The geometry and ecology of curved flowers and their pollinators

#### 3. What is curvature?

Reviewing the literature leads us to ask, “what is curvature?”. Turning to the field of geometry, we find several related definitions, resulting from a history of independent mathematical derivations (reviewed in Coolidge, [1952](#ref-coolidge_1952); Bardini and Gianella, [2016](#ref-bardini_2016)). Here, we follow the conventions of Casey ([1996](#ref-casey_1996)) and Rutter ([2000](#ref-rutter_2000)), and present a definition relevant to the problem of analyzing biological shapes.

Intuitively, when a line deviates from being straight we say it is curved, the extent to which it is not straight is its curvature. More technically, a line deviates from being straight when its first derivative - the tangent (shown by , , in [Figure 3](Figure_3.jpg)) - changes direction (e.g. the difference in direction of to . Therefore, curvature can be thought of as the rate of change in the tangent as we move across the curve. Hence, the tangent of a straight line has the same direction everywhere and a curvature of zero, whereas the tangents of the curve shown in [Figure 3](Figure_3.jpg) will have a non-zero curvature.

To formalize these concepts mathematically we begin by considering an ordinary function of the form , where specifies one value of for each value of . Biological curves, however, often loop back on themselves (e.g. spirals) and are better described by parametric fuctions that allow the curve to have multiple values for a single . Parametric functions use a ‘hidden’ variable that determines the values of and independently. For example, we use the parameter arc length, , along the curve. The position is solely determined by the corresponding arc length, , along the curve. We define the location along the curve by a vector , which is a function of arc length :

Where indicates that our position on the curve is determined by the length of the segment . Although we could parameterize a curve by any arbitrary variable, arc length is a convienient parameter because it allows us to move along the curve at even increments of . This proves useful when taking repeated, equally-spaced measurements along a curve, such as curvature.

If we are interested in the derivative properties of our arc-length parameterized function, we can differentiate with respect to arc length as:

The resultant tangent function is the first derivative of the parametric equation . The tangent contains information about the direction of the curve at position that we will use to calculate curvature.

At the beginning of this section we defined curvature () as the rate at which the tangent is changing direction. We can now formalize this by differentiating with respect to arc length:

Where is the second derivative of the parameteric function :

When the tangent is placed into a cartesian plane its direction is related to the angle formed with the -axis. We can then re-state curvature at a single point as:

This definition provides an intuitive unit of measurement for reporting curvature: degrees of rotation per unit arc length [(Figure 4)](Figure_4.jpg). For example, if arc length has been measured in millimeters, we would report its curvature as degrees per millimeter . Framed this way curvature is a measurement of rotation per distance. In previous defintions (reviewed in the preceeding section) curvature is an indivisble, single property of an entire shape. Here, curvature is a property of every point along the curve. Consequently, we can summarize the *total curvature* (Milnor, [1954](#ref-milnor_1954)) of a specimen. To do this, we sum the individual curvature measurements made along the curve. This is calculated as:

Units for *total curvature* are no longer expressed as because we are not measuring curvature at a single point. Instead we are summarizing all tangent rotations along the curve, expressed simply as .

To account for size variation between specimens, we propose using *total adjusted curvature*, that is, total curvature divided by arc length:

Units for are expressed as . *Total adjusted curvature* also represents mean curvature of the curve.

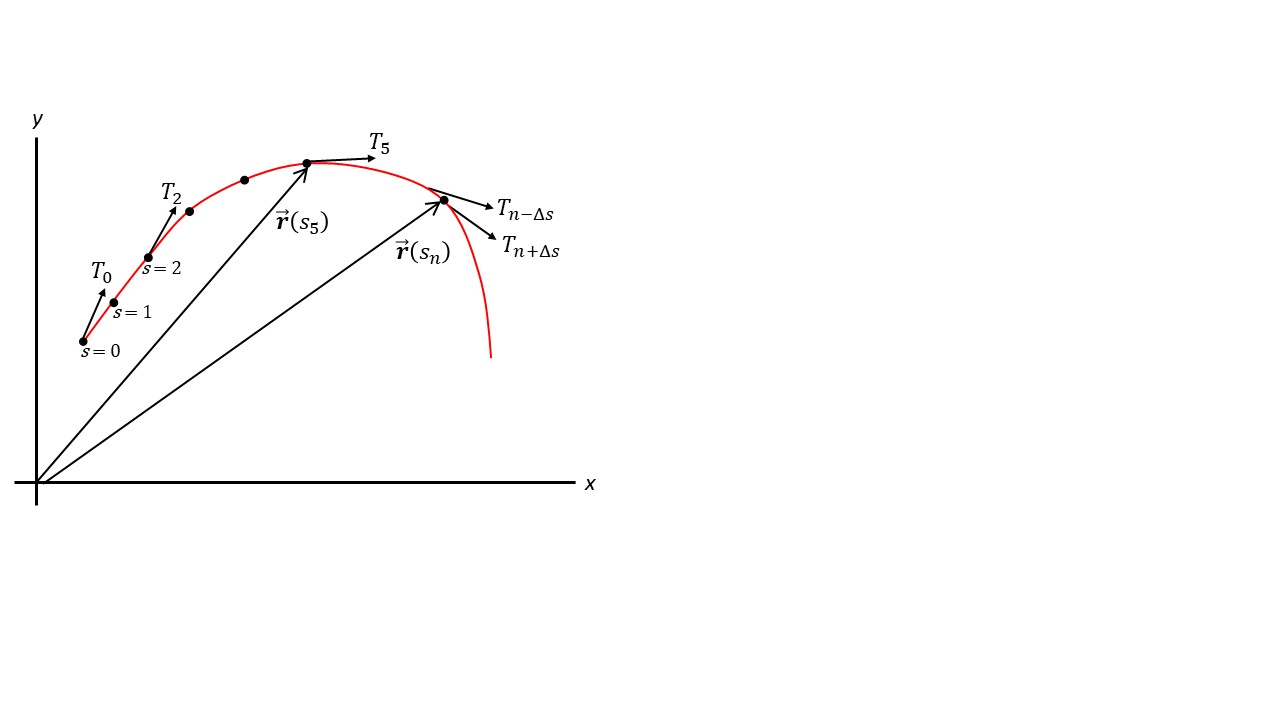


Figure 3. A curve parameterized by arc length (). When , the vector points to the location on the curve . , , and are the tangents ( ) at , , and , respectively. Curvature at is defined in equation (4).

#### 4. A proposed protocol for measuring curvature

As illustrated in the methodology review, our current protocols for measuring flower-pollinator curvature lack a conceptual unity. In each method, curvature takes on a new meaning. Therefore, there are two main advantages of the curvature definition described above. First, curvature becomes a local property of the tissue or organ under study. This means that shape information is gathered at every point along the curve and can be examined and compared to other points within or between specimens. This differs from previous methods that take curvature as a total property of the entire curve. In these measurements curvature cannot be parsed into smaller elements. Second, because the revised definition is explicitly adapted from the field of differential geometry, we benefit from citeable geometric concepts that allow us to be clear about what we mean by ‘curvature’.

In order to apply the above definition of curvature, a biological organ or tissue needs to be reduced to a continuous function. We propose a workflow as illustrated in [Figure 4](Figures/Figure_4.jpg). Cosgrove ([1990](#ref-cosgrove_1990)) uses an analogous approach to study the development of cucumber hypocotyls. By fitting cubic splines to hand-marked seedlings, curvature was computed using the same definition as above. However, since Cosgrove ([1990](#ref-cosgrove_1990)), the entire field of landmark-based geometric morphometrics has unfolded (reviewed in Adams et al., [2013](#ref-adams_2013)). This rigorous, reproducible toolkit has been used extensively in pollination ecology, but has not yet been leveraged to calculate curvature ([Table 1](Tables/Table_1.csv)). Terral et al ([2004](#ref-terral_2004)) use these tools to digitally landmark olive stones and fit polynomials to the landmarks: synthesizing the concepts of Cosgrove ([1990](#ref-cosgrove_1990)) and Terral ([2004](#ref-terral_2004)) produces a modernized method for fitting curves and computing curvature from biological forms [(Figure 4)](Figures/Figure_4.jpg)



Figure 4: Proposed protocol for measuring curvature. 1. A petal of *Epimedium violaceum* is landmarked and rotated. 2. A polynomial curve is fitted to the landmarks. 3. Curvature is calculated as the rate of change of the tangent vector at every point along the curve. Total curvature can be calculated by the methods outlined in Section 3.

Comment on why using we’re using polynomials and not splines, fourier, etc.

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