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Abstract
An insect wing consists of a thin membrane supported by a system of veins, and flow of blood through the system of veins is critical for maintaining healthy insect wings. Better understanding of the insect wing vein circulation requires to know how the efficiency of blood flow in an insect wing relates to the geometric shape of the vein. Our investigation of the wing vein network of a dragonfly *Anax junius* follows the idea of Murray's law, which is established in the study of efficiency of the vein network and the geometric shape of the vein. Instead of using the classic Murray's law for circular cross-sections, we derived a variation of the Murray's law for vein cross-sections of equilateral triangles. Then, we evaluated the conformity of the studied wing vein network to Murray's law by measuring the diameter of veins of the forewing of *A. junius*. Our data suggest that the vein network does not abide by the class Murray's law and support that the shape of the vein is not cylindrical.

Keywords: Murray's law, Hagen-Poiseuille flow, vein network, geometry, transport optimization

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Introduction

An insect wing includes a network of veins in which longitudinal veins are connected to each other by cross-veins. Many insects share the well-defined wing circulatory flow route in which hemolymph enters the wing via the anterior veins, flows toward the wing tip, and returns through the posterior veins back to the thorax [1, 2]. Blood (or hemolymph) flow through wing veins provides water and nutrients to and removes waste products from live cells hosted in veins [1, 3]. Hemolymph flow through the network of wing veins is important for maintaining the health and functionality of insect wings.

The vein system of an insect wing may be viewed as a network and analyzed to better understand the hemolymph flow patterns and hemolymph distribution throughout the insect wing. If one assumes the general shape of any given wing in the vein network takes the form of a cylinder and that the hemolymph flow is laminar, it is well-known that the optimality of the hemolymph flow throughout the wing is determined by the conformality of the geometry of a particular vein intersection to Murray's law [4].

More specifically, Murray's law states that, in a flow network where cost for transport and maintenance of the transport medium is at a minimum, if a given vein of radius r splits into two veins of radii r_1 and r_2, then necessarily $r^3 = r_1^3 + r_2^3$. This is generalized for a single vein of radius r splitting into n branches:

$$r^3 = r_1^3 + r_2^3 + \ldots + r_n^3 \tag{1}$$

The use of the standard version of Murray's law to analyze hemolymph transport has been accomplished in studies such as [5].

However, the cross-sectional shape of veins in an insect wing network is not consistently cylindrical. For instance, the fore wing of a dragonfly *C. servilia* Drury had various cross-sectional shapes for its veins [6]. As such, Eq. (1) based on the circular cross-sections may be valid for limited areas of a wing where vein cross-sections are circular.

In this study, we derived alternate versions of Murray's law for different geometric shapes of the vein. Since dragonflies have been studied most for biomimetic wings [7-11], we chose Common Green Darner (*Anax junius*), a commonly found dragonfly in Nebraska, as a representative insect. Among common regular shapes such as rectangles, ellipses and triangles, the most interesting case is when we assume the vein is of the shape of an equilateral triangle. In this case, the theoretic data suggested by this version of Murray's law is most conformed with the real measurement we obtained from a real dragon wing model.

Materials and Methods

Murray's law for vein cross-sections of equilateral triangles

Murray's law is derived from the Hagen-Poiseuille equation for laminar flow [4, 12-14], which describes incompressible laminar flow of a Newtonian fluid in a cylindrical vein. To derive analogous versions of Murray's law for veins whose cross-sections take on the shape of an equilateral triangle, we follow the results by Murray [13] and Rosen [14] in assuming that the power required to support the system of blood vessels is the sum of the power required to maintain the flow of blood, P_{Flow}, with the power required to maintain the health of the cells that the blood supplies with energy, P_{Supply}. Therefore, the equation for total power is given by

$$P_{Total} = P_{Flow} + P_{Supply} \tag{2}$$

If Q denotes the flow rate through a blood vessel, and ΔP represents the change in pressure, then the power required to maintain the flow of blood through the vessel is modelled by

$$P_{Flow} = Q\Delta P \tag{3}$$

When it comes to the power required to maintain the cells that the vessel feeds, it is assumed to be proportional to the volume of the vessel. That is,

$$P_{Supply} = KV \tag{4}$$

where K is the metabolic factor, which is a positive constant, and V is the volume of the vessel.

Now, denote by r the distance between the center of an equilateral triangle with side length h and any vertex. Then,

$$r = \frac{h}{\sqrt{3}} \tag{5}$$

The volume flow rate Q through a tube where the cross sections are equilateral triangles is given in [15] by

$$Q = \frac{Gh^4}{60\sqrt{3}\mu} \tag{6}$$

where G is the magnitude of the pressure gradient in the flow direction (= $-\mathrm{d}P/\mathrm{d}x$,), and μ denotes the dynamic viscosity of the hemolymph. Both are assumed to be constant. Since G is a constant, one may take $G = -\Delta P/\Delta x$ to lend that for a pipe of length $\Delta x = -l$, and then we have the expression $G = \Delta P/l$. This expression for G is substituted back into Eq. (6) for Q, and then ΔP is solved for:

$$\Delta P = \frac{60\sqrt{3}\,\mu l Q}{h^4} \tag{7}$$

Substituting the expression for ΔP from Eq. (7) into Eq. (3), we have,

$$P_{Flow}(h) = \frac{60\sqrt{3}\,\mu l Q^2}{h^4} \tag{8}$$

Next, the volume of an equilateral triangular prism is given by

$$V(h) = \frac{\sqrt{3}}{4} h^2 l \tag{9}$$

Then, substituting Eq. (9) into Eq. (4),

$$P_{Supply}(h) = \frac{\sqrt{3}}{4} K h^2 l \tag{10}$$

Combining Eq. (8) and Eq. (10) in Eq. (2), the following equation for total power is obtained:

$$P_{Total}(h) = \frac{60\sqrt{3}\mu l Q^2}{h^4} + \frac{\sqrt{3}Kh^2 l}{4} \tag{11}$$

The power to maintain an entire circulatory system is just the sum of the power functions for each individual blood vessel segment. For any blood vessel whose cross-section is an equilateral triangle, there is an optimal side length h of the equilateral triangle such that the power required to maintain the flow of blood through the vessel and to feed the cells is minimized. At such an optimal length h, the derivative of PP with respect to h must be zero. Hence, we differentiate Eq. (11) with respect to h, and set $\mathrm{d}P_{Total}/\mathrm{d}h = 0$ to solve for the optimum h. This lends the equation

$$-240\sqrt{3}\,\mu l Q^2 + \frac{\sqrt{3}}{2}Kh^5 l = 0 \tag{12}$$

Solving Eq. (12) for Q gives the following relation between the flow rate and the optimum side length:

$$Q = \sqrt{\frac{K}{480\mu}}\,h^{2.5} \tag{13}$$

Finally, the new version of Murray's law is retrieved by using the fact that, for a vein of flow rate Q branching off into n branches with respective flow rates Q_1, Q_1, …, Q_n, we have

$$Q = Q_1 + Q_2 + \ldots Q_n \tag{14}$$

and thus, substituting Eq. (13) into Eq. (14) for a branch of side length h branching off into n branches of respective side lengths h_1, h_2, …, h_n, we have

$$h^{2.5} = h_1^{2.5} + h_2^{2.5} + \ldots h_n^{2.5} \tag{15}$$

To recover the standard form of Murray's law, one can replace V in Eq.

(9) by $\pi r^2 l$, where r is the radius of the vein now taking on the shape of a tube, and Q in Eq. (6) by $\pi r^4/8\mu l$, before minimizing resulting power Eq. (2) with respect to the radius of the tube r.

Measurement of vein diameter

A high-resolution picture of a fore wing of *A. junius* was taken using a digital SLR camera (Canon EOS Rebel T3), and the picture was converted to a black-and-white image as shown in **Figure 1**. Measurements of the width or diameter of the wing veins at a particular intersection were made using the measurement tools in Photoshop (Adobe).

Figure 2 shows how the diameter of a given vein segment was measured. First, two different locations in a particular vein segment were selected, and lines were drawn at the two places, edge to edge, at no particular angle. The centers of these two lines are marked as p_1 and p_2 in Figure 2. Second, a line was drawn between p_1 and p_2, as shown is blue. Third, lines were drawn precisely perpendicular to the central blue line, which are the black dotted lines. Fourth, the length of the dotted lines was recorded as the various diameters d_1, d_2, and d_3. Last, the diameter d of the vein segment was determined as the average of these three values. At any given intersection, the diameter of all veins in the intersection are measured in this fashion as shown in **Table 1**.

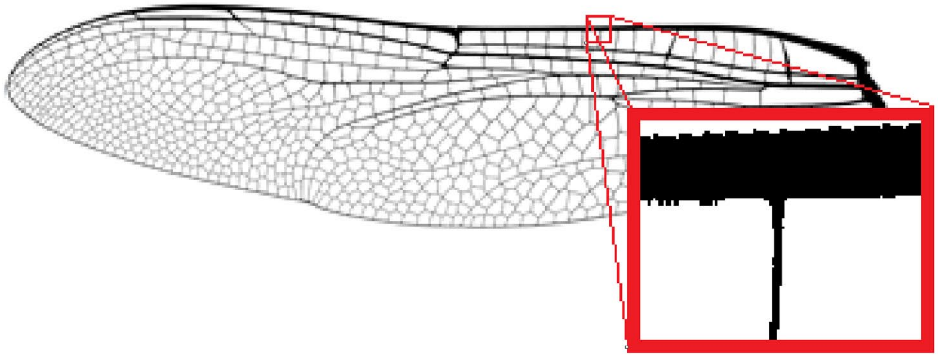


Figure 1. Black-and-white image of the fore wing of *Anax Junius* wing. Inset: An example of the intersection of wing veins for vein width measurement.

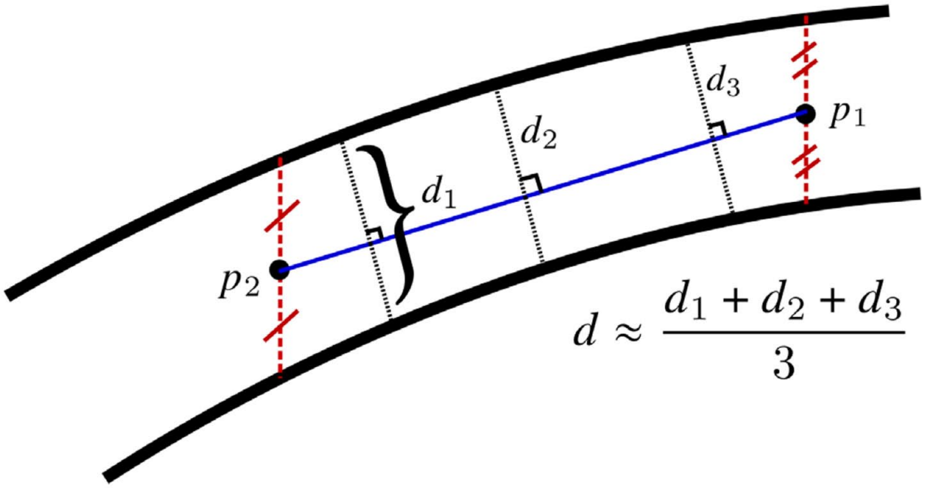


Figure 2. Measurement of the vein diameter using the black-and- white image of the insect wing.

Measurement of conformity to Murray's law

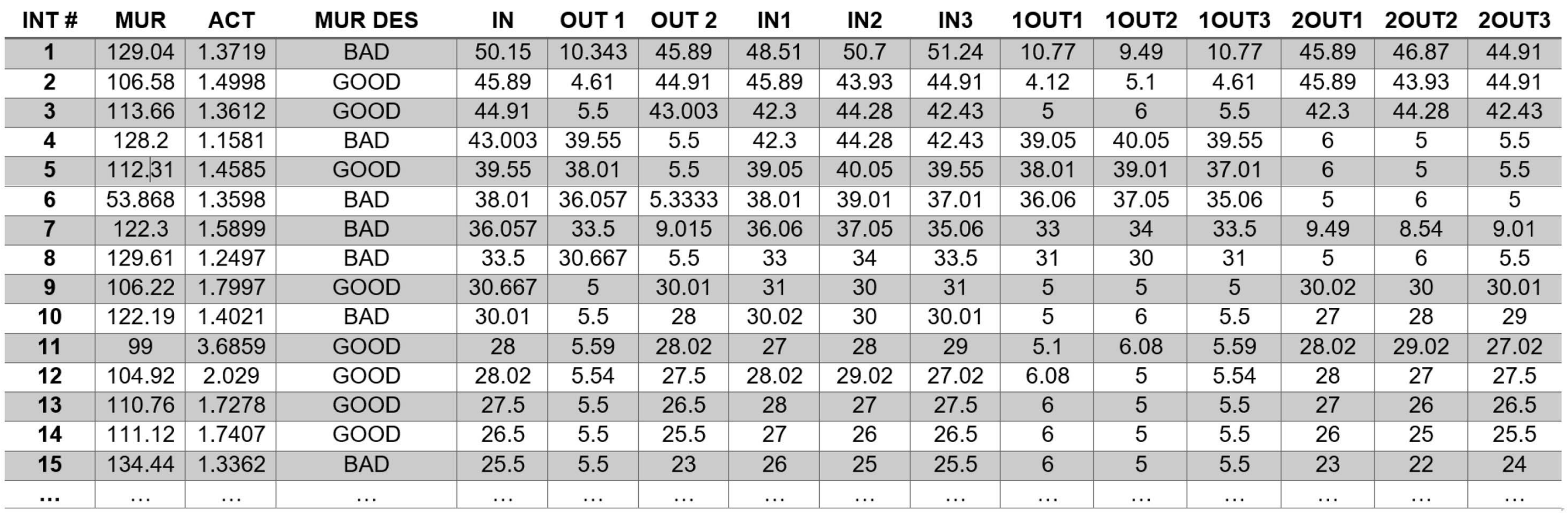
We assigned a conformity rating C at each intersection of the vein network as follows. At each intersection, the measurements for diameter of each adjacent branch were taken as explained above. Let d denote the diameter of the thickest branch which splits into n branches of respective diameters d_1, d_2, …, d_n. Then, a rating of conformity to Murray's law is given by the quotient

$$C = \frac{\sum_{i=1}^{n} d_i^x}{d^x} \times 100\% \tag{16}$$

When $x = 3$, we retrieve the conformity rating for the classic version of Murray's law [i.e., Eq. (1)], where $d_i = 2r_i$. When $x = 2.5$, we retrieve the conformity rating for the variation of Murray's law in Eq. (15) for a vein taking on the cross-sectional shape of an equilateral triangle, where $d_i = 2r_i = 2h_i/\sqrt{3}$.

In both cases, if the value of C is within the range of 100 ± 20%, then the conformity to Murray's law is designated as "good conformity". Any other value of C is "bad conformity". If the intersection has good conformity, then it abides by the corresponding Murray's law for the vein system.

Table 1. Examples of measured vein diameters, conformity to Murray's law, and found "perfect" exponent



INT #	MUR	ACT	MUR DES	IN	OUT 1	OUT 2	IN1	IN2	IN3	1OUT1	1OUT2	1OUT3	2OUT1	2OUT2	2OUT3
1	129.04	1.3719	BAD	50.15	10.343	45.89	48.51	50.7	51.24	10.77	9.49	10.77	45.89	46.87	44.91
2	106.58	1.4998	GOOD	45.89	4.61	44.91	45.89	43.93	44.91	4.12	5.1	4.61	45.89	43.93	44.91
3	113.66	1.3612	GOOD	44.91	5.5	43.003	42.3	44.28	42.43	5	6	5.5	42.3	44.28	42.43
4	128.2	1.1581	BAD	43.003	39.55	5.5	42.3	44.28	42.43	39.05	40.05	39.55	6	5	5.5
5	112.31	1.4585	GOOD	39.55	38.01	5.5	39.05	40.05	39.55	38.01	39.01	37.01	6	5	5.5
6	53.868	1.3598	BAD	38.01	36.057	5.3333	38.01	39.01	37.01	36.06	37.05	35.06	5	6	5
7	122.3	1.5899	BAD	36.057	33.5	9.015	36.06	37.05	35.06	33	34	33.5	9.49	8.54	9.01
8	129.61	1.2497	BAD	33.5	30.667	5.5	33	34	33.5	31	30	31	5	6	5.5
9	106.22	1.7997	GOOD	30.667	5	30.01	31	30	31	5	5	5	30.02	30	30.01
10	122.19	1.4021	BAD	30.01	5.5	28	30.02	30	30.01	5	6	5.5	27	28	29
11	99	3.6859	GOOD	28	5.59	28.02	27	28	29	5.1	6.08	5.59	28.02	29.02	27.02
12	104.92	2.029	GOOD	28.02	5.54	27.5	28.02	29.02	27.02	6.08	5	5.54	28	27	27.5
13	110.76	1.7278	GOOD	27.5	5.5	26.5	28	27	27.5	6	5	5.5	27	26	26.5
14	111.12	1.7407	GOOD	26.5	5.5	25.5	27	26	26.5	6	5	5.5	26	25	25.5
15	134.44	1.3362	BAD	25.5	5.5	23	26	25	25.5	6	5	5.5	23	22	24
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…

INT #: the intersection number, **MUR**: the respective conformity rating C_{MUR} for Murray's law for that intersection, **MUR DES**: evaluation of the conformity, **ACT**: the "actual" exponent for perfect conformity, **IN**, **OUT 1**, and **OUT 2**: the measurements for the diameter (in pixels) of each branch in the intersection used in calculation (**IN** is an average of **IN1**, **IN2**, **IN3**; **OUT 1** is an average of **1OUT1**, **1OUT2**, **1OUT3**; **OUT 2** is an average of **2OUT1**, **2OUT2**, **2OUT3)**, the columns latter to **IN**, **OUT1**, and **OUT2**: the measurements recorded as outlined in the Measurements section.

Result and Discussion

It is reasonable to assume that the conformity rate of Murray's law is directly related to the efficiency of the network. That is, the higher the conformity rate is, the more efficient the network is.

We computed the conformity to the standard Murray's law using Eq. (16), with $x = 3$ [i.e., Eq. (1)], for 165 intersections on the wing image of the *Anax Junius*, and some results are summarized in Table 1 as an example. Out of the 165 intersections examined, only about 60% of the intersections had "good" conformity to Murray's law. In particular, only 60% of the intersections analyzed had a C_{MUR} value [i.e., Eq. (16) for $x = 3$], shown in the **MUR** column of Table 1, lying between 80% and 120%. While this encompasses the majority of intersections analyzed, the slim majority indicates that the vein network does not rigorously adhere to the classic Murray's law.

Then, we computed the perfect exponent for all intersections as follows. Given a particular branch d splitting into n branches $d_1, d_2, \ldots, d_n$, one can solve the following equation for the "perfect" exponent x such that

$$d^x = d_1^{\,x} + d_2^{\,x} + \ldots d_n^{\,x} \tag{17}$$

This was done in Maplesoft using the *fsolve* function:

$$fsolve\,(d^x = d_1^{\,x} + d_2^{\,x} + \ldots d_n^{\,x},\; x = a \ldots b) \tag{18}$$

where the interval $[a, b]$ of solutions for x is enlarged until a solution is located. It needs to be noted that, in some cases, the equation had no solution, for when $d = d_i$ for some $1 \le i \le n$, an exponent x could not be calculated for that particular intersection.

The found perfect exponent values are shown in the **ACT** column in Table 1. About 65% of the intersections analyzed had a perfect exponent less than 3, which further supports our findings that the studied vein network of *A. Junius* does not rigorously follow the classic Murray's law. Instead, the average "perfect exponent" was found to be about 2.33, much closer to the exponent appearing in the equilateral triangle version of Murray's law [i.e., Eq. (15)]. Therefore, our computation suggests that the geometric shape of the vein can be better represented by equilateral triangles rather than circles in terms of the efficiency of the vein network.

Conclusion and Future Work

In this paper, we took geometric measurements of each intersection on the forewing of the *Anax junius.* With these measurements, we analyzed data on the conformity of each intersection to the classic form of Murray's law [Eq. (1)]. Furthermore, we derived a variation of Murray's law assuming the shape of the veins' cross-sections was an equilateral triangle [Eq. (15)]. Then, we analyzed data on the conformity of each intersection to this newly derived equation.

With respect to the above data collection and analysis, the vein network of the *Anax junius* is more reminiscent of a vein network where the veins take on the geometry of a triangular prism rather than a cylinder, where the standard version of Murray's law is applied.

In future research, other versions of Murray's law could be derived for vein cross-sections of other shapes — such as for ellipses. For example, if the shape of the cross section of a vein takes the form of an ellipse with semi-axes a and b, branching off into n veins with likewise geometry, one semi-axis of fixed length b and the other of respective length a_1, a_2, …, a_n, the analogy of Murray's law for ellipses can be derived and stated as

$$\frac{a^2}{\sqrt{a^2+3b^2}} = \frac{a_1{}^2}{\sqrt{a_1{}^2+3b^2}} + \dots + \frac{a_n{}^2}{\sqrt{a_n{}^2+3b^2}} \tag{19}$$

As such, versions of Murray's law such as the one above may be used to compute their own conformity ratings for each intersection on an insect wing.

* * *

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