1940b. A record of birds banded at Avery Island, Louisiana during the years 1937, 1938, and 1939. Bird-Banding, 11: 105–109.
MILLAIS, JOHN G.
1913. British Diving Ducks. Longmans, London.
PAYNE-GALLWEY, SIR RALPH
1882. The fowler in Ireland. London, 503 pp.
PHILLIPS, JOHN C.
1925. A natural history of the ducks. Boston and New York.
ROBINSON, H. W.
1913. Inequality of sexes among diving ducks. British Birds, 7: 20–21.
WETMORE, ALEXANDER
1919. Lead poisoning in waterfowl. U. S. Dept. Agric., Bull. No. 793.

Division of Economic Zoology
University of Minnesota
St. Paul, Minnesota

CERTAIN RELATIONS BETWEEN THE PARTS OF BIRDS' EGGS

BY V. S. ASMUNDSON, G. A. BAKER AND J. T. EMLEN

INTRODUCTION

THICKNESS of shell has been shown by Asmundson and Baker (1940) to have a marked effect on the percentage of shell of avian eggs. They have further shown that changes in shape within ordinary limits have little effect on the percentages of shell, whereas given a constant thickness of shell, the percentage of shell increases markedly with a decrease in volume (size). Actually, however, the eggs of many species which lay small eggs have relatively less shell than the larger eggs of other species (Grossfeld, 1938). The reason for the relatively low percentage of shell on small eggs is not evident from published data since little information is available on the weight of the various parts of the eggs laid by different species of birds and even less on the thickness of shell. Eggs of different species were, therefore, obtained to secure more nearly complete data. While the number of species represented is small and the number of eggs from each species is comparatively small, the data are presented here with the hope that others will take the trouble to collect similar information when a favorable opportunity presents itself.

MATERIAL AND METHODS

Eggs were obtained from nests wherever possible while the nests were being added to. The eggs were removed as soon as possible to a room maintained at 55° F. Nevertheless they varied in age from a few hours to several days when they were measured, weighed and partitioned. Only the Cliff Swallow's eggs had, however, been incubated.

All eggs were measured to the nearest hundredth of a millimeter and weighed to the nearest hundredth of a gram. Density was determined as previously described (Asmundson and Baker, 1940).

An unknown variable was the age of the birds that laid the eggs. Data for the Domestic Fowl (Curtis, 1914; Jull, 1924, and others) show that the amount of yolk as a percentage of total egg weight increases during the first three or four months after egg production starts at about six months of age. Thus, Jull's data show a maximum average difference of about 3 per cent. The eggs from various individuals have yolks that differ on the average by as much as 10 per cent (Curtis, 1914). Age is presumably a minor factor when eggs from wild species are compared since eggs are not usually laid until the birds are about a year old, but individual differences may well be important. Other factors admittedly may also have a considerable influence on the values obtained from small numbers of eggs.

EGG DATA

The data obtained are summarized in Tables 1 and 2. Data for the first four species have been published in part elsewhere (Asmundson and Baker, 1940).

Relation of yolk and albumen.—The yolk is generally regarded as the mechanical stimulus to secretion of albumen, its volume as well as the size of the oviduct determining the amount of albumen secreted. It seemed desirable therefore to attempt to measure the direct relation between the weight of the yolk and the white. For this purpose the data summarized by Grossfeld (1938, p. 78) and the data in Table 1 were used to determine the relation between the weight of the yolk and the weight of the white in eggs from twenty-four species.

Text-figure 1 shows that for the species of birds studied, the relation between the weight of yolk, y, and weight of white, w, is well represented by the equation,

$$w = 1.56y + 0.7 \quad (1)$$

A line was drawn through the data and the constants 1.56 and 0.7 were read off from the graph.

It is a mistake in principle to attempt to fit the curves of Text-figures 1–4 to the data by means of least-squares technique. The

TABLE 1

DATA FOR THE EGGS OF TEN SPECIES

Thickness of shell of turkey eggs and specific gravities are not in all cases based on the total number of eggs shown

	No. of Eggs	*Length* mm.	*Diameter* mm.	*Index* (D/L) %	*Egg Weight* gm.	*Yolk Weight* gm.	*Albumen Weight* gm.	*Shell Membrane* gm.	*Shell* *Weight* gm.	*Shell* *Thickness* mm.	*Specific Gravity* *Egg*	*Specific Gravity* *Shell*
Turkey[1]	196	65.65	47.47	72.3	81.76	25.99	47.21	1.32	7.25	.35	1.075	2.174
Chicken[2]	64*	57.29	41.64	72.7	55.81	17.21	32.97	0.35	5.28	—†	1.082	2.235
Silver Pheasant[3]	7	52.19	39.18	75.1	44.09	17.44	21.47	0.30	4.88	.36	1.083	2.288
Ring-necked Pheasant[4]	23	42.77	33.65	78.7	26.66	8.71	15.15	0.22	2.58	.26	1.085	2.325
Quail[5]	5	35.00	24.19	69.1	10.34	3.17	6.18	0.27	0.72	.21	1.043	1.843
Brewer's Blackbird[6]	4	24.96	18.40	73.7	4.58	0.91	3.33	0.03	0.31	.15	1.057	2.059‡
Mockingbird[7]	4	22.93	18.12	79.0	4.10	0.73	3.05	0.03	0.29	.17	1.032	1.586
Tricolored Red-wing[8]	17	24.58	16.93	68.9	3.67	0.75	2.64	0.03	0.25	.13	1.039	1.511
Cliff Swallow[9]	4	21.06	14.31	67.9	2.16	—	—	0.02	0.15	.11	—	—
Barn Swallow[10]	5	18.79	13.68	72.8	1.90	0.52	1.23	—	0.15—	.15—	1.031	1.4806

* Average for eggs from each of 64 hens or 384 eggs. † The value used in Text-figure 3 is 0.31 (see Asmundson and Baker, '40).
‡ Extremely variable.

1 Meleagris gallopavo
2 Gallus domesticus
3 Gennaeus nycthemerus
4 Phasianus colchicus torquatus
5 Lophortyx californica. .
6 Euphagus cyanocephalus
7 Mimus polyglottos
8 Agelaius tricolor
9 Petrochelidon albifrons
10 Hirundo erythrogaster

method of least squares weights extreme deviations much more heavily than it does small deviations. Since it is desired to obtain trend lines that will hold for most species, and since it is admitted that species differences from this trend exist, it would not be proper to use the method of least squares even though the points were equally stable from a random-sampling point of view. Some of the points are based on very few eggs, and some on many eggs. If each point is given equal weight, for which there is an argument because they are for different species, then too much weight is given to the points subject to large random errors. If each point is weighted by the number of eggs on which

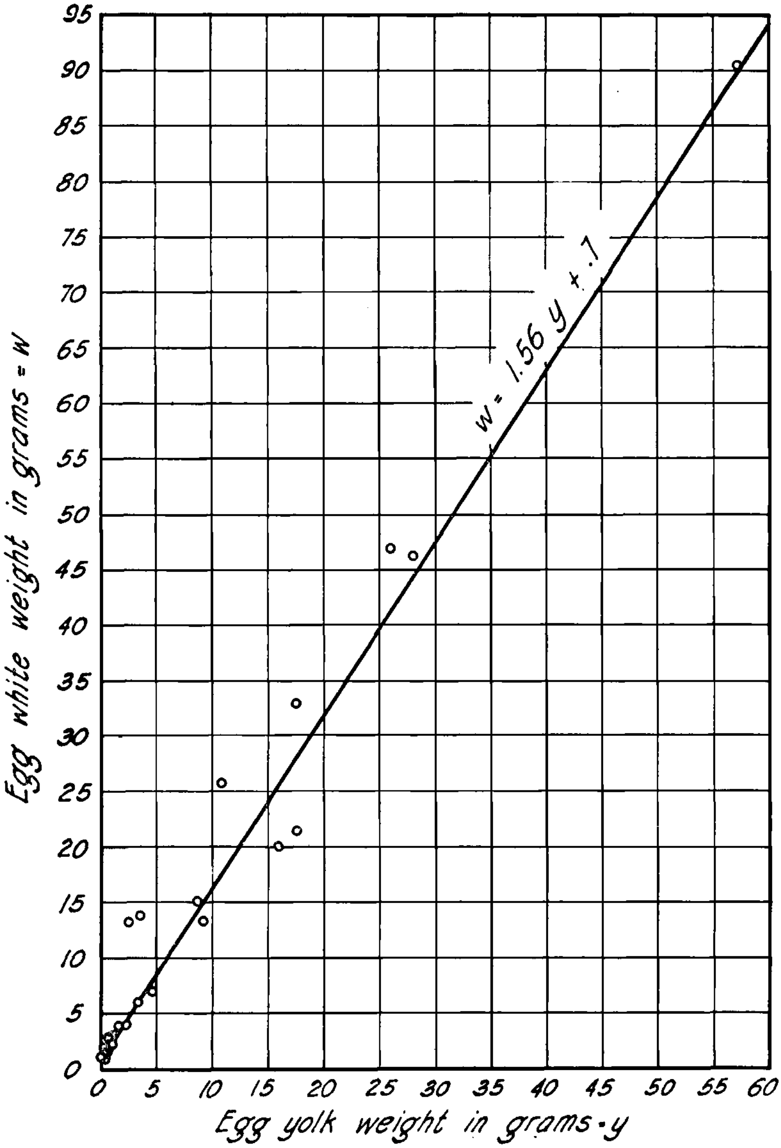
TABLE 2

RELATIVE WEIGHT OF THE PARTS OF THE EGGS OF TEN SPECIES
(SEE TABLE 1 FOR ACTUAL WEIGHTS)

Species	*Percentages*			
	Yolk	*Albumen*	*Shell membrane*	*Shell*
Turkey	31.79	57.74	1.61	8.87
Chicken	30.84	59.06	0.63	9.46
Silver Pheasant	39.56	48.70	0.68	11.07
Ring-necked Pheasant	32.67	56.83	0.83	9.68
Quail	30.66	59.77	2.61	6.96
Brewer's Blackbird	19.86	72.70	0.66	6.77
Mockingbird	17.80	74.39	0.73	7.07
Tricolored Red-wing	20.44	71.93	0.82	6.81
Cliff Swallow	—	—	0.78	6.94
Barn Swallow	27.36	64.74	—	7.89

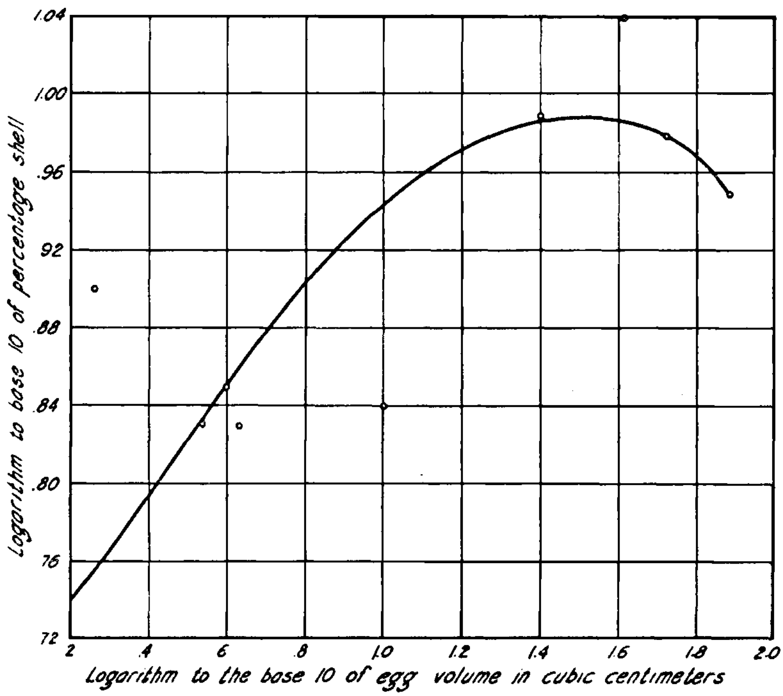
it is based, then too little weight is given to some species. Thus again, least-squares technique may give misleading results unless arbitrary weighting procedures are employed. The curves were drawn with these considerations in mind. For comparison, the least-square constants giving equal weight to each point for equation (1) are 1.55 and 2.05. The effect of using the method of least squares would be to pull the line up away from the lower cluster of points but leave the slope unchanged.

Five or six species show fairly wide discrepancies from the trend line for all species. These discrepancies may represent species differences, random errors, errors of determination or some biological differ-



TEXT-FIG. 1.—Relation of weight of white to weight of yolk for twenty-four species of birds whose average egg sizes range from 1.53 to 161.0 grams.

ences besides species differences. Among the differences which affect this relationship are differences in the age of the females laying the eggs. For instance, Silver Pheasant hens do not lay until they are about two years old; hence their eggs may not be strictly comparable to the first-year eggs of other species. On the whole there is, however, a remarkable conformity with the straight line in Text-figure 1.



TEXT-FIG. 2.—Logarithm of percentage of shell plotted against logarithm of egg volume.

Relation of the shell to egg volume.—It is evident from Table 1 that the weight of shell decreases as would be expected with a decrease in egg weight. Consider equation (7) of (Asmundson and Baker, 1940) which gives percentage shell as,

$$(2) \qquad P = \frac{3^{2/3}\,\pi^{1/3}\left(\lambda + \dfrac{\sin^{-1}\sqrt{1-\lambda^2}}{\sqrt{1-\lambda^2}}\right) D_s\, T_s\, (100)}{2^{1/3}\,\lambda^{1/3}\,V^{1/3}\,D_e}$$

where $P =$ percentage shell. $\lambda =$ breadth/length, $D_s =$ shell density, $D_e =$ egg density, $T_s =$ shell thickness in centimeters, $V =$ egg volume in cubic centimeters which was computed from the weights and specific gravities in Table 1. For the present purpose and data λ is so nearly constant, slight variations make so little difference and the differences are so erratic that the part of (1) containing λ and pure numbers will be designated by K (a constant).

Take logarithms of both sides of (2) and we obtain,

$$(3) \qquad \log P = \log K + \log D_s + \log T_s - \log D_e - \tfrac{1}{3} \log V$$

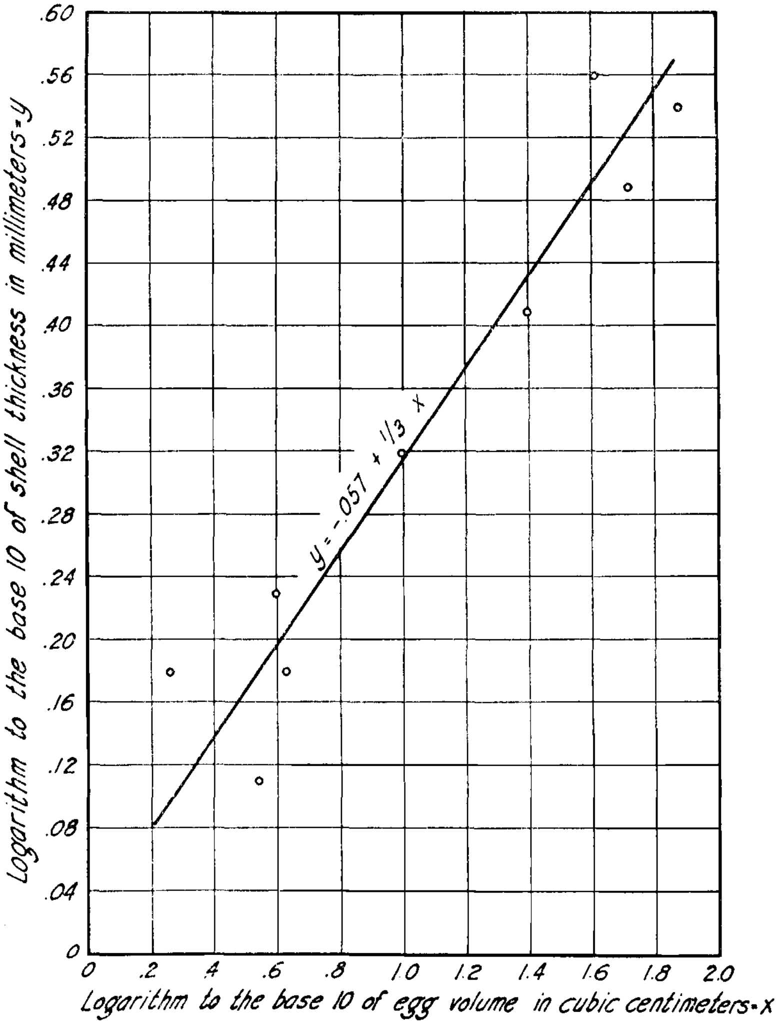
If D_s, T_s and D_e were not functions of V then log P would be a linear function of log V, i.e., the plot of (log V, log P) would be a straight line. Text-figure 2 shows that the plot of (log V, log P) is very definitely not a straight line. It thus becomes of interest to inquire as to what sort of functions of V D_s, T_s and D_e are.

If we plot log T_s against log V (Text-figure 3) we see that a straight line represents the data fairly well. This implies that,

$$(4) \qquad T_s = c \ V_b$$

where c and b are constants to be determined. The graph shows that b may well be ⅓. For comparison it is noted that the method of least squares and equal weights gives $C = +.047$, $b = 0.27$ as compared with the considered values of —.057 and ⅓ shown in Text-figure 3. Points based on very small numbers of eggs are given too much weight by this method (see above). The data are suggestive of the possibility that shell thickness depends principally on the volume of the egg and that species differences are small except as a reflection of the species differences in egg volume. Data for other species may reveal exceptions; hence further data should be obtained before final conclusions are drawn. However, as far as T_s is concerned, log P should still be a linear function of log V since T_s is such a function and it combines with $- \frac{1}{3}$ log V and log K to give a linear function. If $b = \frac{1}{3}$, then shell thickness is a constant proportion of a diameter of the egg and percentage shell depends only on D_s/D_e. If percentage shell is proportional to D_s/D_e, then the curves of Text-figures 2 and 4 could be made to coincide by shifting one scale properly with respect to the other. The agreement is as good as could be expected with the data at hand.

The variation in D_e is only about 5 per cent. Instead of considering D_e and D_s separately, we may consider D_s/D_e. Text-figure 4 shows that log D_s/D_e is a non-linear function of log V. Log D_s/D_e increases to a maximum and then decreases. The maximum density of shell appears to be for eggs about the size of Ring-necked Pheasant



TEXT-FIG. 3.—Logarithm of shell thickness plotted against logarithm of egg volume.

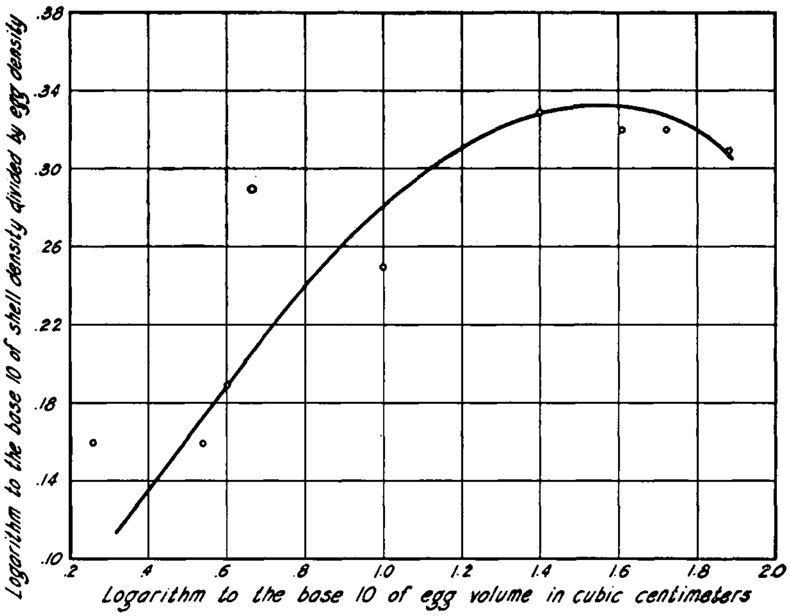
eggs. Thus it appears that D_s is largely responsible for the non-linearity of the (log V, log P) graph.

Relation of yolk, albumen, and shell membrane to egg volume.—Since the relation,

(5) $P + P_y + P_a + P_m = 100$, where P = percentage shell, P_y = percentage yolk, P_a = percentage albumen, P_m = percentage shell membrane,

must hold in every case, it follows that if one of the quantities P, P_y, P_a, P_m is a function of egg volume then some or all of the remaining quantities must be similar functions of egg volume. P has been shown (Text-figure 1 and Table 2) to be a function of egg volume. Therefore, P_y, P_a and P_m must be functions, constant or otherwise, of egg volume also.

Small eggs weighing less than 5 grams tended to have relatively small yolks weighing about 20 per cent of the total weight. The one exception in our data is the eggs of the Barn Swallow where the



TEXT-FIG. 4.—Logarithm of D_s/D_e plotted against logarithm of the egg volune.

yolk weighs 27.4 per cent of the egg weight. Eggs weighing 10 grams or over tend to have yolks weighing about 30 per cent of the total egg weight. Data summarized by Grossfeld (p. 78) have two exceptions to this rule out of fourteen species cited. These facts point to the conclusion that percentage yolk is a non-constant function of egg volume.

The data in Tables 1 and 2 show that the smaller eggs have a lower percentage of albumen than do the larger eggs, so that percentage albumen is also a non-constant function of egg volume.

The turkey egg is known to have a relatively heavier shell membrane than the egg of the Domestic Fowl (Asmundson, 1939). Table 2 indicates that the shell membrane in quail eggs is relatively even heavier than that of turkey eggs. These data do not indicate whether the trend of percentage shell membrane is a constant or non-constant function of egg volume.

Discussion

Two especially important relationships emerge from the data considered in this paper. One is the relation between the yolk and the albumen or white expressed by equation (1) above. The amount of albumen secreted around a small yolk is relatively larger than the amount secreted around a larger yolk which agrees with the data of Pearl (1910) for multi-yolked as compared with single-yolked eggs of the Domestic Fowl. This relation is best expressed by a straight line although there may be significant species differences from the straight-line relationship (Text-figure 1) which fits the data for most species.

The second general relationship is the decrease in thickness of shell with a decrease in volume which is linear when log T_s *is* plotted against log V (Text-figure 3). This relationship is undoubtedly necessary for the survival of the various species since it is improbable that a young bird weighing one gram, for instance, could pick its way out of a relatively thick shell such as is found on a 20- or even 10-gram egg. On the other hand, the larger eggs presumably require a thicker shell than the smaller eggs to protect them against breakage by the parent birds while they are being incubated.

Undoubtedly the eggs of many species differ significantly from one or more of the general relationships found to hold for most species. Such deviations as a result of evolutionary change should not prove detrimental provided they do not interfere seriously with the nutrition of the embryo or its ability to emerge from the shell at the end of the incubation period.

Summary

1. Data are presented for the eggs of ten species of birds. Of these, four were domesticated species or birds kept in confinement. Data summarized by Grossfeld (1938) were also used to calculate the relation between the weight of the yolk and the albumen.

2. For most species the relation between the weight of the yolk and the white is represented by the line

$$w = 1.56y + 0.7$$

where w is the weight of the white and y is the weight of the yolk.

There were some deviations which presumably are due to species, individual, age or other differences.

3. Evidence is presented which indicates that densities of the egg and of the shell are functions of egg volume.

4. Shell thickness decreases with a decrease in egg volume. The plot of log T_s against log V is represented fairly well by a straight line implying that

$$T_s = c\ V^b$$

where c and b are constants to be determined.

5. Percentage shell, percentage yolk, percentage albumen, and percentage shell membrane are similar functions of egg volume.

LITERATURE CITED

ASMUNDSON, V. S.
1939. The formation of the egg in the oviduct of the turkey. Journ. Exp. Zool., 82: 287–304.

ASMUNDSON, V. S., AND G. A. BAKER.
1940. Percentage shell as a function of shell thickness, egg volume and egg weight. Poultry Sci., 19: 227–232.

CURTIS, M. R.
1914. A biometrical study of egg production in the Domestic Fowl. IV. Factors influencing the size, shape and physical constitution of eggs. Arch. Entw. Mech. Organ., 39: 217–327.

GROSSFELD, J.
1938. Handbuch der Eierkunde. Pp. vii + 375; Julius Springer, Berlin.

JULL, M. A.
1924. Egg weight in relation to production. Part 1. The relationship of the weights of the parts of the egg to the total egg weight. Poultry Sci., 3: 77–88.

PEARL, R.
1910. A triple-yolked egg. Zool. Anz., 35: 417–423.

University of California
Davis, California

FUNCTIONAL ASPECTS OF THE INNER VANE OF REMIGES

BY FRANK RICHARDSON

Plate 3, upper figure

THE perfection of bird flight has long been a subject of wonder, and the structure of the wings which make such flight possible has stimulated much research. Nevertheless, the detailed perfection of wing structure is not yet adequately understood. The purpose of this