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THE COMPOSITION OF PETREL EGGS

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ABSTRACT.—Examination of fresh eggs from 23 species of procellariiform birds shows that the relative amounts of albumen and yolk in the egg depend upon egg size, large eggs having proportionately more albumen and less yolk than smaller ones. Similar allometric relationships also exist *within* two species, *Diomedea immutabilis* and *Puffinus griseus.* The proportions of these components in petrel eggs differ from those in the eggs of either precocial or altricial birds in general. The yolk in petrel eggs lighter than 25 g weighs more than that in eggs of similar size produced by typical precocial birds. Shell weight is a relatively constant percentage of egg weight, except for fulmars, which nest among rocks and on ledges: their eggs have heavier and thicker shells than other petrel eggs of similar size.

Heinroth (1922) pointed out that the eggs of altricial birds contain less yolk than those of precocial birds. The yolk reserves carried by the hatchlings in their yolk sacs are also generally larger in precocial birds than in altricial ones of similar body weights. Ar and Yom-Tov (1978) calculated that, on average, precocial hatchlings have twice as much yolk as altricial ones.

Romanoff and Romanoff (1949) compiled data on the weights of egg components with respect to the weights of intact eggs. These may be summarized:

Altricial species—yolk 12–27%; albumen 68–79%; shell 5–10%.

Precocial species—yolk 32–41%; albumen 51–56%; shell 9–14%. They pointed out that the proportions of yolk, albumen, and shell vary with the size of egg in both altricial and precocial species, larger eggs having relatively smaller yolks, larger whites, and heavier shells than small eggs. They also noted, as had Curtis (1912), that similar size-related differences in the egg's constituents exist *intra*specifically in the domestic fowl (*Gallus gallus,* var. *domesticus*).

The study of the egg's contents has been stimulated recently because of its importance to the energetics of parental care and developmental processes (see, for example, Lack 1968a, b, Ricklefs 1977, Ar and Yom-Tov 1978, Carey et al. 1980). In uncovering basic relationships between the egg, its producer, and its product, the order Procellariiformes has special characteristics that may make it particularly useful. First, the group is monophyletic; second, its members exhibit a great range of body weight from about 20 g in the Least Storm-Petrel (*Halocyptena microsoma*) to about 8,700 g in the Royal Albatross (*Diomedea epomophora*); and third, the clutch of all the species consists of only one egg. Despite these advantages, little information is available about the constituents of the eggs of albatrosses, shearwaters, and other petrels.

In this paper, I report the yolk, albumen, and shell weights for eggs of 23 members of this order, including the southern fulmarine species *Macronectes giganteus, Fulmarus glacialoides, Daption capense,* and *Pagodroma nivea* previously studied by Étchecopar and Prévost (1954).

The study was undertaken (1) to test the hypothesis that the proportions of the constituents of the eggs vary in a regular manner among procellariiform species according to the size of their eggs, (2) to seek anomalies requiring further examination, and (3) to determine if the intraspecific trends noted by the Romanoffs in the fowl also exist among petrels. (In this paper, "petrel" is used as a general term for any procellariiform bird.)

METHODS

Freshly laid eggs were hard-boiled, cooled, and after separation, the shell with its underlying membranes, the albumen, and the yolk were weighed. Some whole eggs were weighed under field conditions before and after boiling, using spring balances; others were weighed indoors on Mettler balances, as were all the individual constituents. Boiling reduced egg weight by about 1–3%, probably because of water loss from the albumen. I therefore increased albumen weight by the difference between the fresh and the boiled egg weight, as recommended by Curtis (1912).

Because all the birds were protected, only small numbers of eggs were usually available. They came from breeding places in the Pacific and Indian Oceans, from Antarctica, and from Scotland. Larger samples, e.g., from the Sooty Shearwater (*Puffinus griseus*) and the Laysan Albatross (*Diomedea immutabilis*), consisted

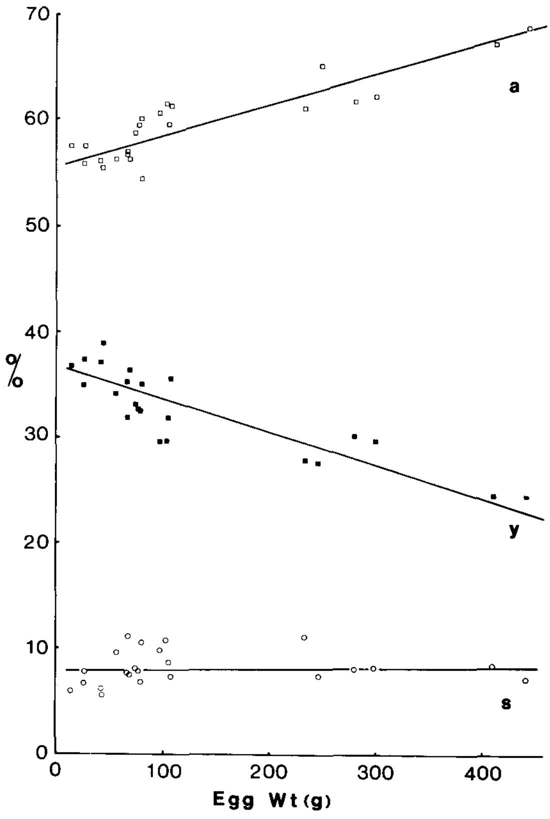

FIGURE 1. The relative proportions of the components making up the eggs of 23 procellariiform species. Circles are values for shell (s), closed squares values for yolk (y), and open squares values for albumen (a). % = (weight of part/weight of egg) × 100.

of surface and/or abandoned eggs. (Burrowing petrels often lay eggs on the surface of the ground: these are not incubated, and some eggs are abandoned even by birds of species that nest on the ground itself. Such eggs are probably laid by the younger members of the colony and tend to be smaller than those of established breeders (Serventy 1967, Warham, unpubl.). Hence, they may differ slightly in composition from the eggs of older birds.

RESULTS

The trends noted by Romanoff and Romanoff (1949) for birds in general also apply to petrels (Fig. 1). Larger eggs contained more albumen, yolk, and shell than smaller ones, but the proportion of albumen was higher, whereas the proportion of yolk was smaller. Shell weight was a relatively constant percentage of the egg's weight, irrespective of the latter's size.

Similar relationships appear to exist *within* species of petrels too, as indicated by my data for the Laysan Albatross and Sooty Shearwater (Fig. 2). In both species, albumen weight and egg weight were highly correlated ($P < 0.001$), whereas yolk or shell weight and egg weight were not ($P < 0.01$ to 0.1).

Logarithmic plots of the data for the species listed in Table 1 (Fig. 3) indicate that the egg's constituents were highly correlated with egg weight. The correlations between the $\log_{10}$ of the component weights and the $\log_{10}$ of the egg weights were very high (r values between 0.983 and 0.999), but again, they were highest for albumen weight, as they were for Sooty Shearwaters and Laysan Albatrosses (Fig. 2).

Comparing incubation periods with albumen and yolk weights disclosed similar relationships. I have satisfactory figures on the "true" incubation periods (i.e., the lengths of time elapsing between the laying and hatching of eggs that receive uninterrupted incubation) of 16 of the species in Table 1. (This definition of the incubation period is important because petrel eggs are resistant to chilling [Matthews 1954] and temporary desertion is quite common in some species, giving the impression of long "apparent" incubation periods.) For these 16 species, the correlation coefficient r between incubation period and albumen weight was 0.957 ($P < 0.001$), and that between incubation period and yolk weight was 0.942 ($P < 0.001$).

DISCUSSION

Considering the small number of eggs that I examined, the data show surprisingly few anomalies, the differences in the proportions of the parts being regular and consistent among eggs of different size. For example, fulmars (*Macronectes, Fulmarus, Daption,* and *Pagodroma*), which have the fastest development rates among petrels both as embryos and chicks (Warham 1968), do not have eggs with abnormally small yolks. Thus, their relatively short incubation periods are not a consequence of eggs with small yolks, which might favor earlier hatching. (The quality or energy content of fulmar yolks may nevertheless differ from those of other petrels.)

The ratios of yolk to albumen in the eggs of procellariiforms range from 0.36 to 0.70, the percentages of yolk from 24.3 to 39.0, those of albumen from 54.5 to 68.5 (Table 1). These values lie between the ranges listed by Romanoff and Romanoff (1949) for altricial and precocial species. Nice (1962:26), commenting on Étchecopar and Prévost's data for penguins and petrels, wrote, "We do not know whether the large amount of yolk is an adaptation to extreme cold or is a characteristic of these birds throughout their range. It may indicate that penguins and albatrosses and perhaps petrels are really more semi-precocial than semi-altricial."

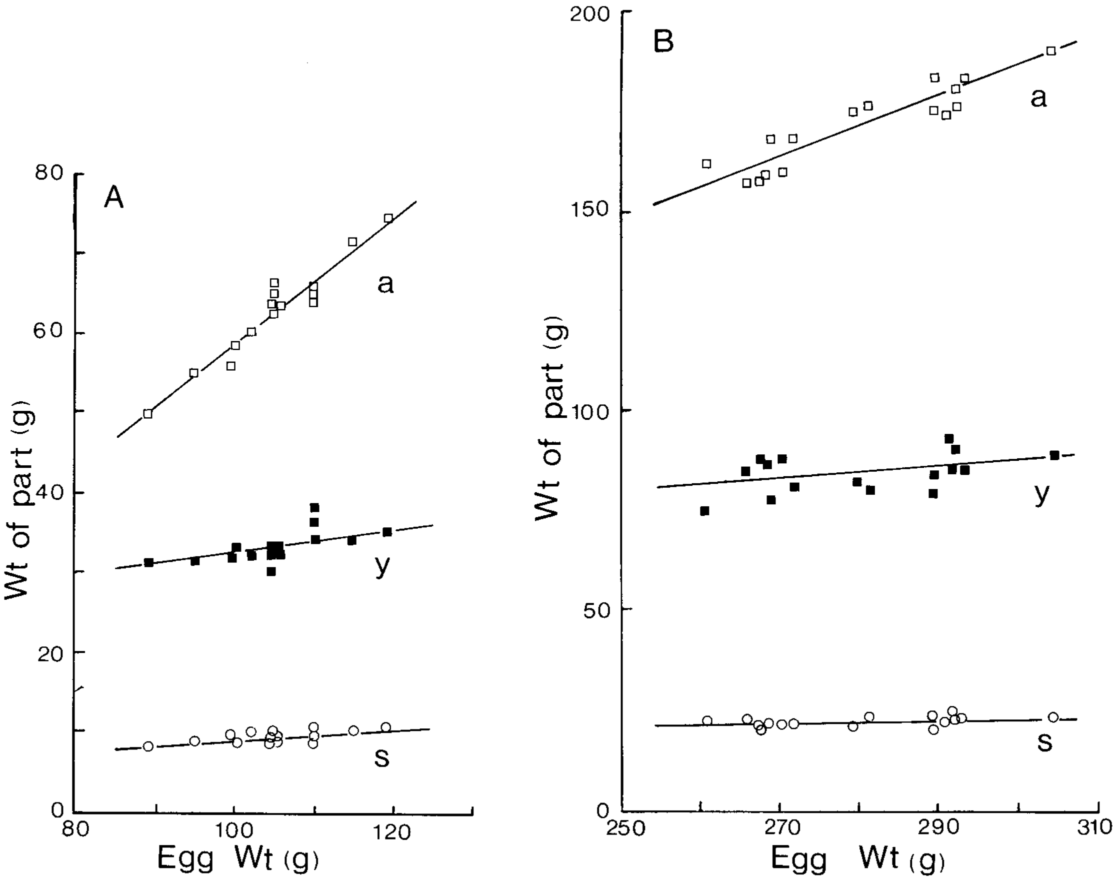

FIGURE 2. Components in the eggs of 15 Sooty Shearwaters (A) and 16 Laysan Albatrosses (B). Symbols as in Figure 1. Equations for the regression lines in A:

Albumen Weight = 0.79 Egg Weight − 20.39 ($r = 0.964$; $P < 0.001$)
Yolk Weight = 0.15 Egg Weight + 17.83 ($r = 0.553$; $P < 0.05$)
Shell Weight = 0.06 Egg Weight + 2.56 ($r = 0.628$; $P < 0.01$)

and in B:

Albumen Weight = 0.78 Egg Weight − 45.49 ($r = 0.918$; $P < 0.001$)
Yolk Weight = 0.18 Egg Weight + 35.55 ($r = 0.462$; $P < 0.1$)
Shell Weight = 0.05 Egg Weight + 9.49 ($r = 0.485$; $P < 0.1$).

My data, however, suggest that the components of petrel eggs do not vary according to climate or latitude, and that their rather high proportions of yolk are characteristic of these birds throughout their breeding range—be it tropical, temperate, or polar.

Nice (1962) recognized intermediates between the "true" altricial and "true" precocial groups. Consequently, she developed a detailed system of classifying neonatal birds based on egg composition and other criteria, such as the chick's ability to move about within its first day or two after hatching. She had little information on petrels, but thought that they belonged in one of her semi-altricial or semi-precocial categories. However, Farner and Serventy (1959) considered the burrowing Short-tailed Shearwater (*Puffinus tenuirostris*) and Fairy Prion (*Pachyptila turtur*) precocial because they attain homeothermy within a day or so after hatching. Clearly, it is hard to define these terms precisely because the states of maturity of newly hatched chicks form a continuum between the extreme precocity of a young megapode (which can fly within a few hours posthatching, is homeothermic, and receives no parental care) and the extreme altricial state of a neonatal passerine (which is wholly dependent on its parents for food and most of its warmth, and does not become homeothermic for some time).

Except, perhaps, for the Subantarctic Diving-Petrel (*Pelecanoides urinatrix*), which is born with a bare crown and a thin coat of down, and is brooded for at least a week (Richdale 1965), all procellariiforms studied thus far

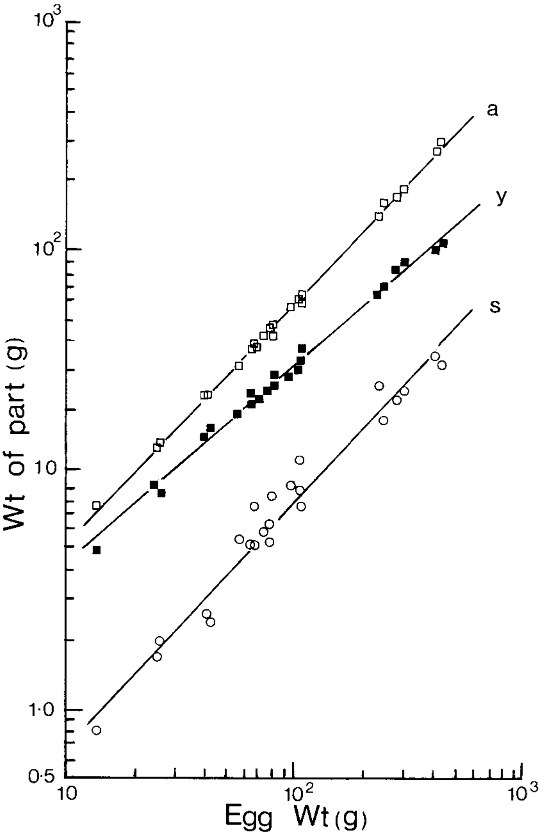

FIGURE 3. Logarithmic plots for the constituents of eggs of 23 species of procellariiform birds from Table 1. Symbols as in Figure 1. Least square regressions:

Albumen Weight = 0.493 Egg Weight$^{1.043}$ ($r = 0.999$; $P < 0.001$)
Yolk Weight = 0.747 Egg Weight$^{0.878}$ ($r = 0.996$; $P < 0.001$)
Shell Weight = 0.058 Egg Weight$^{1.075}$ ($r = 0.983$; $P < 0.001$).

appear to acquire homeothermy within a few days of hatching. This apparently holds even for chicks of surface-nesting species such as Laysan and Black-footed (*D. nigripes*) albatrosses, which are guarded for several weeks (Howell and Bartholomew 1961). Petrel chicks, whether of burrowing or surface-nesting species, are also able to shift around in their nests almost as soon as their down is dry. Chicks of burrow-nesting species are quite active and reach out to collect material from the walls and floor of the nest chamber. Chicks of surface-nesting species are probably less active and are brooded longer, but can usually clamber back into a shallow nest if displaced when two or three days old. Hence, by Nice's criteria, most petrels are semi-precocial.

Ar and Yom-Tov (1978) separated chicks into three categories—altricial, semi-precocial, and precocial—but they included no data for petrels. They defined "semi-precocial" broadly as "species which hatch advanced but [are] immobile and fed by their parents" (p. 657). They also plotted albumen and yolk weights for 53 altricial and 57 precocial species as a function of egg size, as I did in Figure 3 for Procellariiformes. The regression equations relating yolk and albumen weights to egg weights for petrels differ from those developed by Ar and Yom-Tov:

Albumen Weight (g) = 0.493 Egg Weight$^{1.043}$ for petrels
Albumen Weight (g) = 0.724 Egg Weight$^{0.987}$ for altricial birds
Albumen Weight (g) = 0.631 Egg Weight$^{0.954}$ for precocial birds
Yolk Weight (g) = 0.747 Egg Weight$^{0.878}$ for petrels
Yolk Weight (g) = 0.223 Egg Weight$^{0.981}$ for altricial birds
Yolk Weight (g) = 0.279 Egg Weight$^{1.059}$ for precocial birds.

Such differences indicate that (1) petrel eggs have larger yolks and smaller whites than eggs of altricial birds of similar size, (2) petrel eggs weighing less than about 25 g have less albumen than precocial eggs of similar size, but those weighing more than 25 g have more albumen than eggs of equivalent size produced by the precocial species used to generate Ar and Yom-Tov's curve, and (3) petrel eggs weighing less than 55 g have larger yolks than similar-sized eggs of precocial species, so that, as far as yolk content goes, such small petrels are highly precocial. In other words, on the basis of egg constituents, petrels neither fall conveniently into any of Ar and Yom-Tov's categories, nor into the more finely graded ones of Nice. They seem to form a special category of their own.

G. C. Whittow (pers. comm.) informs me that the trend for smaller petrels to be more precocial and the large ones more altricial—in terms of the yolk content of their eggs—conforms with his findings on the energetic cost of prolonged incubation, a cost that is greater in the smaller species.

My finding that larger eggs contain relatively more albumen (Table 1) and that this is related to the duration of their incubation period (from about 39 days in the smaller storm-petrels to about 79 days in the largest albatrosses) requires explanation. The albumen is not only an important store of protein, but also holds in its colloidal matrix about two-thirds of the embryo's water supply (Gray 1926, *in* Needham 1931). The water is used in development and to allow for unavoidable loss through the shell. Thus, the larger the embryo, the larger the water store required, an effect heightened in petrels by their extended incubation pe-

TABLE 1. The composition of petrel eggs. Weights are means ± 1 SD except where raw data were not available or samples contained less than three values.

Species	*n*	Fresh wt.	Shell		White		Yolk	
		g	g	%	g	%	g	%
Diomedeidae								
Diomedea exulans	1	410.0	35.0	8.5	274.5	67.0	100.5	24.5
D. epomophora sanfordi	1	440.5	31.9	7.2	301.5	68.5	107.1	24.3
D. nigripes	8	299.0 ± 14.64	24.6 ± 2.65	8.2	185.5 ± 10.72	62.1	88.9 ± 5.47	29.7
D. immutabilis	16	279.9 ± 12.50	22.6 ± 1.21	8.1	172.4 ± 10.56	61.6	84.9 ± 4.76	30.3
D. bulleri	3	247.5	18.2	7.4	160.8	64.9	68.5	27.7
Procellariidae								
Macronectes giganteus	5	233.8	26.2	11.2	142.5	61.0	65.0	27.8
Fulmarus glacialoides	9	103.4	11.2	10.9	61.6	59.6	30.5	29.5
F. glacialis	4	97.0 ± 4.33	9.6 ± 0.29	9.9	58.7 ± 3.40	60.6	28.7 ± 2.69	29.5
Daption capense	10	67.3	7.6	11.2	38.5	57.0	21.4	31.8
Pagodroma nivea	6	56.8	5.5	9.7	31.9	56.2	19.4	34.1
Pterodroma solandri	2	78.3	5.4	6.9	47.4	60.5	25.5	32.6
P. neglecta	3	68.7	5.2	7.5	38.5	56.2	25.0	36.3
P. hypoleuca	4	41.7 ± 3.09	2.6 ± 0.23	6.3	23.4 ± 1.93	56.1	15.7 ± 1.00	37.6
P. nigripennis	1	42.6	2.4	5.6	23.6	55.4	16.6	39.0
Pachyptila turtur	10	25.1	1.7	6.8	14.0	55.8	9.4	37.4
Puffinus carneipes	12	73.9 ± 7.83	6.0 ± 0.58	8.1	43.4 ± 4.76	58.7	24.5 ± 2.55	33.2
P. pacificus	3	76.9	6.1	7.9	45.7	59.5	25.1	32.6
P. bulleri	6	66.4 ± 2.55	5.2 ± 0.60	7.8	37.8 ± 2.14	57.0	23.4 ± 0.72	35.2
P. gravis	2	107.2	7.8	7.3	61.3	57.2	38.1	35.5
P. griseus	15	105.0 ± 7.27	9.2 ± 0.73	8.7	62.5 ± 5.95	59.5	33.3 ± 1.94	31.8
P. tenuirostris	1	80.0	8.5	10.6	43.5	54.5	28.0	35.0
P. lherminieri	6	25.7 ± 2.02	2.0 ± 0.32	7.8	14.8 ± 1.60	57.5	8.9 ± 0.74	34.7
Hydrobatidae								
Pelagodroma marina	2	13.4	0.8	6.0	7.7	57.4	4.9	36.6

riods. That this water is critical is suggested by Whittow's (1980) finding that total water loss from petrel eggs resembles that of other eggs despite the former's much longer incubation. However, in the two species of petrels that he examined, the eggs contained far fewer pores than birds' eggs in general. Likewise, Grant et al. (1982) found that the water loss of eggs of the Bonin Petrel (*Pterodroma hypoleuca*) was lowered substantially by the relatively small number of pores in their shells and by a low incubation temperature (33.8°C). In petrels, however, the greater amount of albumen in larger eggs may reflect more than the embryo's water needs. For example, the embryo's protein requirement may have favored selection for more albumen during the evolution of the larger petrels.

Why the intraspecific correlations between albumen content of an egg and its weight should be so much higher than those for yolk and shell is obscure. Perhaps larger yolks stretch the magnum more than small ones and stimulate that part of the oviduct to produce more albumen.

H. Rahn (pers. comm.) has found that shell thickness among petrels does not increase as much with increasing egg mass as in other birds, with the result that the relative constancy of the proportions of shell in petrel eggs (Table 1, Fig. 1) would be expected. However, fulmars (*Macronectes, Fulmarus, Daption,* and *Pagodroma*) produce eggs with unusually thick shells (Warham 1968), possibly as an adaptation for nesting among stones and on rock ledges where strong shells would be advantageous.

The highly significant allometric relationships shown in Figure 3, like many allometric relationships between variables of procellariiform birds, emphasize the homogeneity of form and physiology among petrels despite the great range of their body size. Curves like those of Figure 3 may also have predictive value, allowing estimation of component weights without destroying eggs. Also, because yolk-albumen ratios vary with egg size, even within species, it is necessary when comparing the proportions of the parts in eggs of different species either to compare eggs of similar size or to correct for variations in constituents that result from differences in egg size.

Further information about the energetic content of yolks and pore size in egg shells from a range of species of petrels should be instructive, as would data about egg constituents in the least precocial members of the order, the Pelecanoididae, which I find have smaller eggs than other petrels of similar size.

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RECENT PUBLICATIONS

John Gould The Bird Man: A Chronology and Bibliography.—Gordon C. Sauer. 1982. University Press of Kansas, Lawrence. 416 p. $65.00. Gould, an Englishman, was an important figure in 19th century natural history: an enormously productive ornithologist, artist (and employer of artists), and publisher of fifteen magnificent folio sets on birds and mammals. Although he died over a century ago, no major study of him has yet been written. This book makes a big step in that direction, being a voluminous and well-organized compendium about the man and his works. It presents an extensive genealogy of the Gould family, a full bibliographical description of Gould's major published works, a chronology of his life, and, most of all, a detailed bibliography of works by or about Gould, his family and associates, including extensive indexing of references to him in major works by others. Data are set forth in abundance without any attempt to analyze them, that being left for future scholars. They are supplemented with varied and plentiful illustrations: color plates of drawings, monochrome drawings, photographs of people and places, and facsimiles of documents, many of them from the University of Kansas Spencer Library-Ellis Collection or the author's collection. This volume will be an important resource for those who are interested in the history of ornithology.

James Graham Cooper: Pioneer Western Naturalist.—Eugene Coan. 1981. The University Press of Idaho. 255 p. Paper cover. No price given. Idaho Research Foundation, Box 3368, University Station, Moscow, ID 83843. Here is the first well-researched book on James Cooper (in whose honor our Society is named) with much on his father, William Cooper. James, a physician, contributed to our knowledge of molluscs, brachiopods, and chordates in the Pacific Northwest. The Lucy's Warbler and Elf Owl were his most important bird discoveries. While the detailed chronology of Cooper's life contributes to the zoological history of the U.S., it makes for dull reading. Appendix A lists errors in the literature concerning Cooper; Appendix B provides his zoological taxa. Notes on the text, bibliography of works by and about son and father, references, photographs, drawings, and index.—J. Tate.