Palaeo-Math 101

Landmarks and Semilandmarks: Differences without Meaning and Meaning without Difference

In my last essay I showed how it was possible to use the information contained in landmarks to improve the alignment between boundary outline segments that are defined by a series of semilandmarks — the extended eigenshape approach (see also MacLeod 1999). This procedure raises the question of whether there are fundamental differences between landmarks and semilandmarks that should be respected in the context of any morphometric analysis and, if so, what techniques might be available for accomplishing this task. Before beginning this discussion I should, in the interest of full disclosure, point out that while many practitioners or morphometrics recognize a fundamental distinction between landmarks and semilandmarks that's so basic it's hardly ever commented upon, I represent a bit of an anomaly among this practitioner group insofar as I have never really understood either the need for, or the advantages of, drawing such a distinction. In part the existence of this unfortunate blind spot in my own approach to the characterization and analysis of form stems from my personal preference for practicality over theory, consistency over special pleading, and most importantly from my inherent suspicion that fewer errors are likely to be made if an analysis is designed to remain as close as possible to the measured geometries of the forms in question. When I undertake a morphometric analysis I always remain keenly aware that, by choosing to sample a form using either landmarks or semilandmarks, I am always under-representing the true complexity of the geometries presented to us by nature, in some cases profoundly so. If hypotheses are formulated carefully, so that there is a close match between those aspects of the forms under evaluation and those aspects that are actually being measured, this problem can be minimized. But it never goes away entirely.

Over the years I've seen inexperienced practitioners often falling into the trap of assuming that, just because they've decided to measure some specific aspect(s) of an organism's body or a component structure thereof, their results apply to the whole of the body or structure; even to those parts they have specifically not measured or sampled. Because of this I've come to see the decisions we make regarding how to sample a set of forms as the most important decisions made in any morphometric analysis. As a result I've spent an inordinate amount of time pondering the question of how best to represent the shapes nature presents to us given the mathematical tools we've devised for transforming what our eyes see into a form that our computers can help us assess. So, in the last three essays of this column I'm going to indulge myself a bit and focus on areas of morphometric analysis that I see as being among the most advanced and also, counterintuitively, among the most basic.

Let's get started by considering the relationship between landmarks and semilandmarks as tools for characterizing form. You'll remember from our previous discussions that landmarks are specific points on a biological form or image of a form located according to some rule. Landmarks with the same name are presumed to correspond in some sensible way over the forms of a data set.' (Slice *et al.*, 2008, MacLeod 2008). It is commonly accepted across the community of morphometric practitioners that landmarks come in three varieties.

> **Type I** - a mathematical point whose [topological] homology is provided by biologically unique patterns on the form (*e.g.*, juxtaposition of tissue types, small patch of some unusual histology).
>
> **Type II** - a mathematical point whose [topological] homology is provided only by geometric, not biological or histological, criteria (*e.g.*, point of maximum curvature along a boundary).
>
> **Type III** - a mathematical point having at least one coordinate that's 'deficient' in the sense that its location is logically dependent on the location of other landmarks and/or the orientation of the specimen as a whole (*e.g.*, either end of a longest diameter, or the bottom of a concavity).

Type I landmarks are the best landmarks to use, but few locations on any form — and even fewer across forms that represent different species, genera, families, *etc.* — conform to this restrictive definition. Type II and Type III landmarks both represent concessions to practicality in terms of using mathematical points to describe complex geometries. Type II landmarks are difficult to locating precisely and consistently from form-to-form, but in principal are locations that can be represented by a single point. Type III landmarks are even more problematic because they are dependent either on the orientation of the object being measured, or the placement of other landmarks. Indeed, the definition of Type III landmarks often relies on both criteria. Nevertheless, in order to get work done in morphometrics we commonly allow landmarks to be defined by any and all of these criteria. Moreover, once defined in whatever way a data analyst sees fit, the entire set of landmarks is regarded as being equal in terms of the the role each landmark plays in subsequent data analyses with no distinctions are drawn between type I, type II, or type III landmarks once their definitions have been reported in the Materials and Methods sections of a technical report.

Contrast this with the manner in which semilandmarks have been treated in the morphometric literature. While Bookstein (1991) does not use the term 'semilandmark', it is clear from his discussion of type III

landmarks that he includes all “constructions [of landmarks] involving perpendiculars or evenly spaced radial intercepts and the like.”, including “Points taken as “farthest” from other points”, in this category (both quotes taken from p. 65). Bookstein (1991) describes all type III landmarks as being “deficient” in geometric information because their placement depends on the placement of one or more other landmarks. Nevertheless, Bookstein (1991) regards type III landmarks as landmarks and notes that this is a approach to the delineation of form encountered commonly throughout multivariate morphometrics. Subsequently, Bookstein (1997a 1997b) formalized the term semilandmark to refer to corresponding members of a series of points of that are located relative to one another by some consistent rule (*e.g.*, equal linear spacing from preceding point, equi-angular spacing according to a radius vector originating from the centroid of a closed form), with the set collectively expressing the geometry of a curve or curve segment.

Irrespective of the fact that type III landmarks are commonly employed throughout geometric morphometrics and that all type III landmarks are deficient in geometric information via their logical dependence on the locations of other landmarks (or semilandmarks), this sense of problematic usage rooted in the recognition of information deficiency has come to be more-or-less associated uniquely with semilandmarks. The question I’d like to raise, however, is whether it’s really this easy? Are semilandmarks — either individually or as a group — so dependent on the existence of information from other parts of the form that their information content is degraded in practical terms to the extent that they form a unique and somewhat suspect category of geometric information?

Type I landmarks are (rightly) preferred for morphometric analysis because the only criteria used in their location are supplied by the biology of the forms themselves. The classic example is the point of intersection of three bones in the vertebrate cranium. Such a configuration of structures does define a point that corresponds in a topological sense across all forms in which the identify of the structural elements can be determined independently and whose relative configurations are stable across the sample of specimens of interest. As I have argued elsewhere this criterion does not ensure that the point in question conforms to the concept of biological homology which is a hypothesis that equates whole structures to one another rather than individual points on or within structures (see MacLeod 1999). Therefore, attempts to enfold the concept of the landmark in the cloak of unique biological respectability, and exclude semilandmarks therefrom, are ... strained at best. But after dispensing with this morphometric myth (that is neatly skirted around in the formal definition of a landmark, see Slice Bookstein, Rohlf: http://life.bio.sunysb.edu/morph) we are left with practicalities. Landmarks that are located at points internal to the outline or other boundary of a form do indeed exhibit a high degree of spatial freedom with regard to their location relative to other structures. But all landmarks placed on a boundary outline of a form, and that use the existence of that outline or boundary in their definition, exhibit diminished independence of placement that derives from the simple fact that they are constrained to lie on the form’s outline or other boundary.

Once the (to my mind mistaken) notion that all landmarks have anything necessarily to do with biological homology and exhibit inherently greater degrees of independence from aspects of the form than semilandmarks *per se*, we’re in a much better position to appreciate the geometric challenge posed by the need to characterize outlines/boundaries as opposed to point locations internal to an object’s outline and/or away from a boundary of interest. Boundary outlines are often complicated structures whose forms encode information about their own shapes, their own sizes, and their positions relative to other aspects of the form. Most analyses of biological morphology need to locate these structures and represent their forms in order to test reasonable biological hypotheses. But owing to their complexity such structures cannot be represented by a single point location or landmark in the way some (not all) other structures of interest can be located. A representation involving multiple points is required; and therein lies the rub. The problem of semilandmarks in the context of a morphometric analysis does not derive fundamentally from the geometric dependence of the locations of individual semilandmark points relative to one another. Rather, it derives from the fact that, in many instances, so many semilandmark points are used to represent the form and position of a boundary outline that variation in these structures can overpower the information provided by those aspects of the form that can be represented by unitary landmarks. For this reason discussions of the use of semilandmarks inevitably focus on strategies that can be used to down-weight their influence relative to that provided by landmarks. As with so many of the decisions we must make in any form of data analysis, the real issue boils down to a question of balance (see Bookstein 1991, Zelditch et al. 2004).

What are the strategies we might use to achieve an appropriate balance between landmark and semilandmark datasets in the context of a morphometric investigation and how well do they work? Perhaps the simplest is to refuse to allow any of the information contributed by semilandmarks to participate in any way in the analysis of geometric morphometric data. Under this strategy the semilandmark points are, either tacitly or explicitly, regarded as representing an ‘image’ of the form that can be carried along passively in the context of an analysis whose outcome is controlled entirely by the information provided by landmarks. In these cases the point of including semilandmark data at all appears to be either (1) to make more aesthetically appealing graphics and/or (2) to aid interpretation of the landmark-based analytic results. Usually this approach to the “analysis” or semilandmark data is implemented by passively mapping the semilandmark data onto a deformation field such as that specified by coordinate point shape models (see

MacLeod 2009a) or a thin plate spline (see MacLeod 2010, see Fig. 1). Such analyses are sometimes referred to as “image warping”. Of course the problem with this approach is that the biological information encoded by the semilandmark data — information that it often of direct relevance to the analysis being undertaken — is not being used to inform the analytic result.

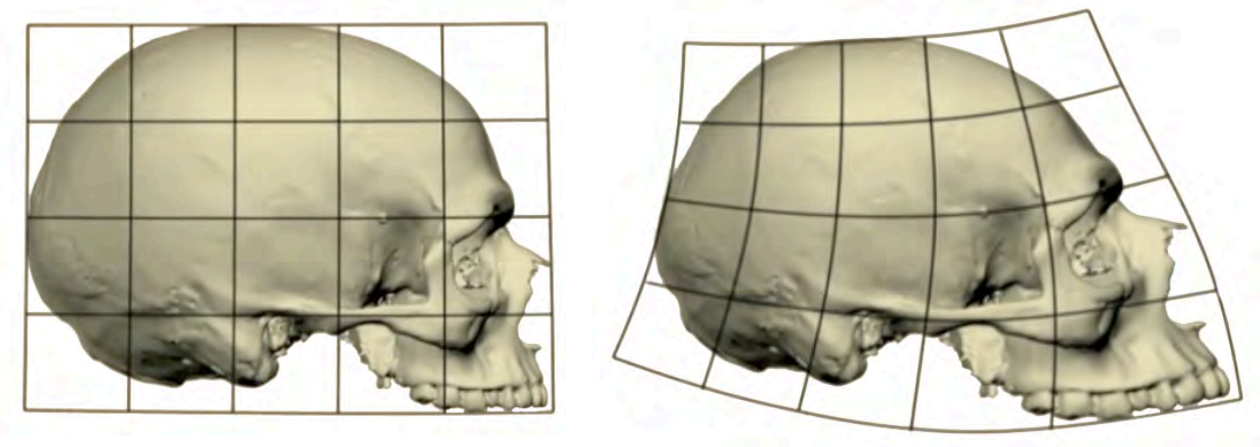

Figure 1. Example of an image of a human cranium being deformed passively using the geometric conventions of a thin-plate spline. This sort of analysis of semilandmark data can be used to inform biological interpretation of the deformation, but in doing so it must be remembered that no information from the image was used to inform the analysis. Graphics from a computer animation created by Rob O'Neill (see http://www.morphometric.com/exhibition/theoryoftransformations/).

In some cases sequestration of the information provided by an assessment of boundary curve form may be appropriate. In other cases it clearly is not. This is a judgement that must be made by the data analyst. Regardless, in all cases is a decision the data analyst makes knowing that other approaches are available that can be used to combine the information provided by these two types of morphometric descriptors.

An obvious alternative series of approaches to the challenge posed by boundary curves involves numerical adjustment of the weight assigned to semilandmark data in the context of an analysis. Zelditch *et al*. (2004) suggest that landmark data be weighted differentially relative to semilandmark data by assigning a weight coefficient to each coordinate point used to achieve procrustes superposition and making a distinction between landmarks and semilandmarks in the design of this weighting scheme. There are two disadvantages to this approach. First, as the resulting shape coordinate data will not lie within the Kendall shape space (see MacLeod 2009b), distortions will be introduced to the ordination of forms within the linear projection space used by geometric morphometricians to represent similarities and differences across a sample of shapes and/or model the character of geometric changes represented by that space. This is, perhaps, not a serious an issue as it might appear on first inspection since the projected positions of specimens within the shape space, and the models calculated on the basis of the shape space, will be accurate representations of the character of shape variation as specified by these weighted data. In other words, not being able to employ the elegance of the Kendall shape space does not mean we are unable to obtain the ordinations and/or models we seek or that these ordinations/model are not useful. A more serious concern has to do, inevitably, with how to go about determining which of an essentially infinite set of possible weighting schemes is most appropriate to our sample and to the biological problem at hand. Unscrupulous practitioners could, of course, inappropriately influence the result of an analysis through informed adjustment of the weighting scheme. But even well-meaning data analyses can employ different, though equally well justified weighting schemes that produce different analytic results. Without biologically informed guidance to specification of the weighting scheme — guidance that is unavailable at present — there is no way to determine which of the many different results that can be generated in this way to believe.

A strategy related to the differential weighting of landmarks and semilandmarks is to allow both types of information to participate in the Procrustes alignment of data collected from the specimens, but to reduce the number of semilandmarks used in the subsequent analysis of these data. Reduction of the discrepancy between the number of landmarks and the number of semilandmarks used in a Procrustes PCA or Procrustes CVA analysis has the effect of down-weighting the influence of the semilandmark dataset in the without requiring specification of a particular weighting scheme. But the problem of choice remains. Which semilandmarks do you remove from consideration and why? What’s the biological justification form removing some, but not others? How does your particular choice in this regard affect the results you obtain. And how to you resolve conflicts between results that are obtained by removing different points from consideration? There are no easy or fully satisfying answers to these questions at present.

For me the way out of this weighting corundum (in most cases) is to focus on the analysis of only those aspects of the form that really are critical to testing specific hypotheses and to use complexity weighting (see MacLeod 2012) to determine the number of semilandmark points necessary to represent the shape of an outline of boundary curve to a consistent level of geometric accuracy for all specimens across a sample. In far too many cases I see analyses in which too many aspects of a form were included in the dataset. This renders the analysis overly complex and can serve to obscure biologically important aspects of form variation in a morass of information from different regions of the form. Qualitative systematists routinely atomize the morphologies of the specimens they analyse into their component parts and conduct what are, in effect, separate analyses of each character and/or character complex. If more morphometricians adopted this approach — as opposed to trying to include all aspects of a form in a single analysis — simpler and more informative comparisons could be made (*e.g.*, compare the results obtained by Naylor 1996 and MacLeod 2002). Improving the focus of a morphometric problem by reducing its scope also, often provides the flexibility necessary to achieve a better balance between data derived from landmarks and semilandmarks, especially when complexity weighting is employed. Indeed, it's often surprising how few semilandmark points are required to represent a seemingly complex curve to an *a priori* specified level of geometric fidelity.

To illustrate this, consider the outline of a bird egg (Fig. 2).

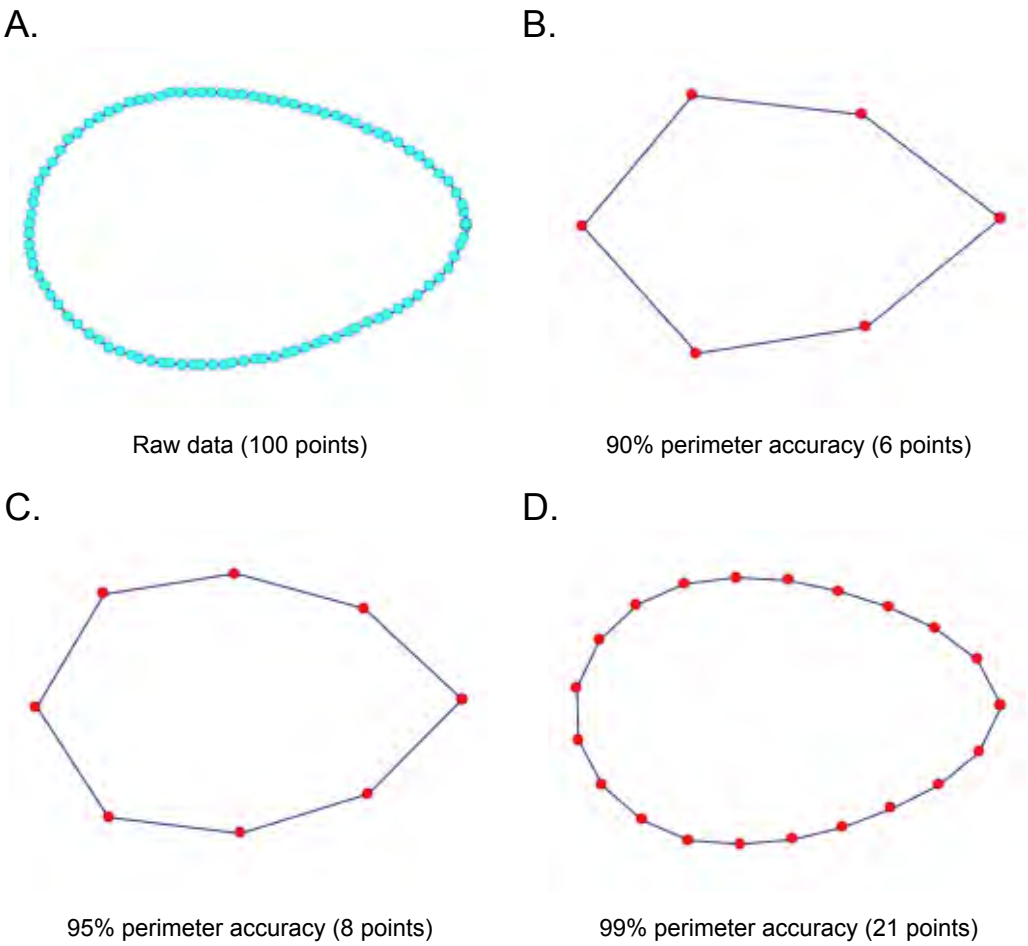

Figure 2. Estimation of the number of equally spaced semilandmark points necessary to represent the geometry of the boundary outline of an *Apus apus* (Swift) egg as assessed by complexity weighting (see MacLeod 1999, 2012). Note that the apparent irregularities in the spacing of the raw data points are due to rounding error in the calculation of the digital plots from which this figure was assembled.

Even more importantly, as the spacing between adjacent semilandmark points increases, the degree of constraint exerted on the location of any individual semilandmark point by points preceding it in the sequence decreases. In this way there exists a complete spectrum of dependencies between landmark points which includes semilandmarks; from type I landmarks whose positions are virtually independent of all other points around them to adjacent semilandmarks along an oversampled outline or boundary curve whose inclusion adds little biological or topological information, but much (needless) computation, to a data analysis problem.

All the semilandmark data weighting methods described above have one thing in common that is also important to appreciate. They all reflect primary assessments of the form or forms in question. Regardless of the density of landmark specification and/or semilandmark sampling, under the schemes proposed above all the data collected represent assessments of observed morphology of the specimens included in the sample. To my mind this is something of an inviolable requirement of all morphometric investigations. We might argue about sampling methods, landmark definitions, and semilandmark spacing schemes. But so long as our data represent observed biological reality at least we're not going to have to argue about the reality of the shapes themselves. While this might seem such an obvious requirement it doesn't need discussion, there is a popular procedure used to analyse semilandmark data that I have concerns about in this area; the so-called sliding semilandmark approach.

The method of sliding semilandmarks was developed by Green (1996) and Bookstein (1997) as a way of addressing the issue of issue semilandmark interdependence. Basically, this procedure takes a series of user-designated semilandmark points that have been transformed into a Kendall shape space via Procrustes alignment and adjusts their positions iteratively along lines tangent to the boundary outline curve, sliding them backwards or forwards along these tangents until the bending energy is minimized between the semilandmark configurations of each specimen and the Procrustes reference configuration (usually the mean shape). This procedure is applied, specimen by specimen, until each specimens' total bending energy is minimized relative to the reference. Once all specimens have been reconfigured in this manner the new shape-coordinate configurations are collected together and submitted to a PCA, CVA, allometric regression or some other procedure to assess modes and patterns of form or shape variation across the sample. As noted by Zelditch *et al*. (2004), the justification for changing the positions of the semilandmarks is that these are, to some extent, the product of a sampling convention (usually equal inter-semilandmark spacing) that is artificial biologically and so contributes a component of shape variation that is not part of the biology of the system. In the view of users of this approach they are "correcting" their data for the artificial constraint of equal semilandmark spacing and achieving a better biological placement of the semilandmarks relative to one another.

While the mathematics that underpin the sliding semilandmark method are unquestionably elegant (though too complex to be described in detail here; see the references I've given above for a full presentation of the mathematics), I remain unconvinced that this approach has either theoretical or practical value. Even more importantly, application of this method produces shape data that might look reasonable on first inspection, but that correspond to no shapes that have ever been observed in nature. Allow me to explain.

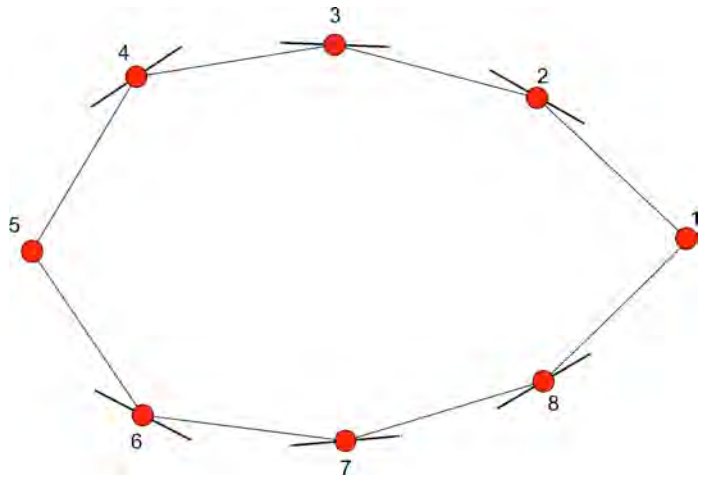

Figure 3. Lines drawn tangent to the curve of an *Apus apus* egg outline sampled using 8 equally spaces points. Here only points 2-4 and 6-8 are regarded as semilandmarks. These tangents are defined as the line that forms a constant angular relations with the chords drawn between the semilandmark in question and points preceding and following it in the point sequence. It is along these lines that adjustments to the semilandmark positions occurs. Note that and change in the position of any of the semilandmarks along these tangent lines takes the landmark away from the measured boundary outline curve. Not also that the orientations of these tangent lines themselves — as assessed under even the comparatively high-relation sampling scheme used here (95% accuracy of the perimeter, see Fig. 2C) — is inaccurate relative to the actual curve (see Fig. 2A).

There are three issues that bother me about sliding semilandmarks, any one of which regard as a fatal flaw. The first, and most obvious, that adjustment of the semilandmark positions is not taking place along the boundary outline curve itself. Rather, the semilandmarks are being slid along tangents to the boundary outline curve. This convention is purely one of computational convenience. It is easier to calculate the new positions of the semilandmarks points if they are adjusted along a linear trajectory than along a complex, curvilinear function. But the situation is, in a sense even worse than this. In implementing of this procedure it

is usually the case that a relatively wide inter-semilandmark sample spacing is used to constrain the boundary outline curve (Fig. 3). The coarseness of this spacing means that the tangents used to constrain adjustment of the semilandmark positions are themselves poor estimates of the true tangents to the boundary outline curve at the semilandmark points. Even if there were not the case, however, adjusting the semilandmarks along tangents to the boundary outline curve forces the points in question to be moved off the boundary outline curve to *positions at which there is no boundary outline curve*. This violates what is, for me, a fundamental requirement of all morphometric procedures; that the forms or shapes submitted to analysis represent the true geometries the forms and shapes present in the sample of biological specimens from which the data were collected (Fig. 4). In addition, constraining the semilandmarks to be slid along "tangents" to the boundary outline curve represents (to me) as artificial a constraint as enforcing strict equality of inter-semilandmark spacing. This procedure does not relax the artificiality of semilandmark placement; it compounds it and does so in a manner guaranteed to produce a result that this both artificial and unreal.

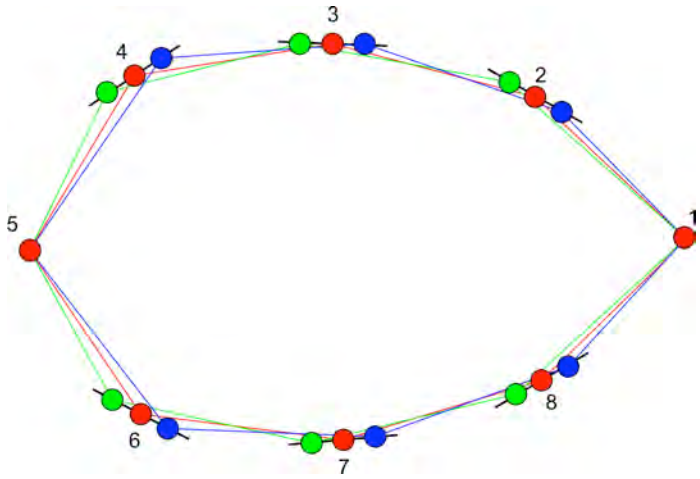

Figure 4. Simple illustration of the range of shape error that can be generated under end-member repositionings of semilandmarks uniformly toward one end of the sample form (blue shifts) or the other (green shifts). Note that representational errors are greatest in those regions of the form where the rate of curvature is the greatest. These are precisely the regions that contain the most shape variation and so are usually of the greatest biological interest.

My second objection to sliding semilandmarks is that the parameter used to control the sliding for the purpose of achieving a more biologically reasonable shape coordinate configuration — bending energy — has no biological status whatsoever. No known developmental, ecological, or evolutionary process operates in such a way as to minimize the bending energy of the mathematical points that morphometricians use to represent biological form(s). Bending energy is nothing more than an arbitrary index that morphometricians use to describe spatial similarities and differences between shapes. This index is the result of a mathematically simple calculation (see MacLeod 2010) and expresses shape change as a deformation metaphorically analogous to the form an infinitely thin, uniform, semi-rigid plate would take if it were bent to touch the ends of the pair-wise form/shape displacement vectors that characterize at each landmark location. Bending energy provides a mathematically convenient means of summarizing overall degrees of form-shape difference as a distance. That's all. Since organismal bodies are not infinitely thin, uniform, semi-rigid plates, and since no biological process takes the slightest account of bending energy as a controlling parameter, the minimization of bending energy has no biological status. For this reason bending energy *per se* cannot be used as a basis for the adjustment of semilandmark positions to a configuration that is any more, or less, biologically reasonable than the original configuration. In addition, the algorithms used to find the minimum bending energy provide neither a unique, nor a global, solution to the minimization problem. Alternative configurations of landmark displacements can have the same bending energy and there is no guarantee that solution found in any specific instance will be optimal globally.

As serious as my previous objections to sliding semilandmarks are, they pale (for me) beside my third objection which is that for the overwhelming majority of cases — especially those cases in which boundary outline curves have been sampled at a level of resolution commensurate with their geometric complexity, the results of sliding semilandmarks to new, bending-energy minimized configurations makes little or no practical difference to the results obtained. Obviously, for a boundary outline curve that has been sampled densely (*e.g.*, Fig. 2A, 2D) there is little scope for the semilandmarks to be adjusted lest they move past each other in the sequence; which would effectively destroy the geometry of the boundary outline. For curves that are less densely, there scope for substantial movement along the (inaccurately placed) tangents. Nevertheless, in practice semilandmarks are rarely slid to radically new positions. To illustrate this, consider the following sample of bird egg outline shapes (Fig. 5).

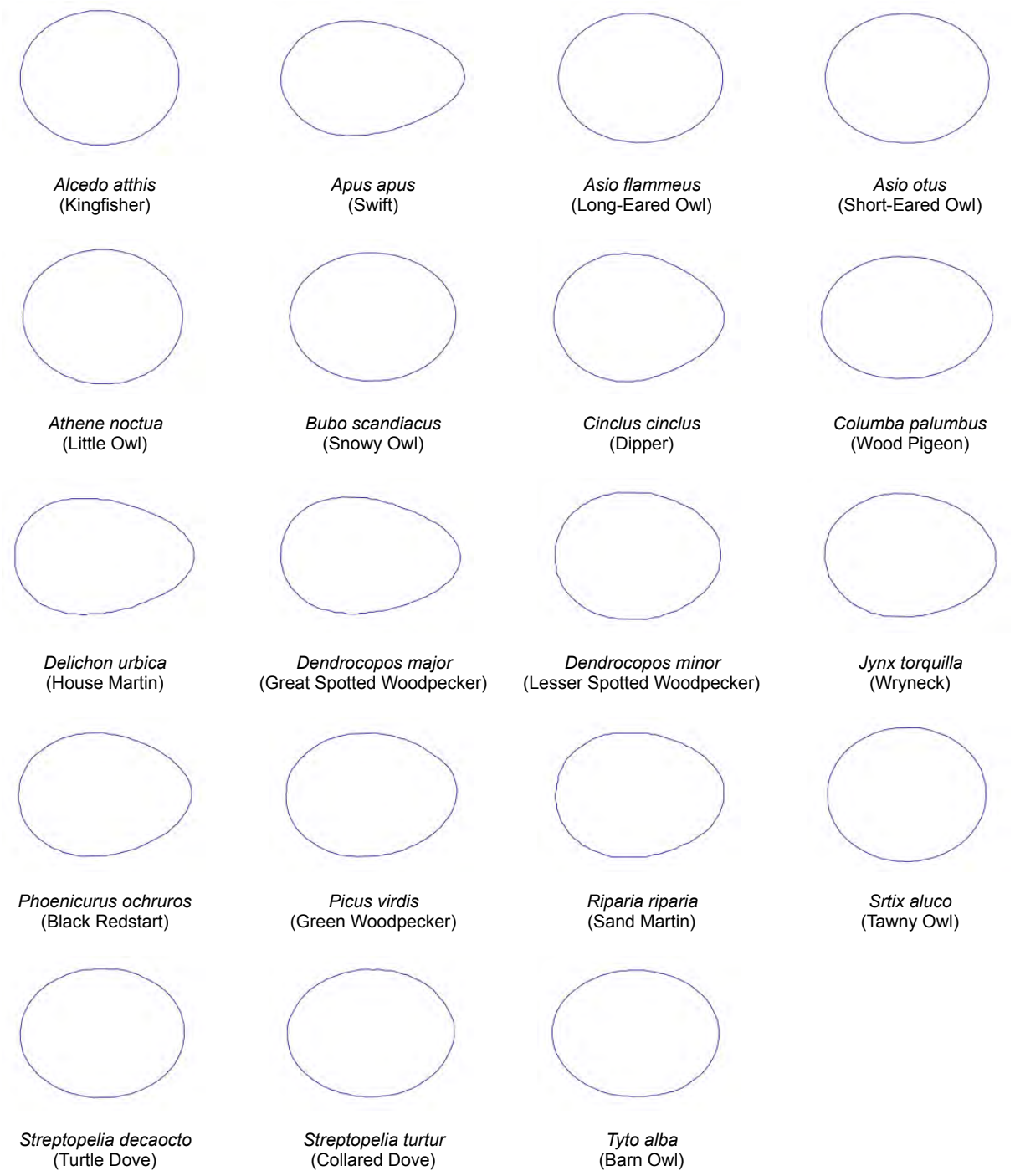

Figure 5. Outlines of a small sample of bird eggs that will serve to illustrate typical results of a sliding semilandmark analysis.

The original outlines were all collected at a resolution of 100 equally spaced points. There were then interpolated to 10 points for the purposes of analysis. This interpolation achieves a geometric accuracy of 97.5 percent of the measured outline's perimeter across the sample. In all cases the point at the narrow end of the outline's major axis was used as the starting point for digitization. Both endpoints of the major axis (points 1 and 5) were regarded as landmark points with points 2-4 and 6-10 designated as semilandmarks.

Jim Rohlf's tpsRelW programme was used to conduct the sliding semilandmark analysis. Both raw Procrustes and sliding semilandmark-adjusted Procrustes datasets were saved and these were submitted to Procrustes PCA analysis to summarize the extent to which semilandmark sliding affected the results. A plot of the ordination results of both analysis is provided as Figure 6.

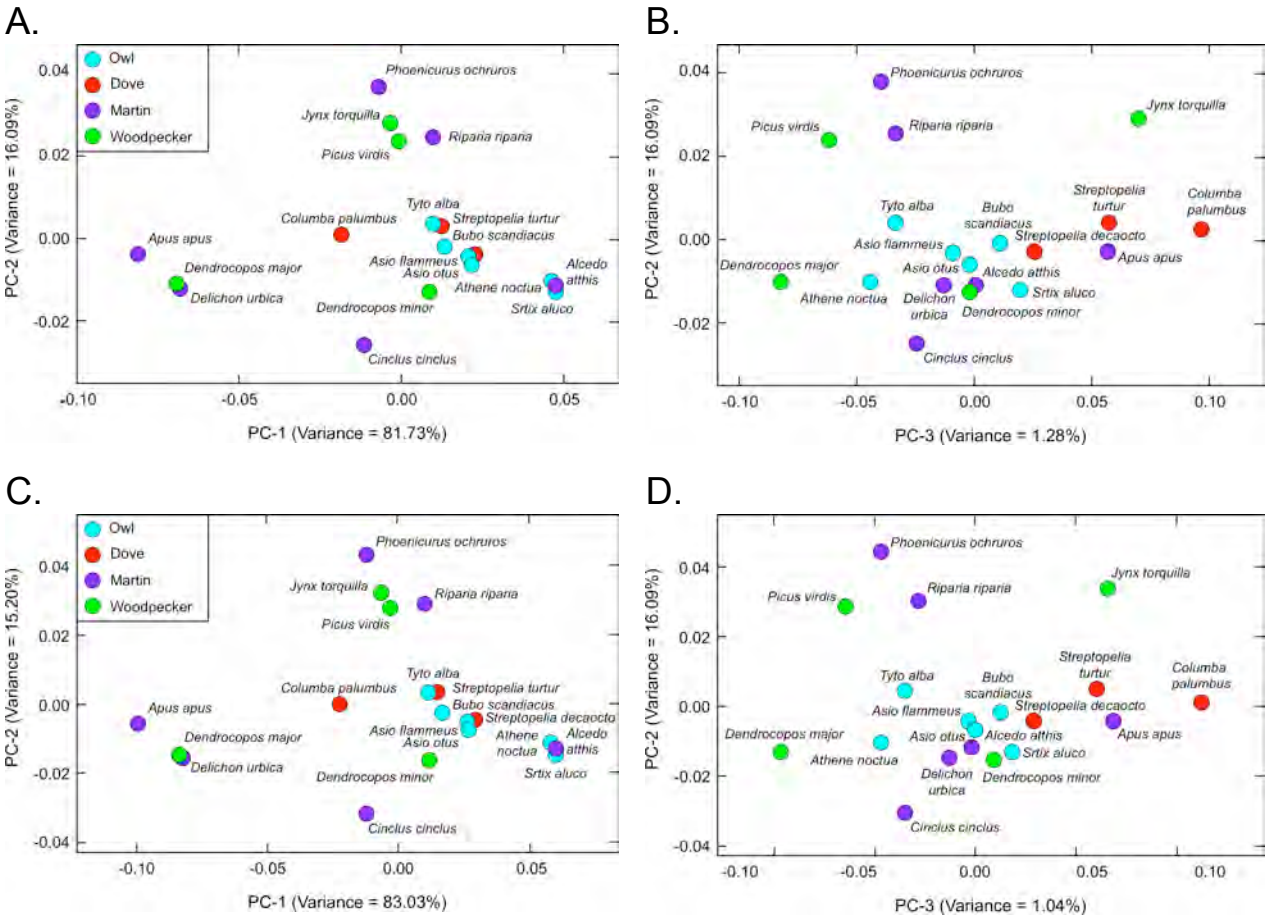

Figure 6. Results for raw (A, B) and sliding semilandmark (C, D) Procrustes PCA analyses. See text for discussion.

As can be seen be close comparison of the PCA space ordinations in figures 6A-6B (raw Procrustes PCA) and 6C-6D (sliding semilandmark Procrustes PCA) the datasets are very similar. Aside from minor differences in the eigenvalue coefficients and and a slight drift of the *Dentrocopus minor* (Lesser Spotted Woodpecker) egg shape toward the *Strix aluco* (Tawny Owl) egg shape on the PC-3 axis they are essentially identical. It is highly doubtful that any important information was gained by by employing the semilandmark sliding procedure. Moreover, then the propensity for — I would say guarantee of — error as a result of the sliding operation is taken into consideration, it is debatable which result is the (marginally) more accurate. Were I a betting man I'd put my money of the raw Procrustes PCA result, always.

The differences between landmarks and semilandmarks are real in the sense that they are different types of mathematical tools that were developed originally to quantify different aspects of biological form. You can use one type of tool to perform the function of the other (*e.g.*, use landmarks to quantify boundary outline curves) in the same way that you can use a screwdriver to hammer a nail into a piece of wood. The question isn't one of capability, but of appropriateness. In the same way that mechanical jobs get done more quickly, more easily, and with a better result when you use the proper tools in the proper way, morphometric analyses/ proceed more quickly, and interpretations are arrived at more easily with less ambiguity, when you use the proper conceptual and mathematical tools. So don't be afraid to use semilandmarks in your analyses. In many situation they will be your only realistic hope of obtaining results that are relevant to the biological problem you're interested in. Even in those cases in which it is profitable to combine semilandmarks and landmarks in the same analysis a little creativity will usually lead to a form sampling solution that allows both types of data to participate in the analysis in ways that enhance and clarify, rather than obscure and complicate, the result.

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