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ERRORS OF MEASUREMENT OF MAXIMUM POSSIBLE PERFORMANCE

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In a previous paper, the author attempted to measure the maximum possible force which individual passalid beetles could exert between their mandibles. This was done by the rough-and-ready method of encouraging each individual beetle to nip ten times on a dynamometer and counting the strongest of the ten nips as representative of the greatest force that the beetle could ever possibly exert in the circumstances; this latter will be called the 'ultimate performance' in this paper. Clearly this measurement, the greatest performance of the ten trials, falls somewhat short of the ultimate performance, and in this paper attempts are made to estimate that shortfall.

The first step in the estimation was to assume that the forces of the ten measured nips of a particular individual were independent samples drawn from some probability-distribution of nip-forces of the general nature of that depicted in Fig. 1; the essential feature of this is that there is a definite force, arrowed in Fig. 1, above which the probability of observing that force is zero. The curve may approach the force axis at an angle or tangentially at that point. The distribution is to be estimated for each individual beetle and the force corresponding to the arrowed point used as the estimate of the ultimate force.

Secondly the assumption is made that, although this force-distribution curve will shift along the force axis according to whether it is to apply to a strong or a weak beetle, and although it will be broad or narrow according as to whether it is to apply to a variable or a consistent individual, nevertheless the form of the curve (i.e. the specification of whether the curve is rectangular, sawtooth-shaped, parabolic, of cosine-form etc.) will be similar for all individuals.

Thirdly, the form of the curve was estimated. To do this, the same individual (selected as appearing to be in good condition

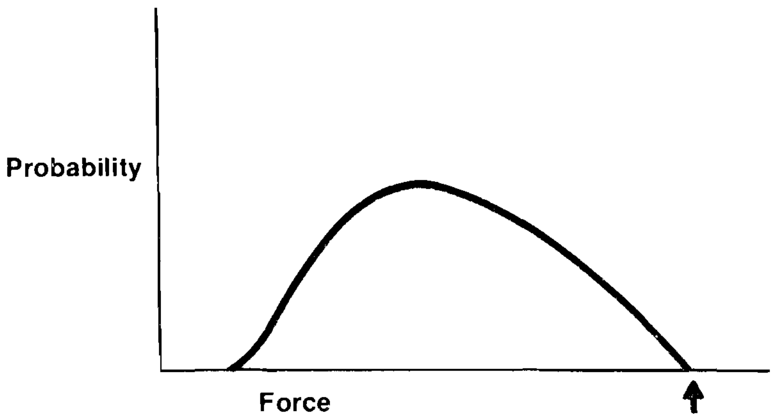
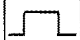
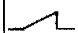
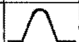
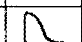


Fig. 1. Suggested general form for the probability distribution of forces measured in a beetle. The 'ultimate performance' is indicated by the arrow.

Table 1 An arbitrary library of distribution functions useful in estimating ultimate performance.

	Shape	Probability distribution function		Mean	Standard deviation	Cumulative distribution function		Shortfall	Coefficient of variability
a		$p = \frac{1}{a}$	$0 < x < a$	.50a	.29a	$\frac{x}{a}$		.091a	.91
b		$p = \frac{2x}{2}$	$0 < x < a$	.67a	.24a	$\frac{x^2}{a^2}$		.048a	.95
c		$p = \frac{2}{a}(1 - \frac{x}{a})$	$0 < x < a$	.33a	.24a	$\frac{x}{a}(2 - \frac{x}{a})$		.27a	.49
d		$p = \frac{x}{a^2}$ $p = \frac{1}{a^2}(2a - x)$	$0 < x < a$ $a < x < 2a$	a	.41a	$\frac{x^2}{2a^2}$ $\frac{1}{2}(-2 + \frac{4x}{a} - \frac{x^2}{a^2})$	$0 < x < a$ $a < x < 2a$	.38a	.49
e		$p = \frac{1}{2} \sin x$	$0 < x < \pi$	1.57	.68	$\frac{1}{2}(1 - \cos x)$		.55	.51
f		$p = \frac{3}{4a^3}(a^2 - x^2)$	$-a < x < a$	0	.45a	$\frac{1}{4}(2 - \frac{x}{a})(1 + \frac{x}{a})^2$		.34a	.53
g		$p = \cos x$	$0 < x < \pi/2$	.57	.38	$\sin x$		.39	.50
h		$p = (2+\sqrt{2}) \sin (x + \frac{3\pi}{4})$	$0 < x < \pi/4$	.27	.19	$(1+\sqrt{2})(\cos x + \sin x - 1)$		.21	.50
j		$p = \frac{2}{\pi} \sin^2 x$	$0 < x < \pi$	1.57	.57	$\frac{1}{\pi}(x - \frac{1}{2} \sin 2x)$		.71	.37
k		$p = \frac{4}{\pi} \cos^2 x$	$0 < x < \pi/2$	.47	.32	$\frac{1}{\pi}(2x + \sin 2x)$		.56	.36
l		$p = \frac{4}{(\pi - 2)}(1 - \sin 2x)$	$0 < x < \pi/4$	.20	.15	$\frac{2}{(\pi - 2)}(2x + \cos 2x - 1)$		.31	.35

and not 'tiring' easily) had the forces of 100 nips measured instead of the customary 10. From the arbitrary library of curves listed in Table 1, the one was selected which showed the best fit between the cumulative frequency distributions of the curve and of the 100 observations. Goodness of fit was measured by the Kolmogorov-Smirnov statistic or a sum-of-squares statistic (both gave the same answer in this case). A power transform was applied to the measured forces to yield a distribution with zero skewness whenever comparison was being made with a theoretical curve that was symmetrical. Once skewness had been dealt with, the standard deviation of the experimental distribution was matched to that of the theoretical, either by scaling the forces (curves e, g, h, j, k & l of Table 1) or by selecting appropriately the width parameter a of the theoretical curve (curves a, b, c, d & f). After this, the means of the experimental and theoretical distributions were matched.

Lastly, having decided on the best approximation to the form of the parent distribution, the appropriate columns of Table 1 were consulted to give a figure for the ratio of shortfall to standard deviation. From each sample-of-ten from a particular individual, the standard deviation (of the parent distribution) was estimated in the usual way, and then this ratio was used to estimate the shortfall. The shortfall was then added to the highest of the ten measurements to give the ultimate force for each individual.

RESULTS

For the set of 100 observations of beetle mandible forces previously referred to, a good fit with the experimental figures resulted from using the theoretical curve:

$$p = 1/2 \sin \left\{ \frac{\text{Force}^{1.27}}{155.71} - 1.284 \right\}$$

where p. δ (force) is the probability of finding an observation within a small range of forces of width δ (force). Forces are measured in grams-weight. The angle whose sine is taken is permitted to lie within the range 0 to π radians, i.e. forces lie within the range 63.9 to 168.8 grams-weight. For forces outside this range, $p = 0$. 168.8 g-wt. represents the ultimate force for this specimen. Raising the force to the power 1.27 corrects for skewness in the force-distribution for this individual and this, together with the sine-shape of the probability function, is presumed to be applicable to all individuals. (This assumption was, in fact, checked, by rescaling results for all individuals to a common mean and standard deviation and showing that a similar theoretical curve gave a good fit.) The factor 155.71 ensured that the function inside the bracket had a standard deviation of $\pm$ 0.68, as is necessary for the sine function, while the subtrahend of 1.284 brings the mean of the quantity within the bracket to $\pi/2$. The figure of 155.71 will, of course, change when the sine fuction is matched to the observations from other individuals. The subtrahend plays no part in the subsequent calculations.

Table 2 shows, in the first column of figures, the forces measured in the strongest of 10 nips by 76 individuals alongside, in the second column of figures, the unbiased estimate of the ultimate possible force exertable by each individual under the conditions of the original experiment, the calculations having been made by the methods above.

DISCUSSION

Among the sources of error in this method, a large one is the sampling error inherent in using only the highest observation of ten as the basis. The last column of Table 1 shows the coefficient of variability for this when considered as a sample from a parent distribution of known mean and standard deviation. It may be objected that the outcome of adding the estimated shortfall to an experimental result is merely to replace a systematic shortfall by a random error that is nor much smaller than the systematic one that it replaces. But judgments are unlikely to be made on the basis of measurements from a single individual, and averaging comparable results from several individuals will mitigate the effect of a random error but not that of the systematic shortfall.

There is much more of statistical interest concerning these distributions with an upper limit than merely the estimation

Table 2

Maximum measured mandibular forces and estimated ultimate forces for 76 individual adult passalid beetles.

Species	Maximum measured force (g-wt.)	Estimated ultimate force (g-wt.)
Didimus alvaradoi Baguena		
	74	78
	61	65
Erionomus pilosus Auriv.		
	156	170
	178	198
	203	223
	170	182
	234	256
	183	197
Erionomus planiceps (Eschscholtz)		
	458	495
	443	489
	514	574
	453	489
	427	466
	304	330
	430	469
	380	421
	269	293
	434	459
	365	390
	360	377
Heliscus tropicus (Percheron)		
	109	120
	106	118
	61	70
	103	112
	173	187
	152	169
	158	171
	121	127
	196	223
	208	225
	219	247
Heliscus Vazquezae Reyes-Castillo y Castillo		
	231	252
	343	374
	119	136
	89	97
	237	254
	263	278
	288	321
	170	188
Odontotaenius striatopunctatus (Perch.)		
	221	240
	182	194
Oileus heros (Truqui)		
	355	399
Oileus rimator (Truqui)		
	83	90
	167	178
	146	162
Passalus punctatostriatus Percheron		
	49	55
Petrejoides orizabae Kuwert		
	88	98
Proculejus brevis (Truqui)		
	209	244
	139	160
	262	313
	205	234
	352	401
	288	336
	156	180
	201	223
	171	187
	171	200
	193	212
	305	340
	269	300
	310	330
	350	386
Proculus beckeri (Zang)		
	1015	1130
	566	640
	897	969
	716	786
Pseudacanthus mexicanus (Truqui)		
	150	173
	254	286
	200	220
	128	139
	173	187
	203	221
Spurius halffteri Reyes-Castillo		
	27	30
	36	39
	53	57
	61	68

of the ultimate performance. For example, it is often an easy matter to devise statistical tests and tables, to allow the use of the estimates of ultimate performance as a criterion of whether two, say, samples-of-ten have been drawn from the same parent population. This is valuable because ultimate performance may well be a biologically-determined quantity in circumstances where mean and standard deviation of a sample-of-ten might depend on changeable or unknown vagaries of measurement technique.

Finally, a mention may be made of the widespread possible value of measures of ultimate performance. In evolutionary terms, it seems possible that survival of individuals of a species could frequently depend on their ultimate performances in life-or-death situations, rather than on average performances. Seen in this light, estimates of ultimate performance acquire considerable interest. It is therefore surprising that standard statistical texts treat as briefly as they do the matter of such estimations.