, an animal's body is treated as a node. It is not necessarily a point-sized node, though, as we will see later; differently shaped body nodes will allow us to handle differently shaped animal bodies (e.g. circular nodes). Second, we imagine that an animal's limbs are fixed in place in their "natural" position, and the point at each limb's tip is treated as a node. The animals studied here have limbs that are approximately uniform in length, and so I assume that body-limb networks have limb-tip nodes that are uniform in distance from the body node. Finally, each limb is treated as a wire connecting the body node to its limb-tip node. In sum, a *body-limb network* consists of: (i) a body node, (ii) limb-tips placed uniformly distant from the body node, (iii) wires connecting the body node to each limb-tip node, and (iv) no other wires. Every limbed animal with uniform length limbs has, then, a corresponding body-limb network defined in the manner just specified (see Fig. 1). An animal's body-limb network can be thought of as characterizing the animal's large-scale morphology.

An *equidistance network* is any network for which there is one node – the body node – from which all other nodes are equidistant. Body-limb networks are special cases of equidistance networks. Other equidistance networks may have wires connecting any pair of nodes; they are not confined, as are body-limb networks, to wires connecting only the body node to other nodes. For example, a single point in the plane with points placed
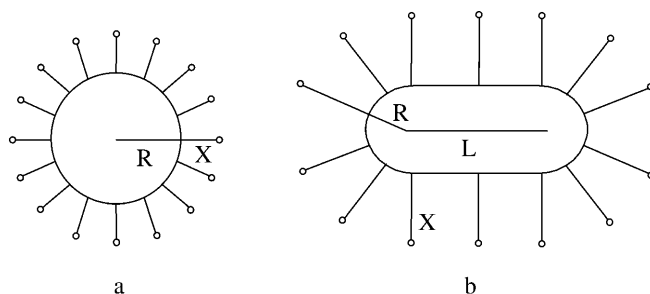


**Fig. 1 a** An example body-limb network with a circle-node, The Max-MST model's predicted "fractional" number of limbs $N_{circle}$ (see text) is the greatest number of limb-wires that can be placed around the circle-node while keeping the distance between the limb-tips greater than $X$. The limb-tips must be separated by at least a distance $X$ because, otherwise, a cheaper wiring network can be constructed by deleting one of the limb-wires and adding a wire between the limb-tip nodes. **b** An example body-limb network with a stretched circle-node. I consider the semicircular ends and straight sides separately. The two semicircular ends are assumed to have the same predicted number of limbs as for a single circle. For the straight sides, limbs on the same side cannot be nearer than $X$ lest it be possible to delete one limb-wire and add a wire between the limb-tip nodes, thereby creating a cheaper wiring layout. Thus there can be $s = L/X$ limbs on each side, where $s$ is the "stretch ratio." In 65 of the cases presented here $s \neq 0$, and to observe in a single plot (see Figs. 2 and 3) how well the data conform to the Max-MST model, the dependence on the stretched circle length can be eliminated by "unstretching" the actual number of limbs as follows: (i) given the limb ratio $k$ and the stretch ratio $s$, the percent error E between the predicted and actual number of limbs is computed; (ii) the predicted number of limbs for a circular body is computed by setting $s = 0$ (and keeping $k$ the same); and (iii) the "unstretched actual number of limbs" is computed as having percentage error from the predicted number of limbs for a circular body. This rids of the dependence on $s$ while retaining the percentage error. [An interactive program may be accessed on-line at http://www.erols.com/ebolz/mst/mst.html allowing one to visualize the large-scale morphology of animals with given values for the limb ratio and stretch ratio.]

around it on a circumference comprises an equidistance network, no matter which pairs of points have wires connecting them. An *X-D-equidistance network* is an equidistance network for which all nodes lie in dimension $D$ and the distance from the body node to the other nodes is $X$. A network is a *spanning tree* if: (i) between any two nodes there is a path, possibly indirect, from one to the other along wires in the network (i.e., the network is *connected*), and (ii) when one leaves a node along a wire, the only way back to that node is along the same wire (i.e. the network has no *cycles*). Informally, a spanning tree is just a way of connecting up the nodes using wires such that there are no loops. Body-limb networks are spanning trees, but some other types of equidistance network are not; e.g. one in which every pair of nodes has a wire directly connecting them (i.e. a *fully-connected* network). There are also non-body-limb equidistance networks that are spanning trees: for example, where a single limb wire emanates from the body node to a limb-tip node, and a wire emanates, in turn, from this limb-tip node and successively connects, one by one, all the limb-tip nodes along the perimeter.

If an animal's actual body-limb network is in dimension $D$ and has limb wires of length $X$, then the set of all spanning tree $X$-$D$-equidistance networks with the

same body node can be thought of as the set of all possible large-scale morphologies for that animal. That is, the set of all spanning tree $X$-$D$-equidistance networks with a given body node is, intuitively, the set of all possible ways for that body to reach out to distances $X$ within dimension $D$. My model, below, says that of all these possible ways – i.e. of all these possible animal large-scale morphologies – one of them, in particular, is actual. One might complain that many of these "possible large-scale morphologies" are implausible as they possess a wire between limb tips (i.e. many of them are not body-limb networks). Real limbs will surely, the complaint might go, travel straight from body to limb tip. However, it is not obvious a priori that this should be the case. A limb whose limb-tip has wires to, say, the two nearest limb-tips would be a sort of branched limb structure, something seemingly not discountable via a priori considerations alone. Nevertheless, the model will do more than conclude the – let us assume obvious – point that an animal's large-scale morphology is a body-limb network. It will tell us which of all possible body-limb networks is the actual one.

A network is a *minimal spanning tree* (MST) if it is a spanning tree that, over all possible spanning trees on those nodes, uses the least amount of wire. Informally, a MST is an optimal way of connecting up the nodes with wires. While body-limb networks are spanning trees, they need not be MSTs. For example, a body-limb network with a point-sized body node and one million limb-tip nodes is not a MST since there are less costly ways of spanning those nodes (see the "six-wire result" in Materials and methods). My model's first principle, or assumption, is that animals have optimally wired large-scale morphologies; that is, animal body-limb networks are MSTs.

A node's *degree* is the number of wires touching it in the network. For example, in a body-limb network the body node's degree is equal to the number of limbs, and each limb-tip node's degree is one. An $X$-$D$-equidistance network has *maximum degree* if its body node has the maximum degree over all $X$-$D$-equidistance MST networks with that body node. Informally, an $X$-$D$-equidistance network has maximum degree if its body node is the most well-connected it can possibly be in any optimally wired large-scale morphology. My model's second (and last) principle, or assumption, is that animals have large-scale morphologies with maximum degree; that is, animal body-limb networks have maximum degree.

Now I may state the Max-MST model in full: an animal's body-limb network is a maximum degree minimal spanning tree. Crudely, the model states that a limbed animal has as many limbs as possible while still being optimally wired. We will see in the next section that the Max-MST model predicts a certain relationship between the number of limbs and the body-to-limb proportion.

## 3 Materials and methods

In this study limbs are assumed: (a) to intersect the animal on a single plane (the "limb plane"), (b) to project out from the animal along the limb plane, (c) to be uniform in length, (d) to be uniform in diameter (i.e. uniform "cost" per unit length), (e) to be straight, (f) to be perpendicular to the perimeter, and (g) to be uniformly distributed around the body node. It is rare that an animal strictly satisfies all of these assumptions, but the animals examined here come close to satisfying them, and for each I assume that all the assumptions hold. A note on (b): Animal limbs are rarely fixed in place, and they very often move out of the plane. However, I consider an animal to satisfy requirement (b) if the limbs are *capable* of lying in the plane. For example, sea stars (Asteroidea) can move their limbs out of the plane, but I treat them as if they are always flat. And an octopus (Cephalopoda), although satisfying (a), usually has its limbs out of the plane; nevertheless, it is able to have its limbs along the plane and so I consider it to satisfy (b). Note that most mammals do *not* satisfy requirement (b), since their limbs are projected ventrally (i.e. projecting down toward the ground). There is a reason besides simplicity for this supposition that the number of limbs is set as if the limbs are always in the plane: over all angles for which the limbs may uniformly be directed out of the plane, the convex hull of the limb-tips (i.e. the geometric figure created by consecutively drawing lines from limb-tip to nearest limb-tip) has the greatest perimeter when the angle is 0°. Thus, it is when the limbs are in the limb plane that, all things being equal, there is the greatest number of limbs needed.

Body-limb networks, and equidistance networks more generally, have been confined to have limb-tip nodes that are points. The body node, however, has not been required to be a point; the body node is free, in fact, to be any shape. In order to apply the Max-MST model to a real limbed animal, assumptions must be made about the animal's body shape, and the body node's shape must be set accordingly. The cross-section of an animal on the plane where the limbs emanate is the only aspect of an animal's shape we are interested in with respect to the Max-MST model; it is this cross-section that is to be modeled by the body node. I will call this cross-section the "body." We wish to allow the body node to vary in shape so as to capture a range of animal bodies.

Let us begin with an animal whose body size is very small compared to the limb length. We can treat such a case as if the body node is a point. Of all possible planar MSTs to which a point-sized node may belong, the maximum number of wires at that node is well-known to be six; this is the Max-MST model's predicted number of limbs for this case. The reason for the number six is that if there are more than six wires, then two must have an angle between them of less than 60°, in which case the distance between the limb tip nodes is less than the length of the limbs, and a less costly spanning tree can be built by deleting one of the limb wires and adding a wire between the limb tip nodes [such a six-wire result applies to some types of neurons (Cherniak et al. 1999)].

Alternative assumptions about an animal's body shape lead to alternative predictions by the Max-MST model. I consider a class of body shapes for which the one above (the point-sized one) is a limit case. I will

introduce the class in two steps that progressively generalize the six-wire case. In all cases the limbs will be assumed to have length $X$.

The first step is to allow the node representing the body to be a circle with radius $R$ rather than a point (Fig. 1a). This allows for the fact that animal body size is sometimes not negligible compared to the limb length. For example, a sea star (Asteroidea) may be idealized to have a body that is a circle (and limbs that project radially and symmetrically around it in a plane). Under this circle-node body shape assumption, the Max-MST model's predicted fractional number of limbs is given by the continuous function $N_{\text{circle}}(k) = 2\pi/\arccos(1 - k^2/2)$, where $k = X/(R + X)$ is the "limb ratio," the ratio of the limb length to the total length from circle center to any limb-tip. As the body becomes small compared to the limb length (i.e. as $k$ approaches unity), $N_{\text{circle}}$ approaches six as in the six-wire case. As the body becomes large compared to the limb length (i.e. as $k$ approaches zero), $N_{\text{circle}}$ approaches infinity.

The second step is to allow the node representing the body to be a "stretched" circle, where the circle-node is cut in half, the two semicircles moved apart a distance $L$, and two straight lines "stretched out" to form the sides of the animal body (Fig. 1b); this collapses to the circle-node case above when $L = 0$. This allows the accommodation of animals whose bodies are extended in length rather than circular. For example, a centipede (Myriapoda) may be idealized to have a body that is a stretched circle (and limbs that project perpendicular to and uniformly distributed along the perimeter). The Max-MST model's predicted fractional number of limbs for the stretched circle-node body shape is given by the continuous function $N_{\text{stretched}}(k,s) = N_{\text{circle}}(k) + 2s$, where $s = L/X$ is the "stretch ratio," the ratio of the stretched length $L$ to the limb length $X$. Note that spherical nodes can in principle be studied using mathematics in Coxeter (1962).

Note that the model does not apply to animals without limbs. The model states that there is a relationship between an animal's number of limbs and its body-to-limb proportion. Without limbs, the model can say nothing. Or, if having no limbs is treated as having limbs with zero limb ratio, then the model predicts infinitely many non-existent limbs. Snakes and other limbless organisms are therefore not counterexamples to the Max-MST hypothesis.

What counts as a limb? 'Limb' is being used here in a general sense, applying to "appendages that reach out." This covers, for example, legs, digits, tentacles, oral arms, antennae and parapodia. Although for any given organism it is usually obvious what appendages should count as limbs, a general rule for deciding which appendages to count as limbs is not straightforward. Some ad hoc decisions were required. For vertebrate legs only the those of Amphibia were studied, as their legs are the least ventrally projected of the vertebrates. For amphibians, the head and tail were included in the limb count because there is an informal sense in which the head and tail also "reach out". Thus, amphibians have six "limbs" in this study. For insects (and other invertebrates with antennae studied here), antennae appear to be similar in "limb-likeness" to the legs, and so were counted as limbs unless they were very small (less than around 1/3) compared to the legs. The head and abdomen of insects were *not* counted as limbs (i.e. they were treated as part of the body) because, in most cases studied, they are well inside the perimeter of the legs and antennae, and thus do not much contribute to "reaching out." The overall fit of the Max-MST model to the data is robust to these where-to-draw-the-line decisions. That is, the Max-MST model is expected only to explain the broad trend in the relationship between limb number and body-to-limb ratio, and not generally to be predictive of the exact number of limbs in any given organism (it is predictive, perhaps, of the logarithm of the number of limbs). Adding or taking away a leg or two here and there does not affect the results.

Digits are treated in the same manner as other types of limbs, the only difference being that only a fraction of the body (i.e. hand) perimeter has limbs (i.e. digits). Digits were studied only in cases where the "hand" is a stretched circle with digits on roughly one half of the stretched circle. For these cases hands may be treated as if the digits emanate from only one "side" of the node. Digits like those on a human foot are, for example, not studied because the foot is not a stretched circle for which the toes are distributed along one half of it.

From published sources (Agur 1991; Barnes 1963; Bishop 1943; Brusca and Brusca 1990; Buchsbaum 1956; Buchsbaum et al. 1987; Burnie 1998; Downey 1973; Hegner 1933; Netter 1997; Parker 1982; Pearse et al. 1987; Pickwell 1947; Stebbins 1954) I measured the number of limbs, limb ratio ($k = X/(R + X)$) and stretch ratio ($s = L/X$) for 190 cases over 15 classes in 7 phyla. Measurements were made on the photographs and illustrations via a ruler with half millimeter precision. The classes were included in this study if six or more data points from within the class had been obtained. Species within each class were selected on the basis of whether usable data could be acquired from the above sources (i.e. whether the limb ratio and stretch ratio were measurable).

## 4 Results

The number of limbs ranged from 4 to 426. Figure 2 shows a scatter plot of the unstretched (see legend of Fig. 1b) actual number of limbs $N$ versus the body ratio (defined as $b = R/(R + X)$ or, equivalently, $b = 1 - k$). One can see that there is a clear trend for a greater number of limbs as the body ratio increases; i.e. more limbs correlates with shorter limbs relative to the body. And as the body ratio approaches zero, the number of limbs tends toward around six, which is what we would expect from the six-wire result. Figure 3 shows a plot of average $\log(N)$ versus $-\log(k)$, along with the best-fit and predicted lines, which can be seen to match closely.

Table 1 shows overall percent error values between the predicted and actual number of limbs. The mean error for all 190 animals is 17.80% (SD $\pm$ 58.29%).
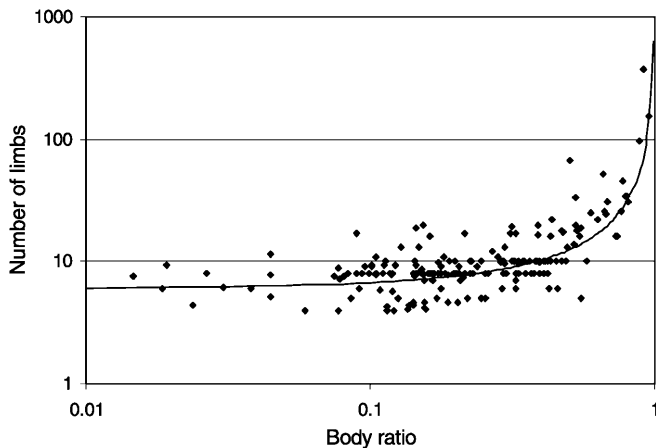
**Fig. 2.** The unstretched actual number of limbs as a function of the body ratio. In order that the digit cases be treated in the same manner as the limbs, the actual number of digits is multiplied by two; i.e. digit cases are plotted as if hands have digits distributed all the way around them rather than half way. The Max-MST model's predicted curve $N_{\mathrm{circle}}(k) = 2\pi/\arccos(1 - k^2/2)$ is shown



**Fig. 3.** The average of $\log_{10}(N)$ values versus $-\log_{10}(k)$, where the $-\log_{10}(k)$ values are binned with width 0.01. $N$ is the unstretched actual number of limbs. Error bars indicate standard deviation (for points obtained from bins with two or more cases). The points plotted in this fashion are expected, according to the Max-MST model, to increase in a nearly linear fashion. The reason is as follows: the Max-MST model's formula $N_{\mathrm{circle}}(k) = 2\pi/\arccos(1 - k^2/2)$ is closely approximated by $N_{\mathrm{approx}} = 2\pi/k$. The percentage difference between them is around 4.72% when $k = 1$ and falls linearly toward zero as $k$ approaches 0. $N_{\mathrm{approx}}$ is linear when graphed here, as its equation is $\log_{10}(N_{\mathrm{approx}}) = -\log_{10}(k) + \log_{10}(2\pi)$. Thus, the Max-MST model predicts a line roughly with equation $y = x + 0.798$. How do the plotted points fit with this predicted line? They indeed appear to be linear ($r^2 = 0.777$, $n = 52$, $p < 0.001$), and the best-fit line, computed using linear regression, is $y = 1.206x + 0.787$; this $y$-intercept corresponds to 6.12 limbs when $k = 1$, fitting well with the six-wire expectation. The percent error of the slopes is 20.60%, and the percent error of the $y$-intercepts is 1.38%. The three rightmost data points exert a disproportionate influence on the best-fit line, and removing them results in the equation $y = 1.112x + 0.807$ ($r^2 = 0.631$, $n = 49$, $p < 0.001$), a percentage error of 11.2% for the slopes, and a percentage error of 1.13% for the $y$-intercepts. All 190 cases plotted without binning leads to $y = 1.171x + 0.795$ ($r^2 = 0.647$, $n = 190$, $p < 0.001$), a percentage error of 17.1% for the slopes, and a percentage error of 0.38% for the $y$-intercepts. (Digits are treated as in Fig. 2.)

Histograms (not shown) of the frequency-distribution of percent error values demonstrate that the values are skewed and that the (natural) log errors better approximate a normal curve (as confirmed by linear regression analysis of a Q-Q normality test). An inverse of the mean of the log errors (the "log transformed mean") is thus a better representative of the mean. The log transformed means can be found in Table 1, and for all 190 animals is 8.79% (SD ± 42.00%). This lower overall error value is reinforced by the similarly sized overall median of 8.85%.

The variance is large in all the analyses just discussed, and is due to two main factors besides measurement error (which is not a significant source of the variance). First, the stretched circle-node characterization of animal large-scale morphologies is an extremely crude approximation. Animal bodies are not exactly stretched circles (neither in shape nor in planarity), their limbs are often not of equal length, they are often not uniformly distributed around the body, and so on (see Materials and methods). Richer and more realistic ways of characterizing animal large-scale morphologies would be expected to lower the variance. Second, an animal's large-scale morphology is a result of many evolutionary pressures in addition to the pressure for a wire-economical shape. We should therefore not be surprised at the large variance, but surprised at the degree to which the Max-MST model's signal can be seen through the "noise."

The Max-MST model's low error values for limbs may be contrasted with high errors in cases of ciliary rings: for 11 cases (among annelids, molluscs and sipunculans) ranging in cilia number from 14 to 211, the mean error is 90.00% (SD ± 132.36) and log transformed mean error is 85.26% (SD ± 90.96%). The Max-MST model therefore does not appear to apply to cilia, although the trend still seems to exist for a greater number of cilia as the body ratio increases.
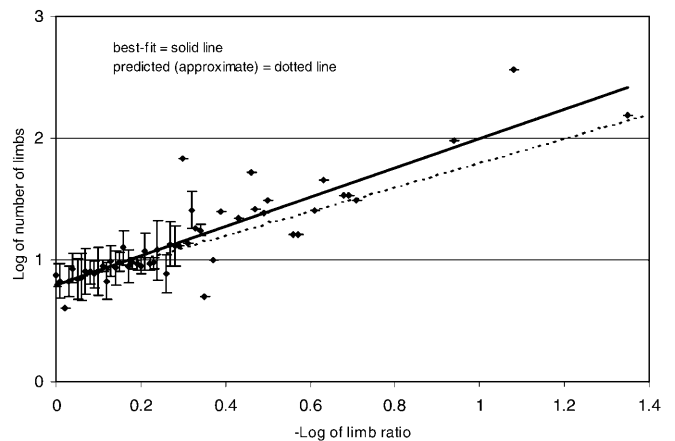
## 5 Discussion

Whereas there are ontogenetic explanations for why organisms have the number of limbs or digits they do (Shubin et al. 1997), there are few adaptation-based explanations for this (Gans 1975; Lande 1978; Gould 1993). The discovery of polydactylous (having more than five digits) tetrapods (four-legged animals) (Coates and Clack 1990) makes the search for an adaptation-based explanation for the pentadactyl (five digit) limb more pressing (Gould 1993). My Max-MST model neither provides an adaptation-based explanation for the pentadactyl limb nor for the number of limbs or digits of animals, generally. Rather, it provides an adaptation-based explanation for the *relationship* between this number and the relative sizes of the body (or hand) and the limb (or digit). However, if an adaptation-based explanation could be given for an organism's body-to-limb proportion, then my model may fill the gap in explaining the number of limbs.

My main points are the following: (i) the large-scale morphology is near-optimal, in the sense of minimally-

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**Table 1.** Summary statistics for max-MST hypothesis, showing percentage errors between the unstretched actual number of limbs and the Max-MST model's predicted number of limbs, where the error is computed as 100(actual − predicted)/predicted. Since the predicted limb numbers tend to be less than the actual numbers, having the predicted number in the denominator increases the error. The log transformed mean percentage errors were obtained by adding 100% to each error (to ensure that it is greater than unity), taking the natural logarithm of each, computing the mean of the logs, computing the exponential of this mean, and finally subtracting 100%. For digits the number of digits is half of what is shown (see legend of Fig. 2)

| Phylum | Class | $n$ | Number of limbs ($N$) | | Percentage error | | | Log-transformed percentage error | |
|---|---|---|---|---|---|---|---|---|---|
| | | | Min | Max | Mean | SD | Median | Mean | SD |
| Class by class | | | | | | | | | |
| Annelida | Polychaeta | 8 | 30 | 426 | 39.10 | 50.29 | 25.79 | 32.77 | 42.02 |
| Arthropoda | Myriapoda | 7 | 28 | 56 | 71.75 | 66.53 | 48.05 | 60.82 | 65.16 |
| | Insecta | 8 | 6 | 8 | −20.57 | 14.06 | −17.65 | −21.73 | 14.65 |
| | Pycnogonida | 6 | 8 | 12 | 36.79 | 26.97 | 30.41 | 34.72 | 25.56 |
| | Chelicerata | 24 | 8 | 12 | 18.09 | 13.71 | 15.73 | 17.30 | 14.10 |
| | Malacostraca | 13 | 8 | 10 | 15.64 | 11.34 | 12.93 | 15.12 | 11.44 |
| Cnidaria | Hydrozoa | 21 | 4 | 68 | 59.83 | 106.40 | 28.71 | 37.07 | 78.57 |
| | Scyphozoa | 18 | 4 | 368 | 30.54 | 98.08 | 5.12 | 10.67 | 62.65 |
| Echinodermata | Holothuroidea | 7 | 8 | 18 | 32.23 | 27.79 | 40.98 | 29.46 | 29.89 |
| | Asteroidea | 22 | 5 | 34 | 8.03 | 51.09 | 0.69 | −1.76 | 45.08 |
| Mollusca | Cephalopoda | 10 | 8 | 8 | 8.34 | 10.04 | 7.49 | 7.91 | 10.19 |
| Vertebrata | Amphibia | 10 | 6 | 6 | −38.87 | 2.74 | −38.33 | −38.92 | 2.76 |
| Tardigrada (digits) | | 8 | 6 | 16 | 3.94 | 21.20 | 3.80 | 2.21 | 19.81 |
| Vertebrata (digits) | Mammalia | 6 | 10 | 10 | 0.08 | 8.02 | −2.81 | −0.17 | 7.72 |
| | Reptilia | 7 | 8 | 10 | 13.37 | 12.14 | 10.99 | 12.83 | 11.87 |
| | Amphibia | 15 | 8 | 10 | −10.44 | 12.13 | −12.58 | −11.22 | 12.31 |
| Phylum by phylum | | | | | | | | | |
| Annelida (parapodia) | | 8 | 30 | 426 | 39.10 | 50.29 | 25.78 | 32.76 | 42.02 |
| Arthropoda (legs) | | 58 | 6 | 56 | 20.62 | 35.38 | 14.62 | 16.41 | 30.91 |
| Cnidaria (tentacles or oral arms) | | 39 | 4 | 368 | 46.31 | 102.40 | 11.56 | 24.17 | 71.30 |
| Echinodermata (arms) | | 29 | 5 | 34 | 13.88 | 42.27 | 10.30 | 5.00 | 45.03 |
| Mollusca (arms) | | 10 | 8 | 8 | 8.34 | 10.04 | 7.49 | 7.91 | 10.19 |
| Vertebrata (limbs, head and tail) | | 10 | 6 | 6 | −38.87 | 2.74 | −38.33 | −38.92 | 2.76 |
| Tardigrada (digits) | | 8 | 6 | 16 | 3.94 | 21.20 | 3.80 | 2.21 | 19.81 |
| Vertebrata (digits) | | 28 | 8 | 10 | −2.23 | 14.92 | −1.33 | −3.34 | 15.00 |
| All cases | | 190 | 4 | 426 | 17.80 | 58.29 | 8.85 | 8.79 | 42.00 |

wired, in many animals over seven phyla; (ii) these animals' bodies have the maximum number of limbs possible in any such optimal body plan; and (iii) animals with such optimal large-scale morphologies satisfy a relationship between the number of limbs and the body-to-limb proportion, so that given one we can approximate the other.

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