TABLE 1. Measurements in millimeters of museum specimens and hybrid.

		N	Culmen Mean (± S.D.)	Culmen Range	Tarsus Mean (± S.D.)	Tarsus Range
American Avocet	♂	10	95.69 (±3.54)	90.1–100.8	94.95 (±3.99)	89.6–104.0
	♀	10	88.90 (±2.66)	82.5– 92.1	87.66 (±3.95)	82.6– 93.5
hybrid			83.6		95.9	
Black-necked Stilt	♂	10	67.27 (±1.87)	64.6– 70.3	111.79 (±2.38)	107.1–116.3
	♀	10	64.49 (±2.33)	60.6– 68.0	98.75 (±6.10)	91.3–108.7

Short (Auk 86:84–105, 1969) said "Artificially induced hybridization proves only the existence of considerable genetic similarity and compatibility." The existence of this hybrid shows great genetic similarity between *Himantopus* and *Recurvirostra*, and supports their placement together in the family Recurvirostridae.

I extend thanks to Joseph Morlan and Malcolm Raff for assistance in observing and photographing this bird, to Ned K. Johnson for permission to measure specimens in his care at the Museum of Vertebrate Zoology, to J. Robert McMorris, Zoologist, and Herman Edwards, Keeper, of the San Francisco Zoo for their courtesy and help, and to Ralph J. Raitt for critically reading this manuscript.

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AREA-VOLUME RELATIONSHIP FOR A BIRD'S EGG

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The surface area A of an egg is slightly more difficult to determine, either by measurement or by calculation, than the volume V. Various methods of determining the volume have been described by Barth (1953), Preston (1974), Paganelli et al. (1974) and Tatum (1975). Recent investigations to determine the area have therefore concentrated on finding a relation between the area and the volume, so that if the latter is known the former could be quickly found. In particular, both Paganelli et al. (1974) and Shott and Preston (1975) have pointed out that there is a general relationship of the form

$$A = kV^{\frac{2}{3}}$$

between A and V for any closed surface, the constant k being determined solely by the shape of the surface and independent of its size. The value of k is least for a sphere, when k takes the value $\sqrt[3]{36\pi} = 4.836$. Both groups have therefore directed their efforts to the determination of k for different shapes of eggs.

Paganelli et al. determined k by actual measurement of A and V for a variety of birds' eggs of different shapes and sizes, and found empirically that for most eggs k is near to 4.951. Shott and Preston, on the other hand, developed a theoretical expression for the value of k for prolate spheroids. With $p = b/a$, where a and b are respectively the semi major and semi minor axes of the spheroid, their expression was equivalent to

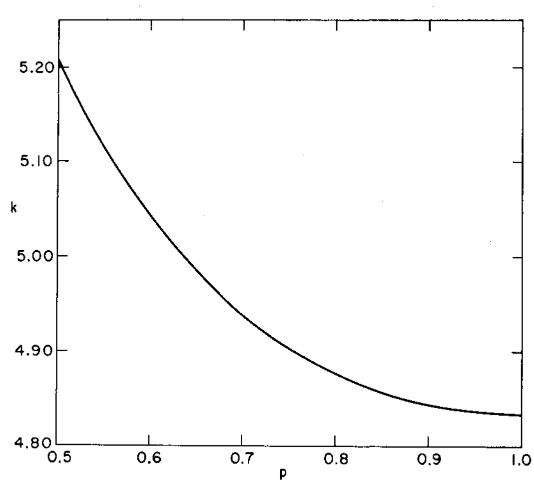

FIGURE 1. The constant k as a function of p for prolate spheroids calculated from the formula of Shott and Preston.

$$k = \left(\frac{9\pi}{2p}\right)^{\frac{1}{3}}\left(p + \frac{\cos^{-1} p}{\sqrt{1-p^2}}\right).$$

This function is illustrated in figure 1. Shott and Preston stated that most eggs have p near to 0.7, and indeed the empirical value of $k = 4.951$ found by Paganelli et al. corresponds to a spheroid with $p = 0.6861$.

Real eggs, however, are not prolate spheroids, which are symmetric objects. Preston (1953) proposed that the shape of many eggs could be fairly faithfully represented by the equations

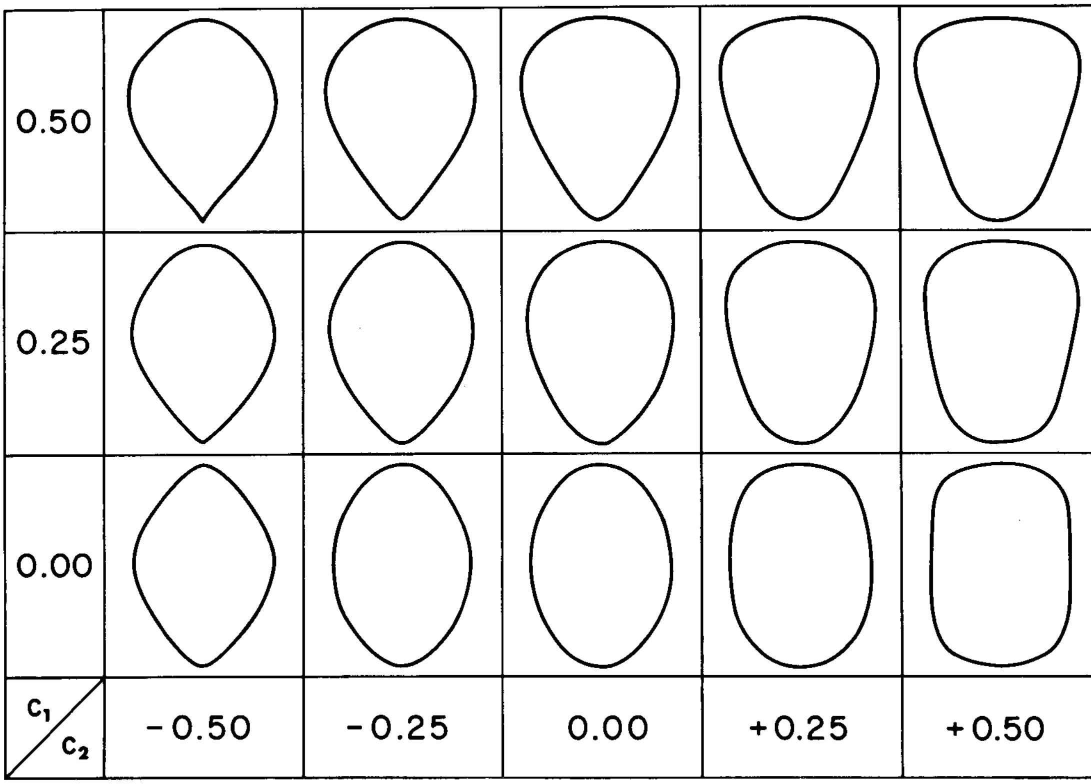

FIGURE 2. The shapes of Preston ovals for different c_1 and c_2. All ovals are drawn with $p = 0.70$.

$$y = a \sin \theta$$
$$x = b \cos \theta (1 + c_1 \sin \theta + c_2 \sin^2 \theta) .$$

These represent an egg of length 2a and of diameter midway between the poles 2b. (Unfortunately Preston [1974] and Tatum [1975] reversed the meanings of a and b. We here return to the original meanings in Preston [1953], also used by Shott and Preston [1975].) For a symmetric egg $c_1 = 0$; for a prolate spheroid $c_1 = c_2 = 0$; and for a sphere, $c_1 = c_2 = 0$ and $a = b$. Further mathematical discussion of this and similar representations was given in Preston (1968), and many data on the shapes of real eggs were given in Preston (1969). Later Preston (1974) and Tatum (1975) developed theoretical expressions for the volume of these ovoids in terms of the parameters c_1 and c_2, showing also how these parameters are obtained from simple measurements on a real egg. Figure 2 shows how the shapes of these ovoids vary with c_1 and c_2; all the ovals in the figure are drawn with $p = 0.7$. (A similar figure was given by Preston [1969] but with a slightly different mathematical representation.)

It occurred to me that it would be of some interest to calculate the value of k for Preston ovoids in terms of p, c_1 and c_2. Not only is this an obvious extension of the theory, but it will also help to determine how well the surface area of an egg can be determined by using a constant value of $k = 4.951$ or by using the formula for prolate spheroids. Using a 200 step Simpson's rule, I therefore evaluated the integral

$$A = 2\pi \int_{-a}^{a} x \left[1 + \left(\frac{dx}{dy} \right)^2 \right]^{\frac{1}{2}} dx$$

for a range of different values of p, c_1 and c_2.

Results are given in table 1 for a range of p from 0.50 to 1.00; $c_1 = 0.00, 0.25, 0.50$; and $c_2 = 0.00, \pm 0.25, \pm 0.50$. A check on the accuracy of the numerical integration is afforded by the agreement to seven significant figures for the cases with $c_1 = c_2 = 0$ and values calculated from Shott and Preston's formula for prolate spheroids.

Examination of the table shows that only quite small errors will be incurred in using a constant value of $k = 4.951$. Even in the very extreme case of an unusually-shaped egg with $p = 0.50$, $c_1 = 0.00$, $c_2 = +0.50$, for which $k = 5.249$, the error would be only 6%; for all other cases covered by the table the error is less. The error incurred in using the spheroidal approximation is less than that incurred in using a constant value of k, although an error of as much as 5% can be found in the range of the table. This again occurs with an unusually-shaped egg, with $p = 1.00$, $c_1 = 0.50$, $c_2 = +0.50$. The correct k is 5.089; the k for a spheroid with $p = 1.00$ (i.e. a sphere) is 4.836. This, however, is a very extreme case and doubtless either method is sufficiently accurate for many biological purposes. Only where accuracy greater than a few percent is required will it be necessary to use the correct values of k.

I wish to thank a referee for a number of helpful comments, which led to substantial improvements in this paper. Since completion of this paper, an important paper on this subject has been published by Hoyt (1977).

TABLE 1. Area-to-volume ratios of eggs of various shapes. The tabulated quantity is $k = A/V^{2/3}$.

b/a	c_1	$c_2 = -0.50$	$c_2 = -0.25$	$c_2 = 0.00$	$c_2 = +0.25$	$c_2 = +0.50$
0.50	0.00	5.183	5.196	5.207	5.223	5.249
	0.25	5.162	5.181	5.197	5.218	5.247
	0.50	5.100	5.138	5.170	5.203	5.242
0.55	0.00	5.097	5.105	5.116	5.135	5.166
	0.25	5.080	5.095	5.111	5.134	5.169
	0.50	5.031	5.066	5.097	5.133	5.178
0.60	0.00	5.030	5.034	5.043	5.064	5.100
	0.25	5.017	5.028	5.043	5.068	5.108
	0.50	4.981	5.011	5.042	5.080	5.130
0.65	0.00	4.978	4.978	4.985	5.007	5.048
	0.25	4.970	4.976	4.989	5.016	5.060
	0.50	4.945	4.972	5.001	5.041	5.095
0.70	0.00	4.940	4.934	4.939	4.962	5.007
	0.25	4.935	4.937	4.948	4.975	5.024
	0.50	4.922	4.944	4.972	5.013	5.072
0.75	0.00	4.912	4.901	4.904	4.927	4.975
	0.25	4.912	4.908	4.917	4.945	4.997
	0.50	4.909	4.927	4.953	4.996	5.059
0.80	0.00	4.894	4.878	4.877	4.900	4.951
	0.25	4.897	4.888	4.894	4.923	4.978
	0.50	4.904	4.918	4.943	4.986	5.053
0.85	0.00	4.884	4.862	4.858	4.880	4.934
	0.25	4.890	4.876	4.880	4.907	4.965
	0.50	4.907	4.917	4.940	4.984	5.054
0.90	0.00	4.881	4.853	4.845	4.866	4.922
	0.25	4.890	4.871	4.871	4.898	4.958
	0.50	4.917	4.922	4.943	4.988	5.061
0.95	0.00	4.884	4.850	4.838	4.858	4.915
	0.25	4.896	4.871	4.868	4.894	4.957
	0.50	4.932	4.933	4.952	4.997	5.073
1.00	0.00	4.891	4.851	4.836	4.854	4.913
	0.25	4.907	4.877	4.870	4.895	4.959
	0.50	4.952	4.949	4.965	5.010	5.089

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