Interpreting the Lists and Equations of Egg Dimensions in Schönwetter's Handbuch Der Oologie

INTERPRETING THE LISTS AND EQUATIONS OF EGG DIMENSIONS IN SCHÖNWETTER'S *HANDBUCH DER OOLOGIE*

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THE MOST COMPREHENSIVE reference work on avian eggshells, Schönwetter's (1960–1992) *Handbuch der Oologie* (= *Handbook of Oology*; referred to hereafter as "the Handbuch") is commonly misread, probably because it is not written in English. Several seminal papers that have drawn on Schönwetter's tables have unwittingly treated its calculated values for shell thickness and fresh egg weights as measured data rather than derived values, thereby potentially compromising the conclusions of those studies. The publication of the Handbuch in German also hinders its dissemination and use, such that its unrivaled collection of data for the eggs of ~10,000 taxa (species and subspecies)—close to the two-thirds of bird species whose eggs are known to science (Walters 1994)—has largely gone untapped and still awaits modern comparative analyses (but see Birchard and Deeming 2009). However, the bulk of the data are presented in tables, which are easily accessible to non-German speakers, once their basic structure and abbreviations have been clarified. In addition to data tables, the Handbuch also contains a collection of equations to calculate shell thickness, egg volume, and fresh egg weight from length, breadth, and shell weight. These equations may be preferable to those routinely used today (e.g., Hoyt 1979) when assessing intraspecific variation or calculating the dimensions of unusually shaped eggs. Here, we provide an explanation of the data tables and clarify the derivation of the equations for egg dimensions with the aim of unlocking this morphological section of the Handbuch for the English-speaking scientific community to enable researchers with no access to a copy of the Handbuch to use its equations.

THE HIDDEN IMPACT OF THE *HANDBUCH DER OOLOGIE*

A book with a worse ratio of impact to recognition than Max Schönwetter's Handbuch (edited by Wilhelm Meise; Steinheimer 2002) will be hard to find in the ornithological literature. Several influential publications in avian biology (Ar et al. 1974, Rahn and Ar 1974, Hoyt 1979; each with 300–500 citations on ISI Web of Knowledge) rely heavily on the Handbuch's lists of shell data and equations, yet few people even know it exists (Hillcoat 2000). In addition, the Handbuch has been used to compile information on eggshells for many standard references, such as the *Handbook of the Birds of the Western Palearctic* (Cramp and Simmons 1978–1994, Hillcoat 2000), which are used regularly to generate data sets for comparative analyses. Although the Handbuch itself is cited less than 100 times in the primary scientific literature (20 since 2005), the diversity of citations demonstrates its relevance to a wide variety of scientific fields, reaching from evolution (Gonzalez-Voyer et al. 2007), molecular phylogenetics (Fregin et al. 2009), and toxicology and environmental pollution (e.g., Becker 1992, Pain et al. 1999) to poultry science (e.g., Ancel and Girard 1992) and zoo keeping (Deeming et al. 1991). Furthermore, recent ecological research also highlights the importance of egg collections for monitoring environmental changes (Scharlemann 2001, Green and Scharlemann 2003).

The text of the Handbuch also contains valuable data, but it is even less well known than the tables of shell morphometrics. Individual species accounts provide detailed descriptions of egg appearance (including color, gloss, pore structure, and surface structure) and a wealth of biological data, based either on Schönwetter's own experience or, where necessary, cited references (Eisenmann 1963). For rare species, these data gathered by Schönwetter and Meise from specimen labels or personal letters (Piechocki 1999) sometimes constitute the only egg and nest descriptions or even the only breeding records available. Furthermore, the Handbuch's general oology section, completed around 1960, provides a comprehensive account of oological phenomena, an overview of which is provided in the table of contents for volume IV (refer to the online Appendix [see Acknowledgments]). Most

importantly, a major comparison of shell structure and coloration (vol. IV, pp. 629–696) highlights general trends and exceptions within groups and provides one of the largest reference collections ever published on the subject. With its wealth of knowledge and historical references, the general oology section therefore inspires a number of scientific questions that could not be addressed when the Handbuch was written but that are accessible today through improved technology and computing power. Unlike the morphometric data, however, reading this section of the Handbuch requires a basic command of the German language.

COMMON MISINTERPRETATIONS OF THE HANDBUCH

Neglecting the Handbuch as a primary source, or referring only to its tables, is not simply a citation problem but has serious scientific implications. Most critically, many users of Schönwetter's (1960–1992) data seem to have been unaware that only length, breadth, and shell weight were measured directly. The shell thicknesses and fresh egg weights given in the tables were calculated from those measurements. This fact has already been pointed out in one of the first reviews of the book (Eisenmann 1963). Hoyt (1979), for example, used Schönwetter's egg-weight data as if they were measurements to confirm the accuracy of his own equation for deriving fresh egg weight from egg length and breadth. Similarly, correlations between Schönwetter's shell measurements and shell thickness and egg weight (Ar et al. 1974, Rahn and Paganelli 1989, Birchard and Deeming 2009) are confounded in that they compare different transformations of length, breadth, and shell weight according to the shape of the egg. These limitations are rarely discussed in these papers, even though the text of the Handbuch describes the equations for calculating shell thickness, volume, surface, and fresh egg weight and their derivation in detail.

Two factors may be responsible for the neglect of Schönwetter's Handbuch. First, the book is written in a language spoken only by a small segment of the scientific commuity and jokingly described as so difficult that "only the dead have time to learn [it]" (Twain 1880). Secondly, outside German-speaking countries it is largely found only in national libraries or natural-history museums (see below for a list of key libraries). However, because most of its data are provided in tables (or, for very rare eggs, in a formalized manner in the species accounts), little explanation is required to make this unique resource accessible. Similarly, once the derivation of the equations is clear, they can be used universally and adapted to calculate various egg properties using measurements not only of blown museum specimens but also of live eggs.

MAKING THE HANDBUCH ACCESSIBLE

Here, we aim to provide the basis for the renewed use of Schönwetter's morphometric eggshell data. To this end we first detail the composition of Schönwetter's eggshell tables and explain the variable notation used in the tables and throughout the Handbuch. Then we assess the equations for shell thickness and fresh egg weight to highlight their strengths and weaknesses. The overall goal is to create a reference to accompany copies of Schönwetter's Handbuch that enables English-speaking scientists to use its tables and equations correctly and to their full potential without the need for expensive and time-consuming translations.

Furthermore, Schönwetter's equations for egg weight and volume, given below, are an important alternative to those published by Hoyt (1979), especially when egg shape needs to be accounted for to achieve greater accuracy.

DATA TABLES AND VARIABLES

Schönwetter (1960–1992) compiled the eggshell data in the tables that form the bulk of the Handbuch from his own collection of 19,206 egg clutches of 3,839 taxa (F. Steinheimer pers. comm.; Projektleitung Naturkundliches Universitätsmuseum Halle (Saale), Germany, where the specimens are stored together with Schönwetter's catalogue and letters). In addition, Schönwetter used various private and public collections in Germany and abroad (e.g., the Museum für Naturkunde, Berlin; the Museum Alexander Koenig, Bonn; Museum für Tierkunde, Dresden; Natural History Museum, Tring, United Kingdom; and Naturhistorisches Museum, Vienna) and data from published accounts and private correspondence (Piechocki 1961, 1999). The taxonomy in the data tables generally follows Peters (1931–1986), and the full list of orders or families covered in each of the Handbuch volumes can be found in the online Appendix. The variables used in the tables and equations are explained in a list on pages vii–viii in the Introduction (Einleitung, vol. I) to the Handbuch. Table 1 provides a literal translation of this list. We have annotated this translation, in square brackets, with information found in the Introduction (vol. I, pp. v–viii), General Oology (Allgemeine Oologie, vol. IV, pp. 591–716), and Mathematical Section (Mathematischer Teil, vol. IV, pp. 1–152) to facilitate understanding of the variables used.

In addition to the basic shell dimensions, Schönwetter's data tables list countries or regions where the taxon occurs. Table 2 mirrors the design of Schönwetter's data tables. As well as detailing the contents of each column, Table 2 explains the German terms that regularly occur in each of the columns. Data in the tables are presented as mean values and ranges but without standard deviations, possibly because they sometimes combine his measurements with published range values. The data sources for the less common species are usually listed in the second column of the data tables or in the species accounts. References for the data tables and species accounts can be found in the Bibliography (Literaturverzeichnis, vol. IV, pp. 587–725).

If information for a species is not listed in the data tables, it may either be presented in the species account or be missing altogether. A taxonomic list of species for which data were not available is given at the end of each volume (vol. I, Non-passerines; vol. II, Passerines to Muscicapidae; vol. III, remaining Passerines). However, recently described species will naturally be missing from this list. Finally, volume IV contains a section called "Additions" (Nachträge, pp. 193–576), which lists in systematic order additional data that became available before 1992 for any species treated in the earlier volumes of the Handbuch. Errors and misprints are also listed in this section under the relevant species name.

COMPOSITION OF EQUATIONS

Schönwetter clarifies how he arrived at the equations used to calculate the values in the tables of egg dimensions in the Mathematical Section (vol. IV, pp. 1–152). In our representation of the

Table 1. Literal translation of the list of variables used in Schönwetter's (1960–1992) *Handbuch der Oologie*. We have set the variables found in the Handbuch's data tables in bold; those found in the main text are in roman. The measurement unit and our own further explanations are provided in square brackets.

Variable	Definition
A	**The long axis, the maximum length of the shell. [mm]**
B	**The broad axis, the maximum lateral diameter of the shell. [mm]**
g	**The shell weight of the egg. This value is indispensible for the identification of many species and allows interesting biological conclusions. It is determined by weighing the clean and completely dry egg shell, best with so-called Swiss pharmacist's scales. One is satisfied with three decimals. [g; in rare cases, mg. The latter is noted next to the respective value. Shells are always weighed with the membrane in place.]**
d	**Shell thickness. It is rarely measured directly; instead it is calculated according to an equation that includes a thickness factor. This factor [m] can be found in a table in section B [vol. IV, p. 82, Tabelle 8] of the main body of the book. [mm]**
e, k	Factors that are crucial for describing egg shape. If both egg poles (measured on the long axis) are about equidistant from the maximum wide axis, the egg is a two-pointer and symmetrically built. Generally, however, the longitudinal section of the egg is an oval or a spinner. In these cases the "Dopphöhe" (= b = distance of the blunt egg pole from the wide axis) is smaller than half the long axis. If the ratio between the longer and the smaller part of the long axis is called e (Szielasko's quotient), $e = a/b$, then the largest values describe spinner-shaped eggs. In addition to the Dopphöhe b, the axis ratio is important as well: $k = A/B$. Relatively round eggs have small values for k; elongate ones, by contrast, have large values. [both dimensionless]
G	**The fresh egg weight in grams. If not weighed directly, it has been calculated using the ellipsoid equation, which has been extended with a variable reduction factor, details of which are given in section B of the main body of the book.**
Rg	**As a percentage, the relative shell weight $Rg = 100 \times g/G$, the percentage of the weight of a fresh egg of the mean size for the species that is attributable to the dry eggshell. *Rg* is interesting because the larger species and eggs typically have relatively higher shell weight; holding the greater egg contents appears to require relatively heavier and stronger shells. However, there are many other question resulting from the *Rg*.**
RG	As a percentage, the relative egg weight $G = 100 \times G$/body weight. For the relative egg weight, I sometimes have mentioned the full body weight in addition to the percentage value.
q	Rey's equation $q = AB/g$ (AB expressed in millimeters, g in milligrams). The heavier the shell in relation to the full egg weight, the smaller the ratio. Especially for cuckoo eggs, q is an important addition to Rg (see above). [dimensionless]
U	The large circumference of the egg. [mm]
u	The small circumference of the egg (with the wide axis as the diameter). [mm]
O	Surface of the egg. [mm²]
Vol	Volume of the egg. [mm³]
γ	Specific weight of the shell. [Greek gamma. In grams. This includes shell and membrane. Tabelle 20 (vol. IV, p. 118) provides the γ Schönwetter deducted for 50 bird families.]
Γ	Specific weight area of the egg. [g]
m	The index m (rarely used) describes the average, for example, g_m = average shell weight. [dimensionless]

Table 2. Key to data tables in Schönwetter's (1960–1992) *Handbuch der Oologie*. Our table structure is an exact copy of that used for the Handbuch's tables. Variables in the table header are explained in our Table 1. The top row shows the table layout, and the bottom row provides translations of German terms used frequently in each column. A decimal comma in the German original replaces the English decimal point.

# [Number of eggs measured directly or from published data]	*Scientific name* Authority min length – max length × min breadth – max breadth [mm] = min weight – max weight [g] (Reference) [if not his own data]	A	B	g	d	G	Rg	Species or subspecies distribution
		#,#	#,#	#,#	#,#	#,#	#,#%	
		[Averages and values calculated from averages, respectively.]						
• – = no data • x + # = unknown sample size plus known sample size.	• nach, n. = following [Author] • bei = in [Reference] • und, u. = and • briefl. = [Author] by letter • Massliste = measurement list • Ei, Eier = egg, eggs • Sammlung = collection • Seite, S. = page • andere = others	(siehe Text) (see text)						• O, Ost; östlich = east; eastern • S, Süd; südlich = south; southern • W, West; westlich = west; western • N, Nord; nördlich = north; northern • Fluss, See, Insel(n) = river, lake, island(s) • Inner, äuβer = central, outer • von – bis = from – to • bzw. = respectively • German and English place names are often similar

equations below, we maintained his numbering of the equations in round brackets to allow easy cross-referencing with the original text. For the same reason, we also maintained his notation of variables. Explanations of these can be found in Table 1 or in our text following the first occurrence of a variable in an equation. Please note that in German a decimal comma takes the role of the English decimal point. For convenience we have used the decimal point throughout. Similarly, we replaced the colon, used occasionally in the original equations as a division sign, with a fraction separator. Finally, the Handbuch equations are inconsistent in denoting multiplication, using variously a multiplication dot, a multiplication sign, or no symbol. We have omitted the multiplication symbols consistently throughout, in keeping with modern scientific notation.

Shell thickness d.—None of the values for shell thickness presented in Schönwetter's tables are measurements. Instead they constitute an eggshell thickness index based on the average of measured values for length A, breadth B, and shell weight g as presented in the tables of Handbuch section A. Shell weight is usually not corrected for the drill hole or other defects of the shell, because Schönwetter found their effect on the weight to be negligible in most cases (vol. IV, pp. 37–39, Tabellen 4 and 5). Similarly, shell thinning through incubation is considered insignificant. However, shell weight and, thus, thickness are inclusive of the inner membrane. The difference between Schönwetter's equation and other thickness indices (Green 2000) is that it includes a "reduction factor" K, a "shape factor" c, and the specific weight of the shell γ (Greek gamma, explained in detail below). These factors allow accounting for the deviations from the "classic" egg shape, which occur in numerous bird species (e.g., elongate in Guillemots [*Uria* spp.] or spherical in jacamars [*Galbula* spp.]; see also Mänd et al. 1986).

The equation Schönwetter used for calculating most shell-thickness values d in the tables is given on page 80 of volume IV as follows, where $k = A/B$ (see Table 1):

$$d = \left(\frac{k}{Kc\gamma}\right)\left(\frac{g}{AB}\right) = m\left(\frac{g}{AB}\right) \tag{43}$$

In the final part of this Equation 43 the term $(k/Kc\gamma)$ is expressed as a thickness factor m. Equation 43 is derived, however, from a more explicit term that is relevant only for very thick eggshells:

$$d = \frac{g}{\left[Kc\gamma\left(B-d\right)^2\right]} \tag{41}$$

Equation 41, curiously, also includes d on its right-hand side, where it serves to calculate a mean of inner and outer surface area in the case of very thick eggshells. For those shells, Schönwetter measured or approximated d prior to calculation. Equation 43 is derived by dropping d and expressing B^2 (Equation 42) as a function of k (= A/B; see Table 1).

$$B^2 = \left(\frac{A}{B}\right)B \tag{42}$$

K, the reduction factor (Reduktionsfaktor), is based on Equation 59 for calculating the surface area O_e of the rotational ellipsoid

(vol. IV, p. 108). Conventionally, surface area is calculated using the half-axes. Schönwetter, however, calculated it in Equation 59 using the full length of the shell A expressed as Bk. The resulting equation is

$$O_e = B^2\left[\frac{\pi}{2}\left(1+\frac{k^2}{\sqrt{k^2-1}}\arcsin\frac{\sqrt{k^2-1}}{k}\right)\right] \tag{59}$$

$$O_e = B^2 K \tag{15}$$

K, the term in square brackets in Equation 59, is therefore a linear function of k. Because k in birds varies only between 1.00 (perfectly round) and 2.00 (very elongate; vol. IV, pp. 13 and 20–24), the equation for K can be expressed as

$$K = 3.14159 + 2.228(k-1) = 0.914 + 2.228k \tag{60}$$

In perfectly round eggs this returns π (3.14159) as the value for K. All values of K for $k = 1.00$ to $k = 2.00$ are listed in volume IV (p. 109, Tabelle 14) in steps of 0.01.

The shape factor c (Gestaltsfaktor) is defined as

$$c = \frac{\text{Egg surface}}{\text{Ellipsoid surface}} \tag{6}$$

The value for the egg surface was derived by Schönwetter from accurate drawings of the longitudinal sections of different egg shapes (vol. IV, pp. 24–25), whereas that of the ellipsoid surface was calculated using Equation 15. In practice, c is determined from a list (Table 3), based on the values k and e (vol. IV, p. 110, Tabelle 15).

For applied purposes and because Schönwetter noticed that "most people do not like to calculate," he combines the term $(k/Kc\gamma)$

TABLE 3. Reproduction of the table of shape factors c in Schönwetter's (1960–1992) *Handbuch der Oologie* (vol. IV, p. 110, Tabelle 15) to calculate c from egg dimensions:

$$\frac{A}{B} = \frac{\text{Egg length}}{\text{Egg breadth}} \quad \text{and} \quad a:b = \frac{\text{Longer part of A as sectioned by B}}{\text{Shorter part of A as sectioned by B}}$$

$\dfrac{A}{B} = k$	$a:b =$			
	1.00	**1.25**	**1.50**	**1.75**
1.10	0.999	0.992	0.990	0.988
1.15	0.999	0.987	0.979	0.972
1.20	0.998	0.983	0.972	0.962
1.25	0.998	0.980	0.966	0.953
1.30	0.997	0.977	0.960	0.944
1.35	0.997	0.975	0.955	0.936
1.40	0.997	0.973	0.950	0.929
1.45	0.997	0.972	0.946	0.922
1.50	0.996	0.970	0.042	0.916
1.55	0.996	0.968	0.938	0.910
1.60	0.996	0.966	0.934	0.904
1.65	0.996	0.964	0.930	0.898
1.70	0.996	0.962	0.927	0.892
1.75	0.996	0.962	0.924	0.886
1.80	0.996	0.961	0.921	0.880

of Equation 43 into a thickness factor m (Table 1). In volume IV (p. 82, Tabelle 8), Schönwetter lists 168 different values for m based on the combinations of $6\gamma \times 4c \times 7k$ values. Today, standard mathematical software (e.g., Microsoft EXCEL) allows us to calculate m for eggs of any measurements rather than rely on tabulated values. In a final simplifying step, Schönwetter transforms the equation for d so that it produces a good approximation of shell thickness for most bird eggs of conventional shape and shell density:

$$d = \frac{0.175g}{AB} \qquad (45)$$

Fresh egg weight G.—In all instances, fresh egg weight G in Schönwetter's tables was calculated (vol. IV, pp. 28–31) rather than weighed directly or determined through weighing the eggshell after filling it with water. Calculation of the egg weight may be preferable to a direct measurement if incubation stage is unknown when the eggs are collected, because eggs lose weight during incubation (vol. IV, p. 30, Tabelle 3). Filling the eggshell with water, on the other hand, requires that the membrane sealing the air cell is destroyed so that the whole egg can be filled, a process that puts older specimens at risk of mechanical destruction or molding. The fresh weight of a newly blown egg, however, can easily and safely be determined by filling it with water.

The equation used for most of the calculations of G in the egg-dimension tables is given in volume IV (p. 31):

$$G = 0.542\phi AB^2 + 0.50g \qquad (21)$$

It is based on the volume of an ellipsoid:

$$V_{EU} = \left(\frac{\pi}{6}\right) AB^2 \qquad (8)$$

Equation 8 is multiplied with ϕ, a shape factor (Gestaltsfaktor) for volume and the specific weight of yolk and egg white, 1.035 ($1.035 \times \pi/6 = 0.542$ in Equation 21), found almost universally across bird species (vol. IV, p. 31). To this weight of the shell-less egg, only half the shell weight g is added, because the other half of g is already taken into account through the equation for the ellipsoid volume. For shells whose specific weight γ differs substantially from 2.0, the term $0.50g$ at the end of Equation 21 should, however, be replaced by

$$\left(\frac{\gamma - 1}{\gamma}\right) g$$

For very large eggs it will be necessary to use Equation 20, which includes shell thickness:

$$G = 1.035 V_i + g = 1.035\,[0.524\phi(A - 2d)(B - 2d)^2] + g \qquad (20)$$

The shape factor ϕ for calculating volumes was defined by analogy to the shape factor c as

$$\phi = \frac{\text{Egg volume}}{\text{Ellipsoid volume}} \qquad (5)$$

As for the calculation of c, the value for the egg was obtained from careful drawings of longitudinal sections of the shell (vol. IV, p. 25), whereas the ellipsoid volume was calculated using Equation 8.

No specific table for values of ϕ exists in the Handbuch; instead Schönwetter notes that ϕ ranges from $1.02c$ to $1.04c$, and he therefore recommends calculating approximate values for ϕ based on the table for the c values (vol. IV, p. 110, Tabelle 15; see Table 3). Some typical values for ϕ and c found across families are also listed in vol. IV (p. 24), where seven types of egg shape are defined.

Because it is easier to measure egg volume than fresh weight reliably, unless laying has been monitored precisely before collection, published accounts on egg dimensions of fresh and historical samples are more likely to provide volumes than fresh egg weights (Schönwetter 1960–1992). The relationship between the two is described by Equation 23c:

$$G = 1.05\phi\text{Vol} + \frac{1}{2}g \qquad (23c)$$

Relative shell weight Rg.—The relative shell weight Rg is calculated from average values of G and g as

$$Rg = 100\frac{g}{G} \qquad (35)$$

Because G is a value calculated on the basis of A and B, Rg is not independent of the size of the egg and cannot be easily compared across species with different-sized eggs. Generally, smaller eggs will have a smaller Rg.

LIMITATIONS OF DATA AND EQUATIONS

To make the best use of Schönwetter's lists and equations, it is important to be aware of their limitations. Three factors influence their accuracy: (1) technology, (2) biology, and (3) methodology.

(1) When the eggshell values for the tables were measured, electronic precision balances, calipers, and micrometers were not available. Instead, mechanical instruments were used, such as Swiss pharmacist's scales (vol. IV, p. 41), which allowed weights to be determined to the milligram. Similarly, length measurements (mm) were taken with an accuracy of up to two decimals or four reliable digits.

At the time the calculations were made, no electronic computers were available, so Schönwetter used the slide rule and value tables (vol. IV, p. 41), like those published in the Handbuch for the shape factor c (vol. IV, p. 110, Tabelle 15; our Table 3). This inevitably required rounding and interpolation if the measurements of an egg fell between the values given in a table.

The technical ability to measure the surface area of an object of irregular shape accurately has only recently been achieved (e.g., Chen et al. 2000). Schönwetter therefore relied on technical drawings to determine egg surface and volume. The factor γ was determined from drawings of egg fragments (created "conveniently" by a mortar-shell explosion in his dwelling) because he deemed the water-displacement method inaccurate because it caused the shell membrane to swell.

(2) The species represented in the Handbuch inevitably reflect the sampling bias of museum collections, either through their geographic restrictions or because some specimens were easier to acquire than others (Graham et al. 2004). For instance, European breeding birds are represented extremely well in the Handbuch,

both in terms of species and subspecies listed and with respect to sample size. This European bias also extends to the species measured to derive constants and equations (Schönwetter 1930). Additionally, for practical reasons, the technical drawings were mostly conducted on medium-sized eggs (vol. IV, pp. 24–27). Finally, the identity of shells of those species scarcely represented in egg collections (i.e., rare species) is often uncertain. Schönwetter tried to combat this problem through comparison with related species; in fact, he recognized a number of misidentified eggs in collections and catalogues using this method (Schönwetter 1928). Other specimens of doubtful identity that have since been reidentified have been listed in the species accounts in the Additions (vol. IV, p. 193–576) by the editor of the Handbuch.

(3) Schönwetter was careful to evaluate his calculations and factors with measurements and gives an estimate of 3–5% as the maximum error for any species or variable (vol. IV, p. 9), lower than the level of natural variability. Sadly, however, a comprehensive list of the species used and the measurements taken to arrive at this estimate has not been provided. The best records we have are for shell thickness, where ~1,350 fragments were measured multiple times with a micrometer or a measuring magnifier and augmented with published data (vol. IV, pp. 79–80). Some of the families, genera, or species used can be deduced from an earlier publication by Schönwetter (1930) or from Tabelle 20 (vol. IV, p. 118) for λ, which was calculated with measured d. Thickness was therefore measured directly for at least 200 species from about 50 families to derive the thickness equations, but these measured data are not presented in the Handbuch tables. The basis of the calculation of ϕ ($\geq$6 species; vol. IV, pp. 25–26) and c is less clear, however.

LIBRARIES OUTSIDE GERMAN-SPEAKING COUNTRIES WITH THE HANDBUCH

No record of libraries that received copies of the Handbuch was available from the publisher, so we instead searched various online catalogues (including www.worldcat.org; see details of other catalogues below) to identify key libraries that could provide access to the Handbuch or parts of it (the online Appendix provides a detailed table of contents to facilitate interlibrary loans of specific sections). We focused our search mostly on English-speaking countries but are aware that copies of the Handbuch are likely to exist in libraries and countries not covered by our search. We used three separate searches in online catalogues, with search terms being "Oologie" as a key word or title and "Schonwetter" or "Schoenwetter" as author.

United States

For holdings in U.S. academic libraries, the catalogues of the 25 top-ranked universities (colleges.usnews.rankingsandreviews.com) and the websites of the major natural-history museums were searched, along with the Online Computer Library Center (OCLC; www.oclc.org). The Handbuch can be found in the libraries of the following colleges and universities: University of California (UC) Berkeley, UC Los Angeles, California State Los Angeles, Carleton College, Colorado State, University of Connecticut, Cornell, Harvard, University of Illinois, Southern Illinois University, Kent State, Louisiana State, Louisiana Tech, University of

Massachusetts Amherst, University of Michigan (including the Wilson Ornithological Society library), Michigan State, University of Rhode Island, San Diego State, University of South Dakota, SUNY at Buffalo, Texas Tech, Texas Austin, Trinity College, and Yale. The Handbuch is also available in the following museums and institutions: Academy of Natural Sciences, American Museum of Natural History, Carnegie Library of Pittsburgh, Library of Congress, Ewell Sale Stewart Library, Field Museum of Natural History, National Institutes of Health, Smithsonian National Museum of Natural History, and Western Foundation of Vertebrate Zoology.

United Kingdom

Academic libraries in the United Kingdom were accessed using Copac (copac.ac.uk/), and the Handbuch was found at Oxford University, the British Library, and the Natural History Museum.

Canada

The following Canadian libraries with holdings of the Handbuch were found using AMICUS (www.collectionscanada.gc.ca/amicus/index-e.html): University of Western Ontario, University of British Columbia, and Royal Ontario Museum.

Australia

In Australia the libraries of all leading (Group of Eight) universities and the Commonwealth Scientific and Industrial Research Organisation (CSIRO) were searched, but only CSIRO Sustainable Ecosystems holds a copy. In addition, the Handbuch is listed in OCLC for the South Australia Museum library and the state library of New South Wales.

DISCUSSION

Almost 50 years after the start of its publication, Schönwetter's (1960–1992) *Handbuch der Oologie* remains the most important work on eggs of wild birds (Kiff and Zink 2005) and an actively used resource (e.g., Lahti 2005, Antonov et al. 2006, Gonzalez-Voyer et al. 2007, Birchard and Deeming 2009). Modern eggshell studies do not exceed the level of precision that Schönwetter achieved with the limited technology at the time (e.g., Nygård 1999, Green 2000, Gosler et al. 2005). This exceptional degree of mathematical accuracy may have been rooted in Schönwetter's profession as a surveyor, but it has earned him the respect of the leading ornithologists of the past century (Piechocki 1961, 1999).

The equations and constants developed by Schönwetter for calculating shell thickness and fresh weight from egg length and breadth compare well with those derived using computers (Paganelli et al. 1974, Hoyt 1979) and with measured data (Rahn et al. 1985). Shell surface area is the critical value for these equations. Because of the small irregularities of egg shape, true surface area will always be problematic to calculate (Shott and Preston 1975) and would require a massive technological effort to measure directly (Chen et al. 2000). The great achievement of Schönwetter's equations is that they aimed to account for the variation in eggshell shape and, thus, surface area, on a species level via shape factors. This addition could make them better suited to interspecific comparisons than many of the more recent routinely applied equations (e.g., for shell thickness; Green 2000). In fact, Hoyt (1979) recommends the use of Schönwetter's shape factors when

calculating fresh weights for eggs of unusual shapes. Unfortunately, Schönwetter does not report the sampling he conducted to arrive at these factors. It is therefore necessary to test the accuracy of the values in Schönwetter's tables through direct measurements, as has been attempted for fresh weight (Rahn et al. 1985) but still remains to be done for shell thickness.

The equations can be rearranged and, using the constants provided in the Handbuch, can serve to calculate values that cannot or could not be measured directly. Thus, they are useful for retrospective or historical studies of eggshells in museum collections as well as field studies. For instance, in a field study, fresh weight calculated using Schönwetter's equations could be compared with the actual egg weight to provide an estimate of the egg's water loss and thus its position in the hatching sequence of the clutch or its laying date. This method could provide a more accurate and safer measure of an egg's development than the height at which it floats in a water column, candling (Westerskov 1950), or frequent repeat nest visits.

Schönwetter's *Handbuch der Oologie* is unrivaled in its comprehensiveness. Furthermore, given the loss of some major European egg collections during World War II and the welcome demise of egg collecting as a hobby, it is unlikely that a similar source of shell data will be gathered again. It is therefore critical to understand the Handbuch's uses and limitations. For the same reason, it would be desirable to make the Handbuch's tables widely accessible in digital form, especially as a resource for modern comparative analyses.

Acknowledgments

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