Flight style in bats as predicted from wing morphometry: the effects of specimen preservation

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(With 5 figures in the text)

An as yet unconsidered potential error in studies that predict flight style from morphological measurements of bats is the effect of the specimen type employed. On the basis of the finding that morphological measurements taken from fluid-preserved bat specimens may not yield values equivalent to those taken from the live animal, we compared the values of several variables (lifting surface area, wingspan, mass, aspect ratio, wing loading and minimum power speed) for live and fluid-preserved little brown bats (*Myotis lucifugus*) with the accepted standards for this species given by Norberg & Rayner (1987). Significant differences were detected for lifting surface area, wingspan, mass, aspect ratio and wing loading values taken from live bats and their respective values reported by Norberg & Rayner. Differences between preserved bats and Norberg & Rayner's numbers were limited to lifting surface area and wingspan (extended wing positions only), aspect ratio (all wing positions), and mass (both 70% ethanol- and 45% isopropyl alcohol-preserved specimens). Thus, Norberg & Rayner's values correspond most closely to values obtained from preserved museum specimens, a fact reflecting the source of their data in this instance. This and other limitations involved in attempting to predict the flight style of bats from a few morphological characters are discussed.

Contents

Introduction

Since flight is the primary means of locomotion of bats, an accurate description of a species' flight performance will yield valuable information about its ecology. However, the secretive and nocturnal habits of bats make it difficult to observe their flight styles directly. Researchers have therefore attempted to predict flight performance on the basis of a few key measurements or morphological indices obtained from the bat wing: wingspan, wing area, wing loading and aspect ratio (e.g. Poole, 1936; Findley, Studier & Wilson, 1972; Lawlor, 1973; Norberg, 1981; Aldridge,

1986; Norberg & Rayner, 1987). In the most comprehensive study of this kind, Norberg & Rayner (1987) predicted the likely flight behaviour of all previously studied bat species, primarily upon the basis of their aspect ratio and wing loading. In so doing, Norberg & Rayner necessarily relied heavily on literature sources for raw data for many taxa.

A potential shortcoming of such studies is that the data (and the ecological conclusions derived from them) are dependent upon the source specimens. In Norberg & Rayner's paper, live animals (e.g. Jones, 1967; Jones & Suttkus, 1971), freshly killed specimens (e.g. Hartman, 1963; Lawlor, 1973), and museum specimens, both study skins (e.g. Farney & Fleharty, 1969) and alcohol-preserved specimens (e.g. Vaughan, 1959, 1966), were used as sources of raw data, and these different sources were often pooled together for a given bat species. However, we (Bininda-Emonds & Russell, 1993) have subsequently found that the representative specimen types for bats (live animal, freshly killed specimen and fluid-preserved specimen) should not be directly compared with one another since the values obtained for the key measurements outlined above often differ significantly between the different types. Therefore, a question equal in importance to 'What flight behaviour can a given species of bat exhibit?' is, 'Does our perception of what this flight behaviour might be change according to the type of specimen we are examining?'

The purpose of this study, then, was to investigate the second question above: do our perceptions actually change? To accomplish our goal, 26 individuals of a single species of bat, the little brown bat (*Myotis lucifugus*), were fixed and preserved according to standard museum techniques. The values for all the variables examined (lifting surface area, wingspan, mass, aspect ratio, wing loading and minimum power speed) were compared to their respective reported values presented by Norberg & Rayner (1987). We then compared the different specimen types to other vespertilionid species of a similar flight style (as evidenced by similar values for aspect ratio and wing loading) and to the values of *Myotis lucifugus* reported by Norberg & Rayner (1987). A point of major significance here is that the same set of individuals yielded the data for all specimen types, thus allowing changes induced during the preservation procedure to be directly monitored.

We hasten to add that this paper is not intended as an indictment of Norberg & Rayner's (1987) approach or conclusions, but is meant to point out some of the limitations of all such studies that attempt to characterize the flight styles of bats by using morphological variables. Norberg & Rayner's contribution is merely the most comprehensive and most recent of these kinds of study and their numbers are often taken as the standard by which to measure one's own data (e.g. Aldridge, 1988).

Methods

A detailed description of specimen collection and preparation, and of the tracing and measuring protocols, can be found in Bininda-Emonds & Russell (1993). Four different specimen types were examined, which represent the sequential stages in the preservation process for fluid-preserved museum specimens: live animals, freshly killed specimens, specimens immediately after fixation and rinsing ('post-fixation') and specimens that have been preserved in alcohol for some time (36-week-preserved specimens). All of these specimen types, with the exception of the post-fixation stage, are routinely used as data sources for bat specimens. Within the post-fixation and 36-week-preserved samples the wings were fixed in 1 of 3 positions: 'compressed' bats are those preserved with the wings folded against the body, 'intermediate' bats are those preserved with the wings partially spread (so that the individual digits are recognizable), and 'extended' (Bininda-Emonds & Russell, 1993) bats are those preserved with 1 wing (here, the left) fully

extended and the other fully compressed. Although the intermediate and extended positions are rarely found in museum collections, we found them to be demonstrably better than the compressed position in preserving the original wing morphometry (Bininda-Emonds & Russell, 1993).

Morphological measurements, indices and flight speeds

Lifting surface area (LSA; analogous to the more equivocal term 'wing area') was defined as in Norberg (1981) (see Bininda-Emonds & Russell, 1993: fig. 1). Wingspan was defined as in Bininda-Emonds & Russell (1993).

Aspect ratio (A), wing loading (Q_s), and minimum power speed (V_{mp}) were calculated as noted in Bininda-Emonds & Russell (1993: 147, equations (1), (2), and (3), respectively). Aspect ratio (A) describes the relative antero-posterior width of the wing (i.e. narrow versus broad) (Findley et al., 1972), and, as such, is a good indicator of the general shape of the wing (Aldridge, 1986). Wing loading (Q_s) describes the body weight supported per unit area of the flight surface (McManus & Nellis, 1972) and correlates with minimum flight, minimum power, and maximum range speeds, turning radius, and general manoeuvrability of a given species (Pennycuick, 1975; Aldridge, 1986; Norberg, 1987). Minimum power speed (V_{mp}) is used to maximize flight time for a given amount of energy (Norberg & Rayner, 1987). The body mass from the freshly killed specimen was used to calculate both wing loading and minimum power speed for all stages.

Aspect ratio and wing loading categories

Norberg & Rayner (1987) based their predictions of a given species' flight performance on its aspect ratio and wing loading, assigning most species to a qualitative category for each variable (generally low, average, or high). No explicit account was given of how membership in a particular category was determined for a given species. Norberg & Rayner (1987: 381–382) state that 'aspect ratio and wing loading refer both to the absolute values of these quantities . . . and to the size-independent measures of these quantities derived from (a) principal components analysis.' Wing loading was further characterized relative to the size of the bat (as represented by mass). We question this latter technique as the mass of the bat is already incorporated into the wing loading. By scaling wing loading relative to mass, one runs the risk of inadvertently creating false trends as the 2 variables are necessarily correlated with each other (autocorrelation). As there was no overall size estimate of the bat available in Norberg & Rayner (1987) that was independent of LSA, we simply judged wing loading according to its absolute magnitude alone.

In order to view the distribution of these categories for vespertilionids (the family to which *Myotis lucifugus* belongs), we plotted histograms of the number of vespertilionid species of a given numerical aspect ratio (or wing loading) according to the category they were assigned by Norberg & Rayner. The boundaries between the categories were quantified by sorting all the aspect ratio (or wing loading) values in ascending order and dividing this series sequentially into categories. The boundaries were set so that each category contained the same number of species as did the original category in Norberg & Rayner's paper (1987). (The 'average to low' wing loading category mentioned by Norberg & Rayner (1987: 397) for vespertilionids of low aspect ratio is obviously an artificial clustering of bats of average and low wing loading in that one instance. In determining the boundaries for the wing loading categories, we assumed that this 'category' contained equal numbers of bats of average and of low wing loadings.)

Statistical analysis

The initial hypothesis for this study was that there would be no differences between the values of any of the 6 variables (LSA, wingspan, mass, aspect ratio, wing loading and minimum power speed) determined at a given stage in our sample and the equivalent values presented by Norberg & Rayner (1987). Only the

results for the live animals and the 36-week-preserved specimens were compared to Norberg & Rayner's values by way of a 2-tailed one sample Student's *t*-test using Systat 5·0 on an IBM PC (Zar, 1984; Wilkinson, 1990). These comparisons were made according to treatment groupings found in our earlier study (Bininda-Emonds & Russell, 1993); live bats were all pooled together, and 36-week-preserved specimens were pooled according to wing position for all variables except for mass, which was pooled according to preservation fluid. A rejection level of 0·05 was used, corrected for multiple comparisons with the Bonferroni method (Eq. 1) (Snedecor & Cochran, 1989):

$$\alpha_C = \alpha_E/r \tag{1}$$

where α_C = rejection level for multiple comparisons; $\alpha_E = 0·05$; r = number of comparisons.

Smooth curves for the histograms were generated by using Systat's KERNEL smoothing algorithm (Wilkinson, 1990). The graph of aspect ratio versus wing loading was created by plotting the individual data points and determining 95% Gaussian bivariate confidence ellipses to view the range of these 2 variables for a number of cases (Wilkinson, 1990). Three sets of ellipses were plotted. The first was for each of the 4 preservation stages. Although we earlier found significant differences between the wing positions in each preservation stage for aspect ratio and wing loading (Bininda-Emonds & Russell, 1993), the wing positions were pooled for each stage to simplify the graph. Additionally, ellipses were plotted for all specimens grouped over all preservation stages (all stages) and for all specimens of all preservation stages except the post-fixation stage (all stages less post-fixation). The exclusion of the one stage in the latter pooled ellipse reflects the artificial nature of the post-fixation stage.

TABLE I

Values of a given variable for a given specimen and the respective value presented by Norberg & Rayner (1987). Values presented in parentheses represent the corrected values of those variables from the sources used by Norberg & Rayner (1987). The 36-week-preserved specimens are compared according to (a) fixation wing position or (b) preservation fluid. Numbers are presented as mean ± S.E. except for Norberg & Rayner (1987) which are presented as means only

(a)

| Variable[1] | Norberg & Rayner (1987) | Live all bats (n = 26) | 36-week-preserved specimens | | |
			Compressed (n = 9)	Intermediate (n = 9)	Extended (n = 8)
LSA	0·0093 (0·0086)	0·0113 ± 0·00013	0·0096 ± 0·00037	0·0101 ± 0·00033	0·0107 ± 0·00023
B	0·237	0·252 ± 0·0012	0·239 ± 0·0047	0·238 ± 0·0038	0·251 ± 0·0025
A	6·0 (6·3)	5·6 ± 0·049	6·0 ± 0·058	5·6 ± 0·041	5·9 ± 0·048
Q_s	7·5 (8·0)	6·9 ± 0·187	7·7 ± 0·252	7·9 ± 0·228	7·6 ± 0·187
V_{mp}	3·248 (3·286)	3·205 ± 0·034	3·288 ± 0·051	3·378 ± 0·040	3·300 ± 0·028

(b)

| Variable[1] | Norberg & Rayner (1987) | Live all bats (n = 26) | 36-week-preserved specimens | |
			70% ethanol (n = 14)	45% isopropyl alcohol (n = 12)
M	0·071	0·085 ± 0·0026	0·091 ± 0·0044	0·114 ± 0·0022

[1] LSA: Lifting surface area; B: wingspan; M: mass; A: aspect ratio; Q_s: wing loading; V_{mp}: minimum power speed

Results

We noted an apparent error in the value for LSA given for *Myotis lucifugus* by Norberg & Rayner (1987). On the basis of their original sources, we calculated that their value for LSA should have been $0.0086 \, m^2$, not $0.0093 \, m^2$ as reported. This lower value for LSA causes Norberg & Rayner's values for aspect ratio, wing loading and minimum power speed to increase to 6·3, $8.0 \, N/m^2$ and 3·286 m/s, respectively (Table I).

Values for four of the six variables (LSA, wingspan, mass and aspect ratio) determined from our sample of live animals were significantly different from those published by Norberg & Rayner (1987) (Table I). Additionally, at 36 weeks of preservation time, LSA and wingspan for the extended bats, aspect ratio for the intermediate bats, and mass for bats preserved in both ethanol and alcohol differed significantly between our sample and their respective values from Norberg & Rayner (1987). Comparisons with the corrected values did not change this pattern greatly,

TABLE II

t values from a two-tailed one-sample Student's t-test comparing values of a given variable for a given specimen type with the respective value presented by Norberg & Rayner (1987). Comparisons were made between (a, b) the actual value published in Norberg & Rayner (1987) or (c) the corrected value determined from the original sources used by Norberg & Rayner (if applicable); see Table 1. The 36-week-preserved specimens were compared according to (a, c) fixation wing position (b) preservation fluid

(a)

Variable[1]	Live all bats ($n = 26$)	36 week-preserved specimens		
		Compressed ($n = 9$)	Intermediate ($n = 9$)	Extended ($n = 8$)
LSA	16·10*	0·72	2·36	6·05*
B	12·72*	0·34	0·30	5·86*
A	−7·47*	−0·48	−8·53*	−1·36
Q_s	−3·16	0·63	1·67	0·68
V_{mp}	−1·26	0·78	3·24	1·83

(b)

Variable[1]	Live all bats ($n = 26$)	36-week-preserved specimens	
		70% ethanol ($n = 14$)	45% isopropyl alcohol ($n = 12$)
M	5·35*	4·54*	19·03*

(c)

Variable[1]	Live all bats ($n = 26$)	36-week-preserved specimens		
		Compressed ($n = 9$)	Intermediate ($n = 9$)	Extended ($n = 8$)
LSA	21·70*	2·63	4·52	9·17*
A	−14·36*	−6·30*	−16·74*	−8·51*
Q_s	−5·74*	−1·28	−0·45	−1·90
V_{mp}	−1·26	0·03	2·29	0·49

*, $P < 0.05$ (adjusted for multiple comparisons)
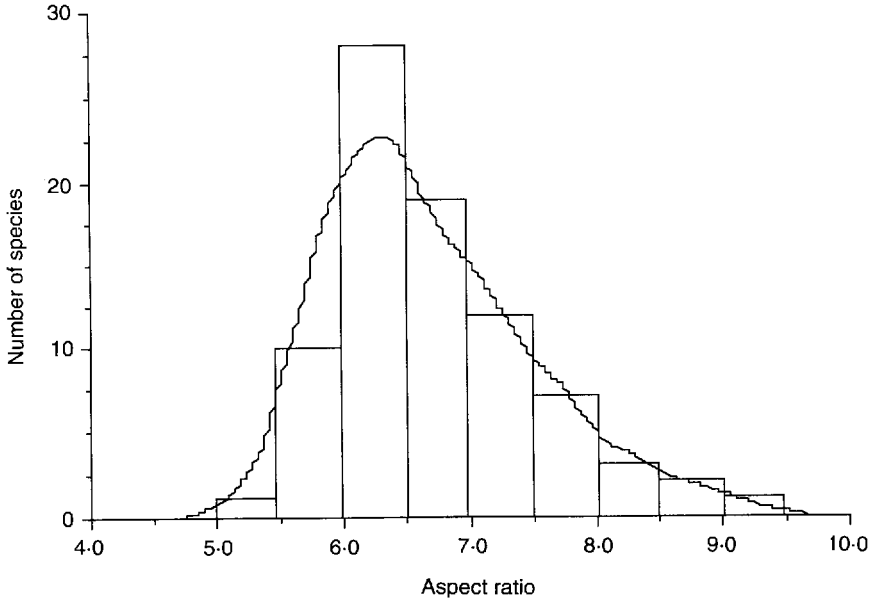[1] See Table I for explanation

FIG. 1. Histogram of the number of vespertilionid species of a given aspect ratio. Only those species assigned a qualitative category by Norberg & Rayner (1987) are included (see Fig. 2).

producing only a few additional differences to those already found. Wing loading in the live animals was now found to be significantly smaller than the corrected Norberg & Rayner (1987) value. Also, our values for aspect ratio in all preserved bats (regardless of wing position) were significantly smaller than the corrected value from Norberg & Rayner. Only minimum power speed never differed significantly between our sample and either its respective or corrected value from Norberg & Rayner (1987) (Tables I and II).

The vespertilionids (or at least that portion of the family that was placed into the qualitative categories by Norberg & Rayner (1987)) span a wide range of both aspect ratio and wing loading values (Figs 1 and 3). However, the categories employed by Norberg & Rayner do not subdivide the respective continua with any apparent utility (Figs 2 and 4). The categories for each index overlap greatly and do not display any obvious discontinuities. This is especially true for wing loading, where the mode for all categories except for high is at about $7 \cdot 0$ N/m^2. As might be expected, the clumped 'average to low' wing loading category displayed a bimodal distribution, although the distribution of the average category completely encompassed that of the low category. Our method estimated the boundaries for the aspect ratio categories to be as follows: low, less than $6 \cdot 1$; average, $6 \cdot 1 - 7 \cdot 3$; and high, greater than $7 \cdot 3$. Likewise, the boundaries for wing loading categories were estimated to be as follows: very low, $< 6 \cdot 45$ N/m^2; low, $6 \cdot 45 - 7 \cdot 5$ N/m^2; average, $7 \cdot 5 - 10 \cdot 3$ N/m^2, and high, $> 10 \cdot 3$ N/m^2.

A plot of aspect ratio versus wing loading demonstrated clear differences among the different specimen types for *M. lucifugus* employed in this study (Fig. 5a). Only the 95% confidence ellipses for the post-fixation and 36-week-preserved bats overlap, and then only to a small degree. The ellipse representing the freshly killed specimens is reasonably well removed from the ellipses of the remaining specimen types. Both of the two pooled ellipses are centred around an aspect
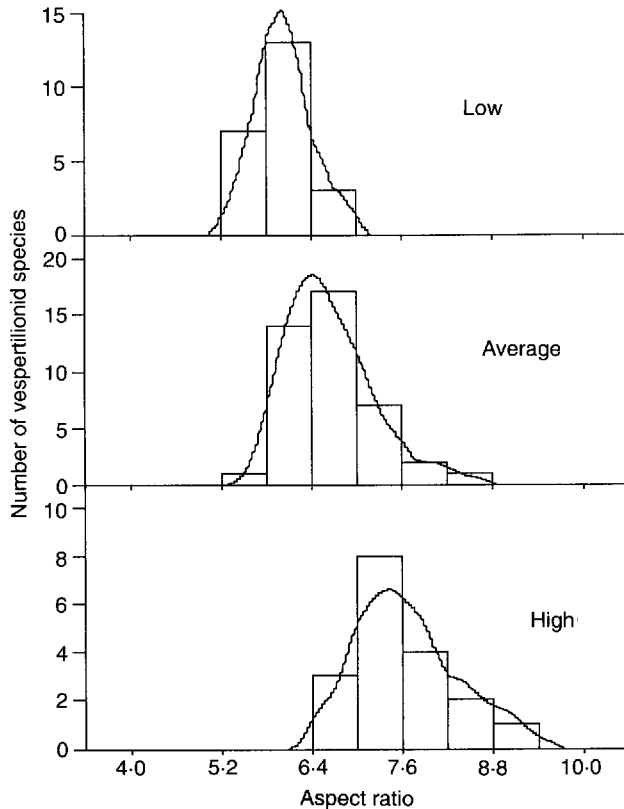
FIG. 2. Histograms of the number of vespertilionid species of a given aspect ratio. Species are separated out according to the aspect ratio category they were assigned by Norberg & Rayner (1987): low, average and high.

ratio of about 5·8, with the all-stages ellipse shifted to a slightly higher wing loading than the all-stages less post-fixation ellipse (7·5 N/m^2 versus 7·25 N/m^2, respectively).

The extent of these differences is magnified even more when our estimates of the aspect ratio and wing loading boundaries are superimposed on Fig. 5a (Fig. 5b). The confidence ellipses traverse the low to average wing loading boundary, essentially separating the preserved (post-fixation and 36-week specimens) from the non-preserved (live animals and freshly killed specimens) *M. lucifugus* specimens. The pooled ellipses reflect this distinction. The all-stages ellipse, with its equal representation between preserved and non-preserved specimens, straddles the boundary while the greater proportion of non-preserved stages in the all-stages less post-fixation ellipse shifts it exclusively into the low wing loading category (Fig. 5b).

When several other vespertilionids of similar aspect ratio and wing loading, based upon Norberg & Rayner's data (1987), are likewise added to Fig. 5a (Fig. 5b), the confidence ellipses are now seen to overlap the points of four different species (*Myotis emarginatus, Myotis volans, Pipistrellus hesperus* and *Plecotus auritus*), but not the point for *Myotis lucifugus* reported by Norberg & Rayner (1987) which falls just beyond the 36-week-stage ellipse. The point corresponding to the corrected *M. lucifugus* numbers is even further removed from the cluster of ellipses, falling in a completely different aspect ratio category (average versus low) (Fig. 5b).
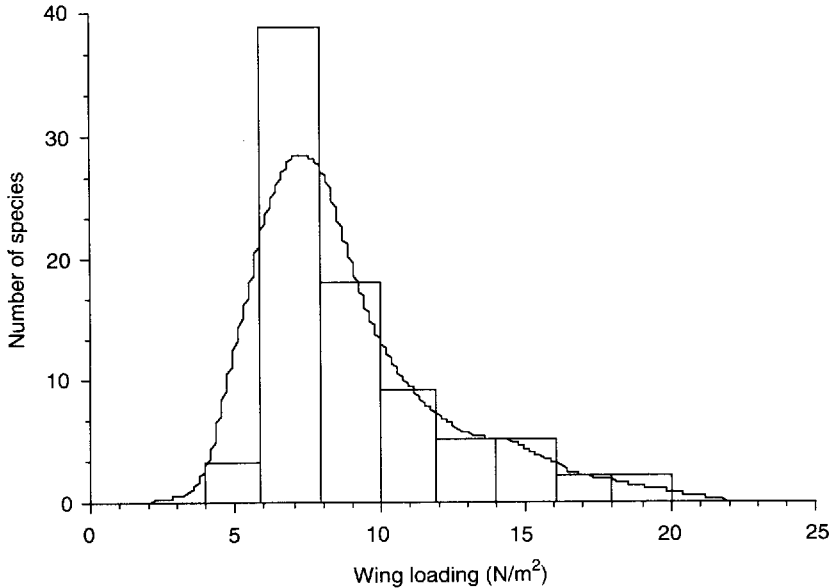
FIG. 3. Histogram of the number of vespertilionid species of a given wing loading. Only those species assigned a qualitative category by Norberg & Rayner (1987) are included (see Fig. 4).

Discussion

With this study, we further corroborate our previous assertion that one must be wary of the types of specimens from which data are obtained (Bininda-Emonds & Russell, 1993). Marked differences in a number of variables exist between the values published by Norberg & Rayner (1987) for *Myotis lucifugus* and those of our own sample of 26 bats. Moreover, these differences generally stem from the disparity between the different specimen types. The differences we observed in this study were larger and/or more numerous when we compared values for live bats with Norberg & Rayner's numbers (Fig. 5a, Tables I and II). As all three of Norberg & Rayner's sources for *M. lucifugus* used preserved museum specimens of some sort (study skins and skulls— Farney & Fleharty (1969); fluid-preserved specimens—Vaughan (1966) and Strickler (1978)), this result should not be altogether too surprising. The differences are more extreme when the corrected values for Norberg & Rayner's (1987) estimates are considered, especially since these force the species into the average wing loading category (Fig. 5b: Mylu(2)).

One encounters additional difficulties with *M. lucifugus* as its ranges of aspect ratio and wing loading values both fall closely adjacent to our estimates of the boundaries between Norberg & Rayner's categories for each index. We encounter a somewhat perplexing problem here. Even though both the preserved and non-preserved samples are composed of the same set of individuals, we would be justified in deducing slightly different flight styles for each of the two samples. (Unfortunately, Norberg & Rayner (1987) do not make a distinction in flight style between low and average wing loading for vespertilionids of low aspect ratio, so the extent of the problem for *M. lucifugus* is unknown.) We are, in effect, basing our perception of the flight style of a live individual (or a species as a whole) on what we do to it after its death. So, although the case for *M. lucifugus* could be more extreme than that for most bats, the differences between the specimen types is real and problematic.
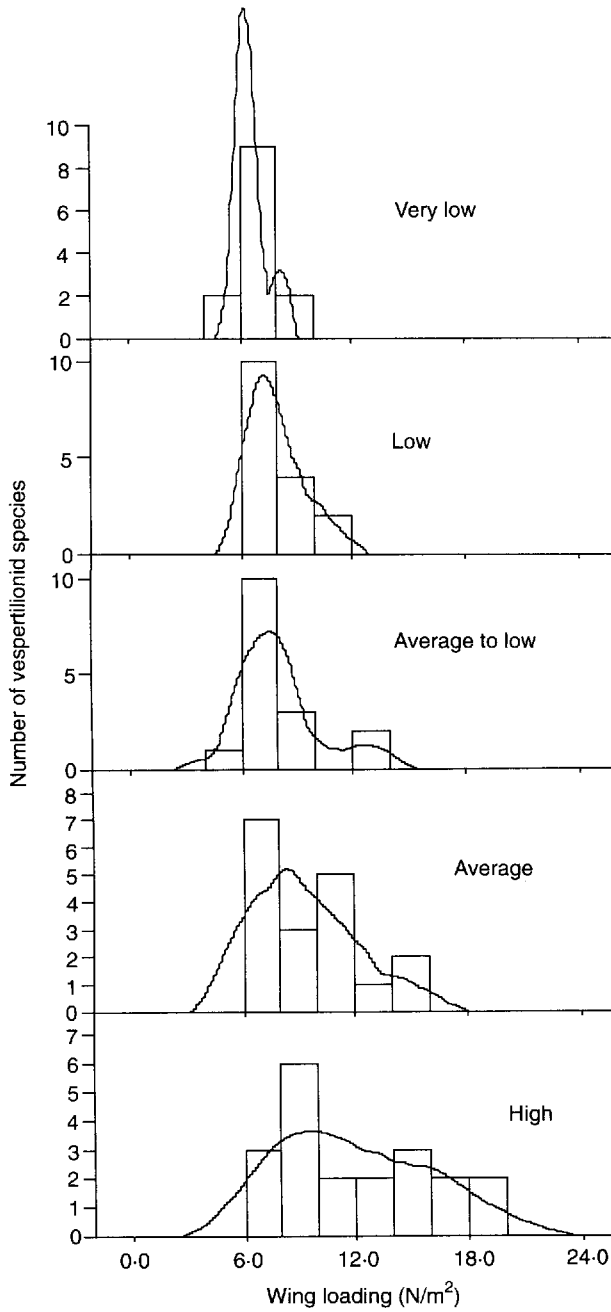
FIG. 4. Histograms of the number of vespertilionid species of a given wing loading. Species are separated out according to the wing loading category they were assigned by Norberg & Rayner (1987): very low, low, average to low, average and high.
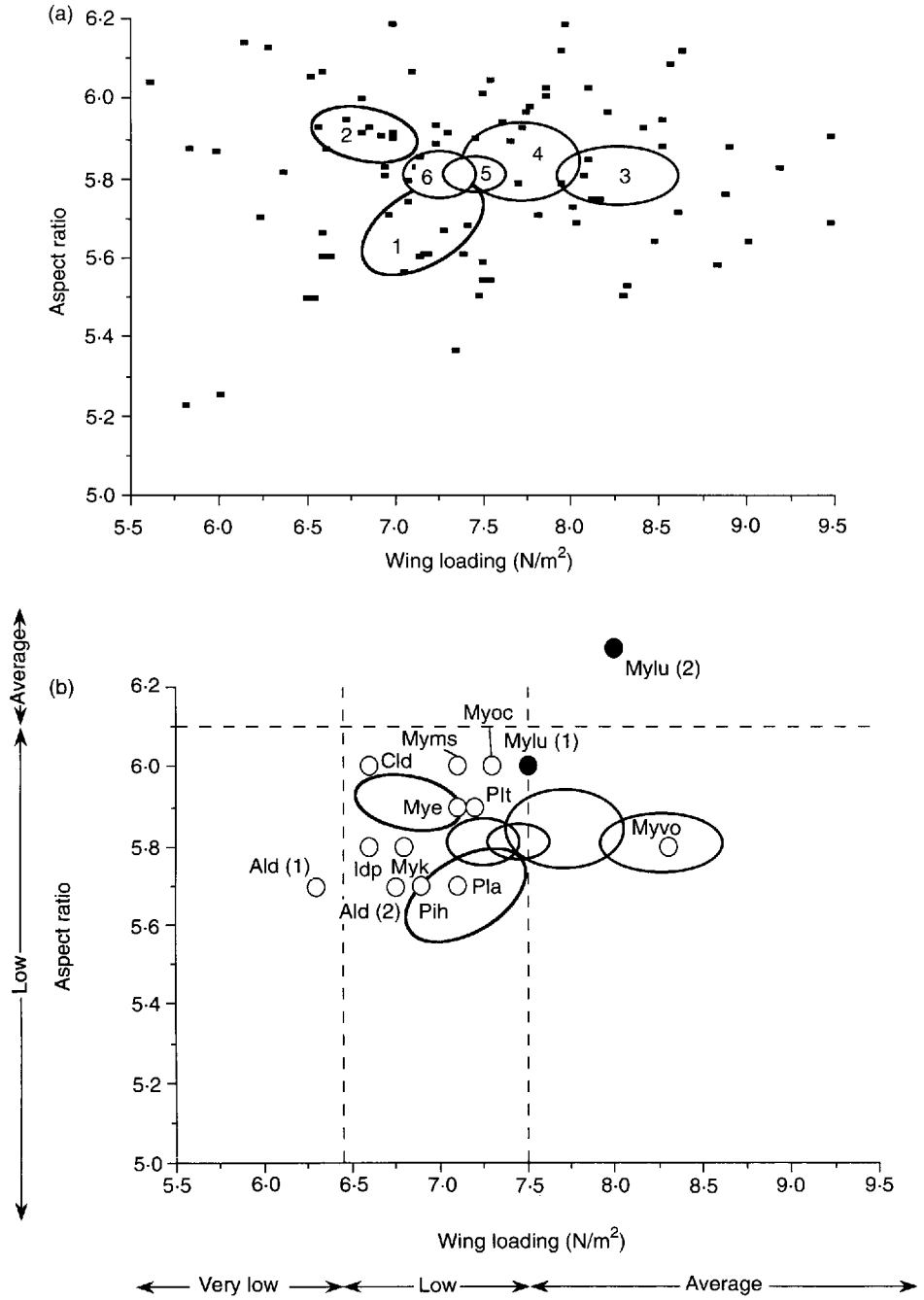
Fig. 5

One possible solution to the above problems might be to adopt a standard frame of reference when dealing with such morphological data. It is universally recognized that masses taken from fluid-preserved specimens are erroneous. Perhaps an equivalent situation should be recognized for wing measurements of fluid-preserved bat specimens. Thus, like mass, wing measurements should only be taken and recorded from live animals or freshly killed specimens. A more complete discussion of this and a proposed standardized protocol can be found in Bininda-Emonds & Russell (1992).

Altogether, this should prompt some degree of caution whenever researchers compare their results with those of others. For instance, we feel that Aldridge (1988: 511) may have been overly cautious when he described a live *M. lucifugus* with a wing area of $0\cdot0112$ m^2 and a mass of $7\cdot7$ g as having 'a lower wing loading ($6\cdot29$ N/m^2) and aspect ratio ($5\cdot70$) than is the norm for the species'. (We infer Aldridge's use of the word 'norm' to mean Norberg & Rayner's numbers.) Aldridge's numbers accord fairly well with our values for the live bats measured in this study (Table I), especially when we calculate that Aldridge's bat should have had a wing loading of $6\cdot74$ N/m^2, given its mass and wing area. Thus, Aldridge was describing an individual that was apparently reasonably normal for live *M. lucifugus* (Fig. 5b).

Studies that seek to predict bat flight styles on the basis of morphology are necessarily simplified; however, we feel that the limitations inherent in these simplifications are often not fully realized. The space a given species occupies on a graph such as Fig. 5a (which in essence can be extrapolated to describe a species' flight envelope) is typically presented as a point value representing the 'population norm'. But, this point is, in reality, a cloud that encompasses the normal range of individual variation within the species. (It becomes even more complicated when we realize that this cloud will shift position slightly as an artefact of the specimen type we are examining.) In the case of data compilations such as that of Norberg & Rayner (1987), this simplification is often unavoidable as many of the original sources lack error intervals for their data (e.g. Vaughan, 1966), and, in any case, the individual data points are usually irrecoverable for the authors to derive their own error intervals from a true pooling of the data. Unfortunately, this just aids in perpetuating the representation of the flight envelope as a point rather than a cloud.

Aspect ratio and wing loading have repeatedly been shown to have the strongest correlations with flight style (Findley *et al.*, 1972; Pennycuick, 1975; Norberg & Rayner, 1987). As a result, there has been a tendency to categorize the flight style of a species of bat according to its aspect ratio and/or wing loading characteristics (e.g. Struhsaker, 1961; Findley *et al.*, 1972; Lawlor, 1973; Norberg & Rayner, 1987). Such a practice is immensely practical as a simplifying and generalizing tool, but it too has limitations. Often, the resultant difference in flight style between the categories is not explicitly stated. In Norberg & Rayner's paper (1987), for instance, no clear

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FiG. 5. Aspect ratio versus wing loading for (a) various *Myotis lucifugus* specimen types examined in this study and (b) various vespertilionids from Norberg & Rayner (1987) with ellipses from (a) and our boundary estimates for the aspect ratio and wing loading categories superimposed. Numbers in the ellipses in (a) to the following preservation stages: 1— live animals, 2–freshly killed specimens, 3—post-fixation stage, 4—36-week-preserved specimens, 5—all stages pooled, 6—all stages pooled except post-fixation stage. The various vespertilionids are abbreviated as follows: Cld, *Chalinolobus dwyeri*; Idp, *Idionycteris phyllotis*; Mye, *Myotis emarginatus*; Myk, *Myotis keenii*; Mylu (1), *Myotis lucifugus* (Norberg & Rayner's (1987) original values); Mylu (2), *Myotis lucifigus* (corrected values for Norberg & Rayner (1987)); Myms, *Myotis mystacinus*; Myoc, *Myotis occultus*; Myvo, *Myotis volans*; Pih, *Pipistrellus hesperus*; Pla, *Plecotus auritus*; and Plt, *Plecotus townsendii*. Values from Aldridge (1988) for a live *Myotis lucifugus* are also included (see discussion): Ald (1), Aldridge's (1988) original values; and Ald (2), corrected values for Aldridge (1988).

distinction is made between the flight style of vespertilionid bats possessing very low versus low wing loading, or, as we have already mentioned, between low and average wing loading for vespertilionids with wings of low aspect ratio. Furthermore, even the overall utility of such categories may be in doubt if they are not clearly distinct from one another, as was the case for the vespertilionids in Norberg & Rayner's paper (1987) (Figs 2 and 4).

A more serious difficulty lies in extrapolating qualitative flight styles from these categories (e.g. a bat with low wing loading will fly slowly). While such a statement is generally true, what exactly is meant by the term 'slowly' is unclear. We must be explicit about what our frame of reference is. A bird with a 'low' wing loading may fly 'slowly', but it will still fly faster than most bats with 'high' wing loading as the wing loadings of birds generally exceed those of most bats (Poole, 1936). In reality, both aspect ratio and wing loading should only be used to make relative qualitative statements of this sort (e.g. of two bat species, the one with the lower wing loading can fly more slowly than the other). However, wing loading has an additional desirable quality. It can be used to make specific quantitative statements about flight speeds and turning radius because of its algebraic relationship with these variables (Pennycuick, 1975; Aldridge, 1987; Norberg, 1987).

Our objective is not to criticize unduly studies that make predictions of flight style based upon morphometric characters. Today, these studies are grounded in good aerodynamic theory and may well yield reasonably accurate predictions on the whole. We merely wish to point out that we should avoid making an already complicated field of study even more complex by ignoring an important source of potential error. For instance, any predictions that we make are likely to represent only a portion of the bat's total flight envelope, as the techniques employed generally ignore the fact that the LSA, and thus the flight characteristics of the bat, are altered during flight (Norberg, 1976). This portion that we can easily predict probably corresponds to one or a limited number of ecological roles (e.g. foraging or migration or normal transit or escape from predation). However, in order to serve the remaining ecological roles, the bat may be able to expand its flight envelope by actively changing the camber of the wing (Vaughan, 1970) and/or the proportions of the subunits of the LSA (Findley *et al.*, 1972). These changes, and the resultant changes to the flight envelope, will be more difficult to predict. The key is to fix the easily predictable portion of the flight envelope as accurately as possible. Our major point here is that the accuracy of this initial placement, and thus the foundation for any ancillary predictions, may be in doubt if we continue to ignore the effects of specimen preservation.

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