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THE TIMING AND ENERGETIC CONSEQUENCES OF EGG FORMATION IN THE ADÉLIE PENGUIN

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ABSTRACT.—To study the timing of egg formation in the Adélie Penguin (*Pygoscelis adeliae*), we gave 150 females an oral dose of Sudan black dye before they laid their eggs. This lipophilic dye is incorporated into yolk synthesized on the day of dosing and deposited on the developing ovum as a blue layer. First, second, and third fresh eggs laid by dosed birds were collected. Analysis of the timing of egg formation revealed that rapid yolk deposition (RYD) on the first ovum began 10–12 days prior to cessation of feeding. Second and third yolks were initiated sequentially at 3-day intervals. The total time necessary for RYD was 14–17 days, and was followed by a 5- to 7-day lag period between yolk completion and laying. In total, 19–24 days were required to produce each egg. Within clutches, second and third eggs were smaller than the first egg, owing to reduced albumen content, while yolk mass remained relatively constant. We determined the daily energy, protein, and lipid input into a clutch and estimated that the use of a female's body reserves during a 12-day fast requires 307 g of muscle tissue. Of this, approximately 123 g of muscle (40%) are required to produce the 24 g of protein contained in egg components deposited during the fast. Both the long lag period and the 3-day interval between laying eggs may be adaptive in reducing the daily protein demand for egg production.

The cost of egg production in wild birds has been the subject of considerable attention (see King 1973, Ricklefs 1974, and Murton and Westwood 1977, for reviews), but the importance of nutrient requirements for egg formation in such species has remained elusive and poorly understood. Egg formation in domestic hens, selected for rapid egg formation and prolonged productivity, cannot represent the avian model for this function, particularly when considering the temporal and energetic constraints attendant on most wild species. Our recent research (Grau 1984; Astheimer, in press) indicates that the process of egg formation is not evolutionarily static; there appear to be many species-specific variations which involve modifications both in the timing of formative events and in the rates of material deposition, either within the follicle or in the oviduct. Such differences would naturally affect any energy assessment of the daily production cost of a clutch.

We chose to investigate the timing of egg formation in the Adélie Penguin (*Pygoscelis adeliae*) to clarify the dynamics of egg production in a seabird that lays a two-egg clutch. We had previously concentrated on Cassin's Auklet (*Ptychoramphus aleuticus*), which provided a simple model for egg formation of a single-egg clutch (Astheimer et al. 1980). An attempt to study this problem in eggs of the Fiordland Crested Penguin (*Eudyptes pachyrhynchus*) was limited to collection of single eggs of this species' two-egg clutch owing to permit restrictions (Grau 1982). A preliminary study showed Adélie Penguins to be tractable experimental subjects (Grau and Wilson 1980) and, moreover, their highly synchronized reproductive timetable was delineated by distinct breeding events that could be related to the timing of egg formation. Adélie Penguins nest colonially on exposed islands and peninsulas in antarctic waters. Spring arrival often requires that the penguins cross many kilometers of sea ice on foot. After a brief prelaying period, during which courtship and nest construction occur, the female normally lays a two-egg clutch with a 3-day interval between eggs. Following clutch completion, she departs the rookery, ending her two- to three-week fast.

Our purposes here were to (1) determine the timing of egg formation, (2) relate timing to the sequence of breeding events before laying, (3) compare differences within clutches in timing and egg composition, and finally, (4) estimate the daily and total nutrient costs of egg production for a female Adélie Penguin.

METHODS

In order to determine the timing of egg formation events, we needed to incorporate date markers within the yolk structure while yolks

were developing in the follicles. To couple unique yolk layers with particular breeding events, Gilbert's (1972) dye-feeding technique, resulting in a distinct dye ring within the yolk, was combined with potassium dichromate staining (Grau 1976), a process which enhances contrast between yolk rings. Research was conducted at Cape Crozier, Ross Island, Antarctica (72°29'S, 169°24'E) between 30 October and 20 November 1981. We chose experimental birds from a subsection of the rookery on a northeast-facing slope, 100–130 m above sea level. Our field party arrived in late October, coincident with the arrival of large numbers of penguins. Daily counts of individuals and pairs in a small sub-colony (peak = 140 pairs) at the same slope position as our experimental area, as well as periodic checks elsewhere in the rookery, provided us with general breeding chronology for the population.

To correlate breeding events with yolk deposition dates, we marked 58 arriving birds with rhodamine B, a water-soluble magenta dye. We selected birds of smaller body size and less aggressive behavior, anticipating that most of them were females. During the following 10 days, 26 individuals of this group were found, paired and occupying nest sites in our research area. These, and a larger, previously unmarked group of females, were then treated as described below.

We identified paired females by their smaller stature compared with their mate, by copulatory mud marks on their backs, and by less aggressive defense of their nest sites when approached by an observer (Sladen 1958). We selected females from pairs exhibiting a strong pair bond, as evidenced by successful copulations, frequent performance of the locomotory-hesitance display (Ainley 1974), and the presence of pebbles at the nest site. Pairs were typically observed for 1–5 min before capture for dosing. Females were caught in a large handheld net and removed at least 5 m from the local group for marking and dosing.

A single No. 0 gelatin capsule, containing 150 ± 15 mg of Sudan black B, was administered orally. This lipophilic dye binds to yolk lipids which are transported, via the blood, to the ovary. The dyed lipids are deposited on the developing yolk as a layer of blue yolk. Transit time of the dye is rapid, approximately 4–7 h in auklets (Astheimer et al. 1980), and incorporation into the yolk was presumed to be an accurate dose date marker, as in domestic fowl (Gilbert 1972). After laying their first egg, 24 birds were given 45 mg of rhodamine B in a No. 1 capsule, either at the initial ($n = 15$) or at a second dosing ($n = 9$). Rhodamine is proteophilic and the presence of rhodamine-stained albumen was assumed to indicate that albumen synthesis was occurring during the dose day. All capsules were placed well down the esophagus and were followed by water and throat massage to insure swallowing. Rhodamine dye was applied to the breasts of dosed birds using a dot code to identify individuals, and numbered stakes were secured at nest sites. Upon release, the birds were observed for 5–10 min to determine whether or not they returned to their nests and were accepted by their mates, as evidenced by mutual greeting. Some males were hesitant in welcoming their mates and a few females were driven away and not seen again. Nearly all females recognized their mate's "ecstatic vocalization" (Ainley 1974) and returned to their nest within minutes of release. A total of 150 females were dosed, including the 26 marked upon their arrival.

After dosing, we checked nests daily for the presence of marked females and fresh eggs. A three-meter bamboo pole was used to coax birds to rise off the nest so an egg could be detected. Care was taken to create the least disturbance possible. Within 6 h of collection, eggs were weighed using a dial-torsion balance with precision to 0.01 g and measured with vernier calipers to 0.01 mm. Laying dates and egg measurements were recorded for 94 pairs, including 82 first eggs, 54 second eggs, and 12 third eggs. Forty-eight two-egg and 12 three-egg clutches were collected. Eggs were kept cool (5–10°C) until they could be taken to the laboratory.

LABORATORY ANALYSIS

Eggs were degassed under vacuum overnight, then frozen at −20°C for at least 48 h. Shells and albumen were removed and yolks were fixed in 4% formalin at 65°C for 16 h. Albumen color was noted and samples were fixed in formalin. Fixed yolks were then weighed, and halved through the blastoderm. Half of each was placed in 6% potassium dichromate for 16 h at 65°C. Shells, air-dried at 65°C, were weighed and shell thickness measured at three positions along the equatorial plane using a Federal thickness comparator. Albumen mass was taken as the difference between total fresh mass and the combined mass of shell with adherent membranes and fixed yolk.

Central slices of both dichromate-stained and unstained yolk halves were photographed and the slides enlarged to produce color Xerox prints. We used the latter to count pairs of pale- and dark-staining yolk rings, to locate the position of the dye ring, and to measure the relative thickness of each yolk layer. Both natural

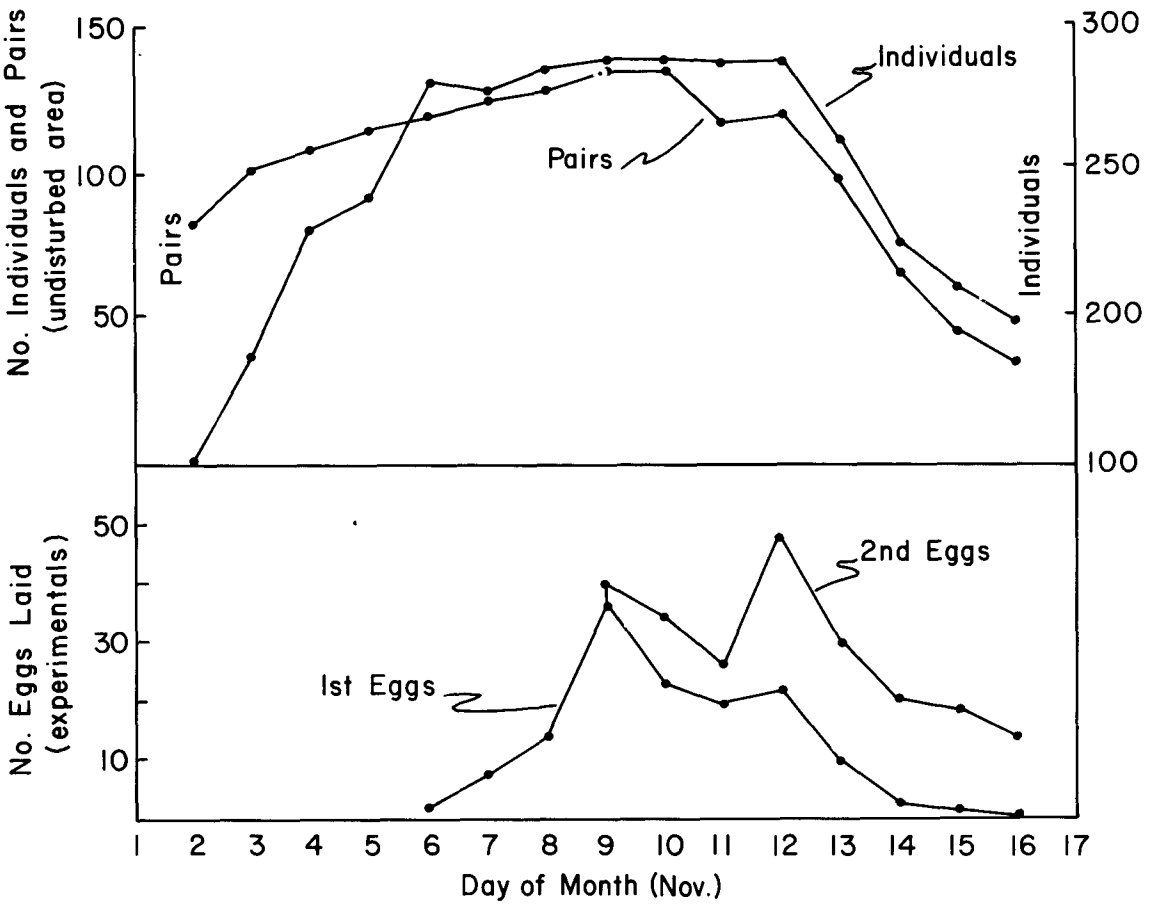


FIGURE 1. A—number of pairs and individuals present in the undisturbed subcolony; B—number of first and second eggs laid by experimental birds, showing synchrony of laying in the two groups. (Note: females usually depart after completing the clutch, thus the distribution in B has been shifted back by one day to make the data comparable.)

pigments and experimental dyes tend to dissolve in formalin and lose intensity during storage, whereas the slides provided us with a permanent record of yolk color and dye ring position.

The Xerox copies were also used to estimate the daily volume of yolk material deposited on the enlarging yolk. We measured daily increments (one pair of pale and dark yolk rings per day) along a representative radius drawn on the Xerox enlargement. Actual yolk radii were calculated using the formula for spherical volume, substituting yolk mass × yolk density for volume to provide a more reliable estimate of daily yolk volume (yolk density = 1.035; Romanoff and Romanoff 1949). Using yolk mass to estimate total yolk volume, as well as daily yolk volumes, served as an internal correction which compensated for compression of yolk and for the presence of small air bubbles captured during processing. The ratio of yolk radius to print radius was used to scale calculations of successively larger spherical volumes. Each sphere was defined by the external margin of a yolk layer. The volume of a single yolk layer was obtained by sequentially subtracting the volume of inner from outer spheres.

Assumptions made in this technique were that: (1) yolk was transferred evenly across the follicle wall, and (2) the proportional radii, as measured from the Xerox enlargement, were representative of uniform yolk thickness throughout the sphere. Follicles are known to assume a slightly elliptical conformation (Gilbert et al. 1982), but we could not detect any regular change in shape in the fixed yolks, most of which had circular rings in at least one plane. Errors due to assumptions of sphericity do not significantly affect the estimate of daily yolk deposition (Astheimer et al. 1980). For the following, means are expressed with ± the SE of the mean (Sokal and Rohlf 1982).

RESULTS

The first eggs were discovered on 6 November, with 11 single eggs found in 5,000 nests checked. Attendance of pairs in the undisturbed colony rose slowly to a peak on 10 November, which coincided with peak laying

TABLE 1. Yolk ring analysis.

	Egg 1		Egg 2		Egg 3		All eggs	
	Days	*n*	Days	*n*	Days	*n*	Days	*n*
Total yolk rings	15.2	79	15.0	43	14.5	8	15.0	140
End-of-feeding (EF) ring	10.2	79	7.9	47	5.0	7	—	—
Lag time	5.7	46	5.9	42	5.7	8	5.7	93
Total days for egg formation	20.9	46	20.9	42	20.3	8	20.8	96

among the dosed birds (Fig. 1). Since egg-laying is synchronous within this population (Ainley and LeResche 1973), similarity in laying time between the undisturbed and dosed birds indirectly shows that handling and dosing had little or no effect on the timing of egg-laying.

Analysis of the light- and dark-staining rings revealed that the mean total number of ring pairs (and therefore the number of days required to form a yolk) was 15.0 ± 0.1 days (n = 140). The number of days required for yolk deposition did not differ significantly according to position within the clutch (Table 1). Of those females that had their first and/or second egg removed, 56.3% laid a third egg and none laid a fourth, suggesting that no more than three follicles develop during a single breeding season. This is similar to Taylor's (1962) data where 65% of female Adélie Penguins were induced to lay a third egg after removal of the first. After the clutch of two eggs is laid without loss, the third yolk probably becomes atretic and is resorbed (Gilbert 1979). The yolk structure of the third egg was frequently difficult to interpret because rings were often convoluted and indistinct, perhaps indicating that some degree of atresia had begun after the second egg was ovulated or laid.

Eggs within a clutch were laid at intervals of 3.0 ± 0.1 days (n = 46) between the first and second eggs, and 3.3 ± 0.1 days (n = 19) between the second and third eggs. Removal of eggs did not affect the laying interval. Of the eggs laid by females of known arrival dates, the time between arrival and laying the first egg was 9.9 ± 0.1 days (n = 25).

Ninety-four eggs, or 63.5% of those collected, contained a layer of yolk dyed with Sudan black. We considered the innermost margin of the dyed yolk to represent yolk deposited before dosing (Fig. 2). Counting ring pairs exterior to this, the date of yolk completion was determined. Within two- and three-egg clutches, the number of ring pairs (or days) between the dye layer in the first, and that in second, eggs was 3.3 ± 0.3 days (n = 18) and, between second and third eggs, this was 3.5 ± 0.2 days (n = 8).

Natural pigments, such as the dietary carotenoids originating from euphausiids, are also retained in yolk structure (Roudybush et al. 1979) and the position of such rings can be compared within a clutch. In Adélie Penguin yolks, an abrupt transition exists between red-orange pigmented yolk toward the center, and less distinctly layered, more homogeneous yolk toward the periphery. This transition probably represents the cessation of feeding and the beginning of migration across the Ross Sea ice. Comparisons of the fatty acid composition of pigmented and unpigmented yolk corroborate this, with pigmented yolk containing twice the percentage of three long-chain fatty acids commonly found in penguin prey items (8.5% of total fatty acids in pigmented vs. 3.6% in unpigmented yolk; Astheimer and Grau, unpubl. data). By counting inward from the outermost

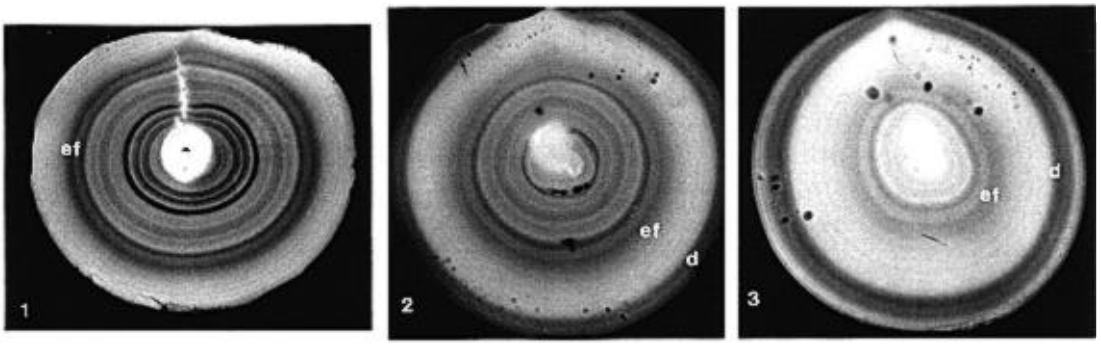


FIGURE 2. Central sections of yolk from first, second, and third eggs laid by the same female showing the relative positions of the end-of-feeding (ef) and dye (d) rings. The first egg of the clutch (1) does not contain a dye ring. Enlargements are not evenly scaled.

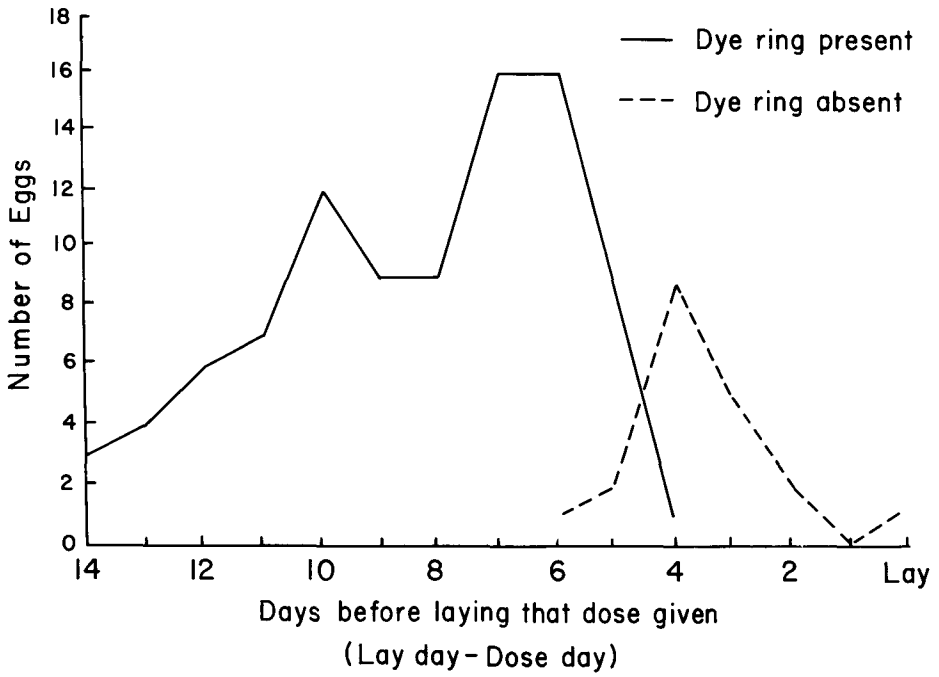


FIGURE 3. The existence of a 5–6 day lag period is demonstrated indirectly by the absence of dye in eggs laid 1–5 days after dosing (broken line), while all eggs laid 5–14 days after dosing contained a dye ring (solid line).

yolk ring to the margin of the orange-pigmented layer (the end-of-feeding or EF ring), we could establish the time between cessation of feeding and yolk completion. Similarly, depending upon whether or not a dye-ring was present and the bird's arrival date was known, we could determine the intervals between EF and arrival, EF and dosing, and EF and egg-laying (Table 1). From the position of the EF layer alone, it was apparent that when penguins ceased feeding, they had an average of 10.2 ± 0.25 days (n = 79) of yolk growth on the largest ovum (C-1) in the clutch, 7.6 ± 0.37 days (n = 36) on the C-2 ovum, and 4.7 ± 0.49 days (n = 6) on the C-3 ovum. The differences, 2.6 C-1 to C-2 and 2.9 C-2 to C-3, approximate a 3-day pause between initiation of yolk deposition in each follicle, which coincides with the interval between laying each egg. When differences between the EF layer were examined within a clutch, the 3-day interval was unequivocal: 3.0 ± 0.1 days (n = 37) between first and second eggs and 3.4 ± 0.2 days (n = 8) between second and third. The approximately 3-day differences between both the dye ring and the EF-ring in consecutive eggs within a clutch indicated that the laying interval results directly from a 3-day hiatus in the initiation of rapid yolk deposition between each of the follicles.

The interval between yolk completion and laying was 5.7 ± 0.01 days (n = 93). We have termed this segment of time the "lag period" (Astheimer et al. 1980, Grau and Astheimer 1982). It includes the time required for passage through the oviduct as well as any delay in ovulation. The duration of the lag period appeared to be constant in Adélie Penguins, with no significant differences related to clutch position (Table 1).

The length of the lag period can also be inferred, independent of dye ring position, by comparing the number of days elapsed between dosing and laying in eggs which contain a dye ring (Fig. 3). Eggs laid 1–5 days after dosing generally did not contain dye in the yolk, indicating that rapid yolk deposition had ceased and, therefore, the dye was not transferred through the follicle wall onto the ovum. Only eggs from birds laying a subsequent egg, which did contain dye, were included in the dye-absent category, thus assuring successful uptake of the dye. This restriction limited the sample in the dye-absent group to 21 eggs. Eggs laid 6–14 days after dosing invariably contained a dyed yolk layer. As we could not anticipate how long after dosing a particular penguin would lay its first egg, we had no control over the spread of egg-laying relative to dose date. The two peaks in the number of dye-containing eggs laid did not correspond to first and second eggs. The apparent 5-day lapse in dye uptake correlated well with the 5.7-day lag period (Fig. 3).

Eggs from rhodamine-dosed birds yielded inconclusive information regarding albumen

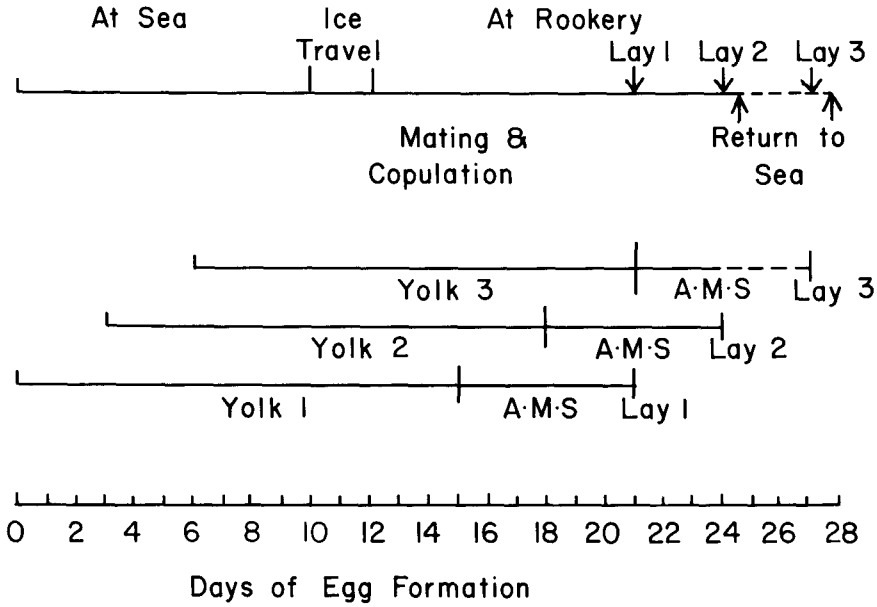


FIGURE 4. A—albumen color intensity (1 = white, 2 = light pink, 3 = pink, 4 = dark pink) in eggs laid by birds dosed with rhodamine 1–5 days before laying. B—model of the timing of egg formation during the lag period. AMS = period of albumen, membrane, and shell formation.

synthesis. Of 16 eggs laid within 5 days of dosing, 13 showed pink-stained albumen. Unlike yolk, albumen has no structural properties to prevent diffusion of water-soluble rhodamine; hence, we could not accurately determine the date of albumen deposition. Instead, we assumed that the presence of stained albumen indicated that albumen synthesis occurred within a day of dosing. When albumen color was ranked by visual assessment of color intensity (1 = white, 2 = light pink, 3 = pink, and 4 = dark pink) and plotted against the number of days elapsed between dosing and laying, a significant negative correlation was found ($r = -0.84$; Fig. 4A). The darkest pink albumen was found in eggs from birds dosed 3–5 days before laying; the lighest pink albumen in those of birds dosed 1–2 days before laying. We interpreted this to indicate albumen was synthesized in the earlier half of the lag period (3–5 days before laying) and that shell formation probably occurs only during the last day before laying (Fig. 4B). No rhodamine was found in the shell. That rhodamine had, in fact, been absorbed was evident in the blood-shot appearance of the scleras and the unusually bright pink feet of dosed birds.

Albumen was green in 5 third and 3 second eggs. Coincidentally, five of these birds were of known arrival date and had been at the

TABLE 2. Composition of Adelie Penguin eggs.

Measurement	Units	Egg 1		Egg 2		Egg 3	
		$n = 79$	SE	$n = 53$	SE	$n = 12$	SE
Total mass	g	122.9	1.09	114.8[c]	1.72	109.1	3.13
Maximum		142.1	—	138.1	—	122.3	—
Minimum		99.5	—	82.8	—	89.9	—
Shell mass[a]	g	15.7	0.19	15.1	0.29	13.8	0.54
Yolk mass[b]	g	26.0	0.27	25.8	0.38	23.6	0.68
Albumen mass	g	81.2	0.89	73.1	1.62	71.7	2.93
Length	mm	69.8	0.26	68.7	0.40	67.4	0.71
Width	mm	55.7	0.19	55.0	0.53	53.3	0.73
Shell thickness	mm	0.699	0.006	0.696[d]	0.009	0.674	0.013
Percent composition							
% Shell mass	g	12.8	0.11	13.2	0.18	12.7	0.37
% Yolk mass	g	21.2	0.23	22.6	0.35	21.9	0.90
% Albumen mass	g	65.9	0.25	63.5	0.72	65.5	0.98

[a] Includes shell membranes.
[b] Mass of yolk fixed in formalin.
[c] $n = 54$.
[d] $n = 50$.

TABLE 3. Regression analysis of egg components in 12 three-egg[a] clutches.

Independent variable	Dependent variable	r^2	F	0.01	n
Egg number	Total mass	0.50	34.13	*	33
	Albumen mass	0.40	22.83	*	33
	Yolk mass	0.09	3.34	n.s.	33
	Shell mass	0.26	11.04	*	33
	Shell thickness	0.06	2.05	n.s.	33
Total mass	Albumen mass	0.90	306.27	*	36
	Yolk mass	0.07	2.45	n.s.	36
	Shell mass	0.66	64.86	*	35
	Length	0.46	26.63	*	33
	Width	0.55	38.58	*	33
Albumen mass	Yolk mass	0.01	0.10	n.s.	36
	Shell mass	0.50	33.25	*	35
Shell mass	Shell thickness	0.64	55.76	*	33
Length	Width	0.19	7.38	n.s.	33

[a] The third egg was induced by removal of the first and/or second eggs as they were laid.

colony for 14–16 days before laying the egg in question. The green tint has been seen in the albumen of eggs laid by Cassin's Auklets dosed with rhodamine (Astheimer, unpubl.) and is probably caused by a metabolic product of rhodamine.

EGG COMPOSITION

Our values for total egg mass and external measurements are smaller than those reported by Reid (1965) and Taylor (1962) for first eggs (Table 2), but neither compares composition of eggs within clutches. The sequential within-clutch decrease in total egg and albumen masses and egg length are evident in Table 3. These three components were the only ones that differed significantly between the first and second eggs of 40 two-egg clutches. The decrease in total mass resulted primarily from a reduction in albumen mass. Within a clutch, albumen mass averaged 7.5 g (9%) more in first than in second eggs, and 5.4 g (7%) more in second than in third eggs, thus accounting for 82% and 58% of the respective differences in total mass. In contrast, yolk mass remained fairly constant.

Regression analysis of data from 36 eggs in 12 three-egg clutches (Table 3) clarified the interdependence of egg components, total mass, and clutch position. Albumen mass was significantly correlated with clutch position, total mass, shell mass, and egg length and width, while yolk mass was poorly correlated with the above components. When similar tests were applied to all first and second eggs, independent of clutch position (Table 4), it was evident that yolk mass was correlated with total egg mass, further emphasizing the effects of population variability and the importance of comparisons within clutches. Yolk mass was relatively fixed for an individual female, at least for a given clutch; whether or not yolk mass varies with age is unknown.

DISCUSSION

Our sample of 148 Adélie Penguin eggs represents the largest we have examined from a single population. The number of yolk ring pairs, the timing of their deposition, and the constant nature of the lag period, both between and within clutches, supports our contention that egg formation in most seabirds is a conservative process, apparently unaffected by environmental conditions (Grau 1984; Astheimer, in press).

For the Cape Crozier population of Adélie Penguins, yolk formation began while the females were at sea. The proximal cue for fol-

TABLE 4. Regression analysis of first and second eggs.

Independent variable	Dependent variable	Group	r^2	F	0.01	n
Albumen mass	Yolk mass	1st eggs	0.00	0.35	n.s.	78
		2nd eggs	0.01	0.48	n.s.	46
Total mass	Albumen mass	1st eggs	0.90	682.44	*	78
		2nd eggs	0.85	247.20	*	46
Total mass	Yolk mass	1st eggs	0.12	10.44	*	78
		2nd eggs	0.10	4.79	n.s.	46

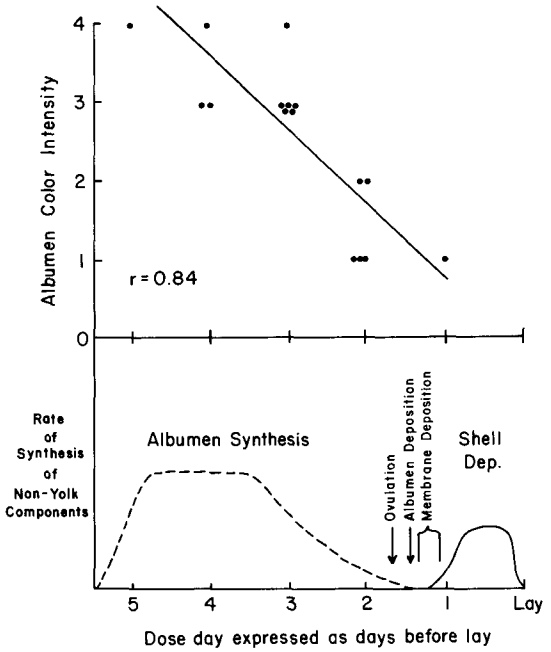


FIGURE 5. Summary of the timing of egg formation in relation to breeding events in the Adélie Penguin. AMS = period of albumen, membrane, and shell formation.

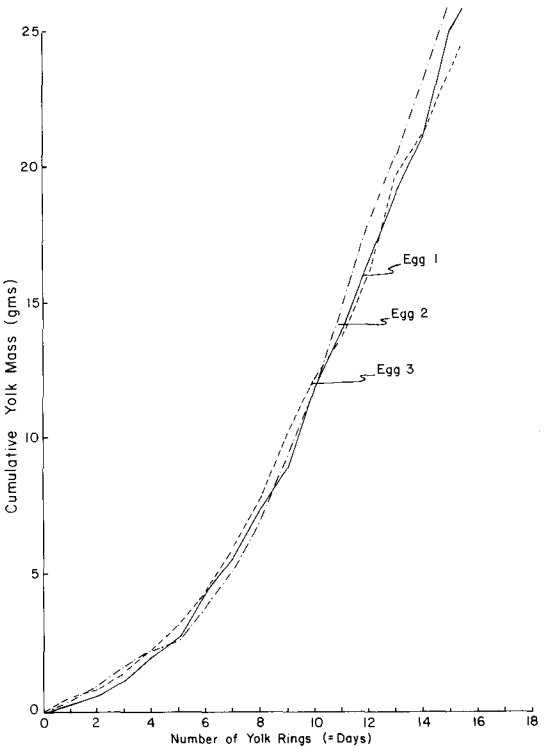


FIGURE 6. An example of cumulative yolk mass produced by a single female. Three eggs of the same clutch show similar yolk growth rates over the 15-day period of yolk deposition.

licular development is not known, but the latitudinal gradient in the dates of rookery occupation and breeding suggests an underlying photoperiodic cue (Ainley et al. 1983). Although sea ice conditions, storms, and presence of snow on the colony can have strong local effects on breeding initiation (Gwynn 1953, Ainley and LeResche 1973), the penguins' strict adherence to a "time schedule" is consistent with the high degree of laying synchrony within a given rookery. Even so, the position of the EF ring in eggs laid by our sample population was surprisingly regular. The difference between the date indicated by the EF ring and that of arrival, estimated as only 1–2 days, was presumed to approximate the time between the birds' last meal at sea and their arrival at the rookery. Because the quantity of krill consumed in this "last supper" cannot be determined, however, one cannot assume that digestion was completed within a day. The EF layer, then, is best considered as marking the start of the prelaying fast.

The presence of a dye ring in the yolk is essential for determining the length of the lag period. In domestic galliforms, the yolk is ovulated and remains in the oviduct for approximately 24 h before egg-laying. Eighty percent of this period is required for shell deposition (Gilbert 1979). If Adélie Penguins ovulated within hours of yolk completion, as do domestic fowl, the ovum would rapidly be fertilized and would remain in the oviduct for the next 5–7 days of the lag period. Because none of the collected fresh eggs showed signs of accelerated pre-ovipositional embryonic development compared to the blastoderm of a fresh chicken egg, it seems unlikely that ovulation occurs that early. Rather, the completed ovum is probably held in the follicle until about one day before laying (see Fig. 3). This hypothesis was substantiated by serial examination of Cassin's Auklet reproductive tracts at various stages of egg formation (Astheimer, unpubl.).

Our data show that the laying interval in Adélie Penguins is the direct result of the regular 3-day spacing in the onset of follicular development (Fig. 5). Differences in the positions of the EF and dye rings, and the dates of yolk completion within a clutch, support this. Williams (1981) speculated that long intervals between eggs, common in penguins, may result from a limited supply and/or ability to mobilize sufficient calcium and phosphorous for shell formation. Our data, however, suggest that the interval is set at the follicular level, and, thus, is not subject to variability by the proximal nutritional status at laying (Astheimer, in press), although the evolutionary significance of such factors cannot be precluded.

Growth rates of the yolks within a clutch are

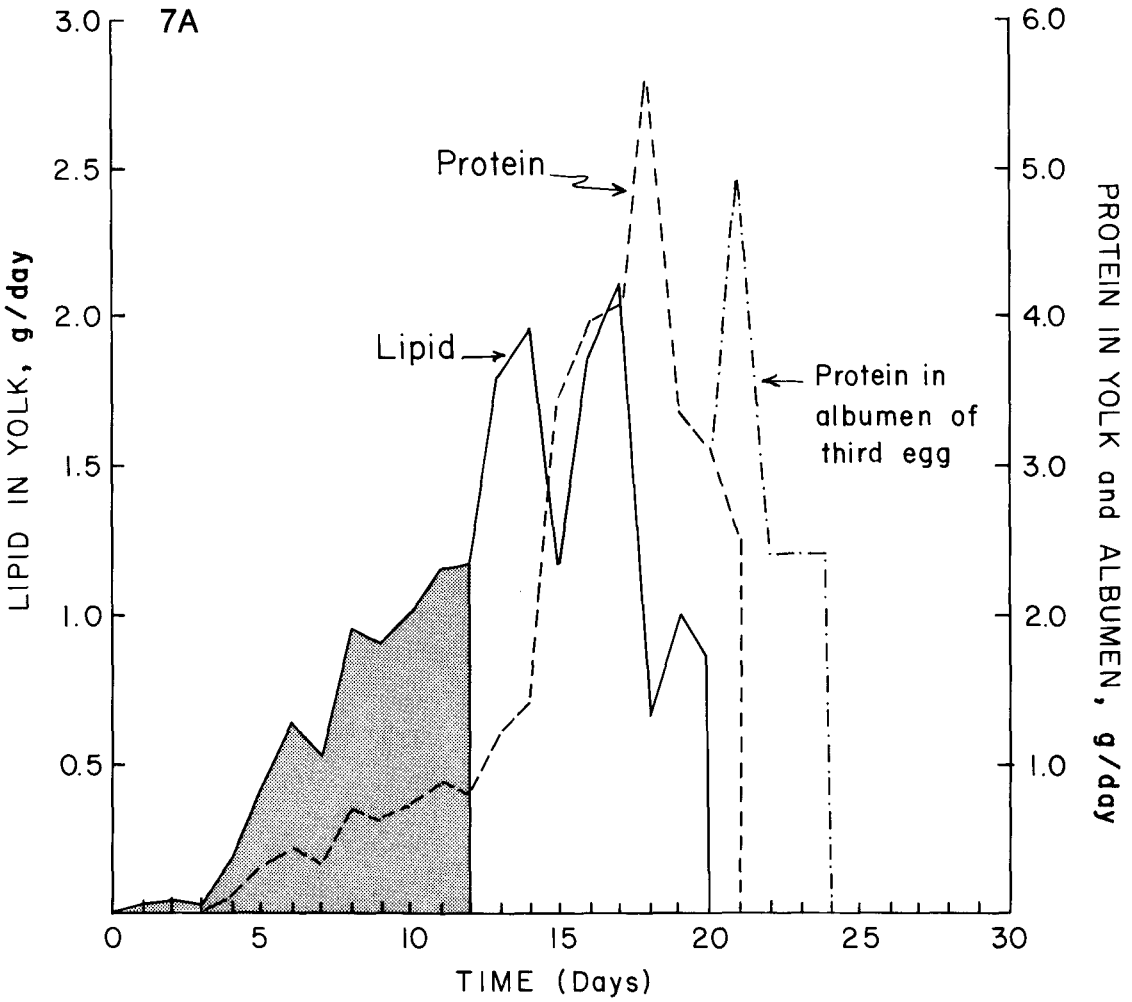
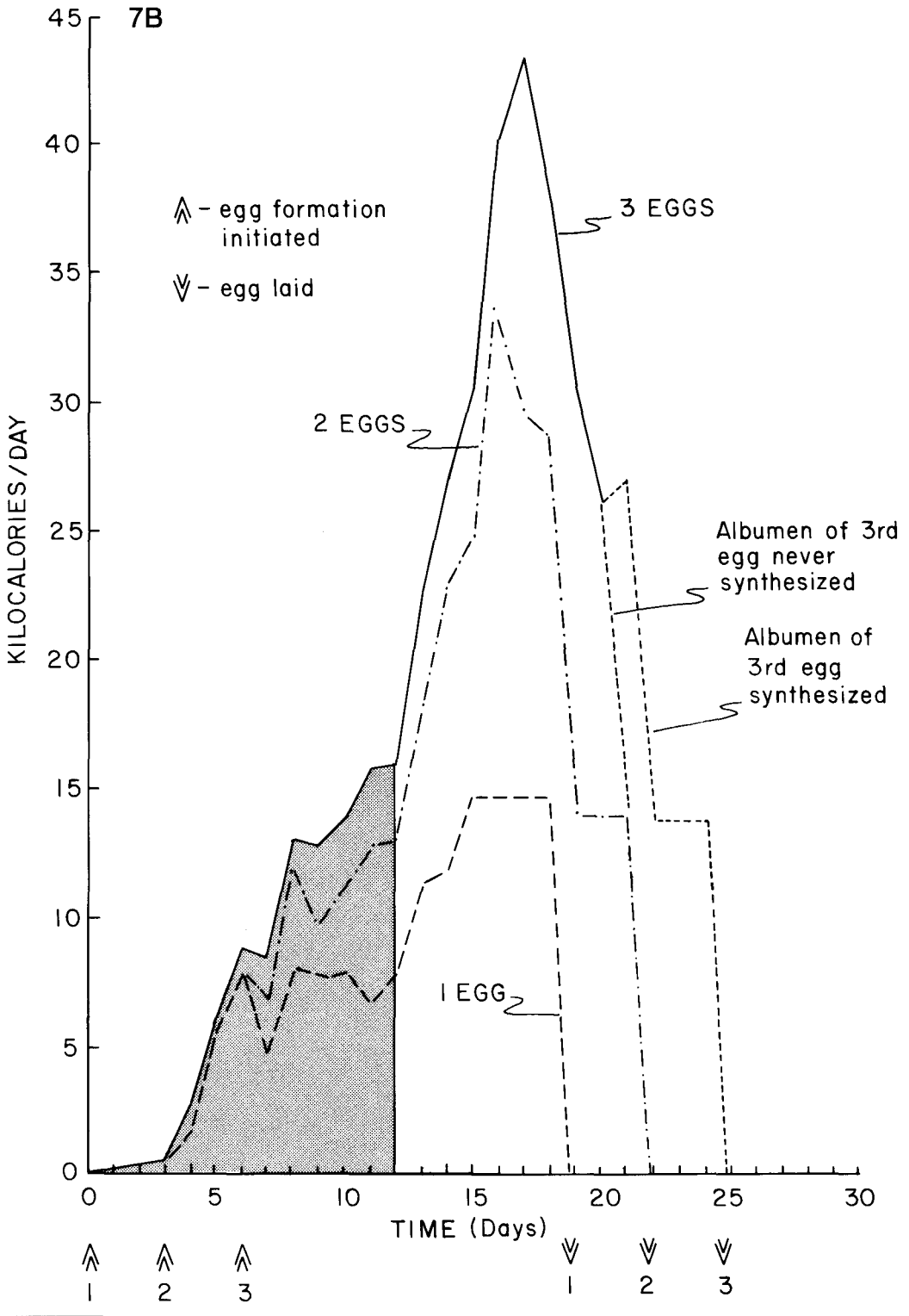


FIGURE 7. An example of the daily deposition of protein and lipid (A) and the kilocalories (B; p. 265) incorporated into the clutch plotted in Figure 5. The clutch includes deposition of three yolks, with albumen synthesis of the third included separately. Shaded portion represents yolk deposition occurring before this bird arrived at the colony. On the basis of the end-of-feeding (EF) ring, this bird probably ceased feeding on day 10.

nearly identical, though the final masses diverge slightly (Fig. 6). From the mass of yolk deposited daily, we determined the daily amount of lipid and protein and the corresponding energy values. Albumen protein was assumed to be synthesized evenly during the lag period. Non-lipid dry matter of yolk (20.5%; Grau 1982) and albumen (12%; Reid 1965) was assumed to be protein, with a gross energy equivalent 5.65 kcal per g, while that of the lipid fraction of yolk (28%; Grau 1982), equivalent to 9.5 kcal per g (Ricklefs 1977). From these calculations, the daily amount of nutrients incorporated into the clutch can be evaluated (Fig. 7A and 7B). Deposition of yolk on a third follicle was included in the daily summations, as it represents a cost to the bird during the fasting period, although it may be resorbed after the two-egg clutch is laid. The curves presented for Adélie Penguins resemble those for the Fiordland Crested Penguin (Grau 1982). It is striking that 75% of the energy content of the clutch (245 kcal of 325 kcal total in the example in Figure 7) is deposited after the females have arrived at the rookery (after day 12).

To evaluate the energy cost of egg production, we estimated the daily energy expenditure (DEE) from existing data on weight loss in female Adélie Penguins during the prelaying fast. Published estimates indicate a mean daily weight loss ranging from 64 to 72 g/day (Sladen 1958, Johnson and West 1973, Bougaeff 1975). The problem of partitioning weight loss among lipid, protein, and water components was addressed by Croxall (1982). Here, we have adopted the assignments of Groscolas and Clements (1976), who found material loss constituted 55.5% lipid, 9.2% protein and 35.3% water in fasting male and female Emperor Penguins (*Aptenodytes forsteri*) during the breeding season. When applied to a 4.5-kg Adélie



Penguin undergoing a 20-day prelaying fast (Sladen 1958), the expected 1,400-g weight loss would be comprised of 777 g lipid, 129 g protein, and 494 g water, representing a caloric expenditure of 395 kcal per day. Females of known arrival date were present at the Cape Crozier rookery for 11–15 days, and in the following estimates we have assumed that females lose 70 g of body mass daily during a 12-day fasting period, or a total of 840 g.

Existence metabolism of incubating Adélie Penguins has been estimated at about 380 kcal/day (Croxall 1982) or 1.5 × the basal metabolic rate (BMR) of 252 kcal/day measured by

TABLE 5. Comparison of component mass and estimated water composition in fresh and hatching first and third Adélie Penguin eggs.

Component	Contents water %	First egg		Third egg		Difference	
		Total mass	g water	Total mass	g water	Total mass	g water
Fresh egg	—	122	—	105	—	17	—
Albumen	87%[a]	81	70.5	68	59.2	13	11.3
Yolk	52%[c]	26	13.5	24	12.5	2	1.0
Total contents	—	107	84.0	92	71.6	15	12.4
Hatching egg							
Conductance loss	15.5%[a]	—	18.9	—	16.3	—	2.6
Chick[g]	81[bde]/79[be]	74.4	60.3	66.1	52.2	8.3	8.0
Residual yolk[fg]	47[b]/44[c]	13.7	6.4	9.6	4.2	4.7	2.2
Total contents	—	88.1	85.6	75.7	72.7	13.0	12.9

[a] Reid 1965.
[b] Tullet and Burton 1980.
[c] Grau 1982.
[d] Ricklefs et al. 1978.
[e] Simkiss 1980.
[f] Reid and Bailey 1966.
[g] Calculated with lower percent water content in the chick and residual yolk in the third egg.

LeResche and Boyd (1969). The estimated DEE (395 kcal) during the prelaying period, inclusive of egg synthesis as well as breeding activities, is only slightly higher (1.6 × BMR). The energy equivalent of the mean material deposition in a clutch is 22 kcal per day during the fasting period (from Fig. 6), which, when adjusted for 75% conversion efficiency (Brody 1945), represents a daily cost of egg production of about 30 kcal or 7–8% of the DEE. The use of a 75% conversion efficiency may result in overestimating these costs, as Adélie Penguins are deriving proteins and lipids for egg production from endogenous stores, whereas Brody's estimate was based on efficiency of egg production by chickens using dietary proteins and lipids. However, because appropriate published estimates are unavailable and because it is likely that synthesis of yolk and albumen proteins does incur some cost, we employ this value, recognizing the potential error.

Assuming muscle composition of 25.2% protein and 5.65% lipid (based on prelaying female Canada Geese, *Branta canadensis*; Raveling 1979), and adipose tissue to comprise 84% extractable lipid (Watt and Merrill 1963, Johnston 1970), we determined that a female would catabolize 307 g of muscle tissue during the 12-day fast. Allowing for 75% conversion efficiency, 123 g of muscle are necessary to provide the 24-g of protein contained in the yolk and albumen produced during the fast. The muscle requisite for egg formation during this period, then, represents 40% of the total muscle catabolized. In contrast, only 4% of the lipid used during the fast is needed in egg synthesis. When this evidence for the high protein requirement of egg formation is coupled with (1) a serial decrease in the albumen mass within a clutch of three eggs, (2) the relatively low frequency of a third egg being laid after removal of the first and/or second, (3) the annual variation in ice conditions, and (4) the necessity of crossing sea ice in order to resume feeding after laying, it appears that a female's protein reserves, or her physiological ability to mobilize them, may play a critical role in the evolution of the timing of egg formation in this species.

Adélie Penguin chicks hatching from the larger, first eggs have higher fledgling success than those from smaller, second eggs (Lishman, in press). We estimated chick and residual yolk hatching masses for average first and third eggs (initial masses: 122 and 105 g, respectively). Such differences in mass (17 g), although not common, can occur even between first and second eggs (13% of clutches in the present study). We partitioned the fresh and hatching egg into components, including conductance water losses during incubation, to compare the water balance through incubation. This disclosed that the difference in water content between a large and small egg at hatching (10.3 g) constitutes a large proportion (83%) of the total difference (12.9 g; Table 5).

Within a clutch, differences in fresh egg mass primarily reflect a difference in water mass rather than in the amount and/or quality of the nutrients available to the embryo (Table 5). About half of the water in the albumen is laid down in the magnum portion of the oviduct (Gilbert 1972); the remainder is added through the process of "plumping," which occurs just before shell formation (Draper 1966). The latter process is poorly understood, but the amount of water added is partially controlled by the amount of dense albumen laid down in the magnum. Regulation of the amount of albumen synthesized and stored in the magnum may result in differences in albumen masses within a clutch. Paludan

(1951) suggested that the laying and/or presence of a first egg in the nest may result in a hormone-mediated reduction of ovarian function. This would not affect yolk deposition in Adélie Penguins, since the two remaining yolks are nearly completed when the first egg is laid. Such a reduction in activity may cause a decrease in albumen synthesis, however, eventually resulting in the addition of less water in successive eggs. Alternatively, or simultaneously, available protein for albumen synthesis may actually be limited in these fasting birds. In either case, the net result is a series of successively smaller eggs within a clutch.

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The Condor 87:268

RECENT PUBLICATIONS

Biology of the peregrine and gyrfalcon in Greenland.—William A. Burnham and William G. Mattox. 1984. Meddelelser om Grønland, Bioscience 14. 25 p. Paper cover. $3.85 plus postage. Source: Secretary, Commission for Scientific Research in Greenland, Øster Voldgade 10, DK-1350 Copenhagen K., Denmark. Based on a ten-year study, this paper reports on the nesting requirements, density, prey, interspecific competition, pollutant levels, and migration of Peregrine Falcons and Gyrfalcons in West Greenland. The authors' hard-earned data are integrated with those in the literature. Maps, photographs, references. For a non-technical, evocative account of these birds, read Harris's book (noted in Condor 84:236).

Transactions of the Forty-seventh Federal-Provincial Wildlife Conference.—1983. Canadian Wildlife Service. 280 p. Paper cover. No price given. Catalogue No. CW69-3/47E. Source: Minister of Supply and Services [Ottawa, Canada]. This volume is a complete record of the conference, which had as its theme, "Wildlife management—today and tomorrow." It includes discussions of the roles of federal and provincial wildlife agencies, forest industry, and citizens. Also given are the reports of many agencies or organizations and the recommendations by the Conference. Although most of the specific points apply to Canada, many general ideas about land use and wildlife management apply equally to the U.S.

Wildfowl 35.—Edited by G. V. T. Matthews and M. A. Ogilvie. 1984. Wildfowl Trust, Slimbridge. 184 p. Paper cover. $15.00. Source: Administrative Officer, Wildfowl Trust, Slimbridge, Gloucestershire GL2 7BT, England. This volume matches its predecessors (noted in Condor 86:186 and previously) in size, scope, and appearance. Opening with a humorous yet wise critique of American waterfowl hunting regulations by the late John Lynch, it proceeds with 17 articles on the populations, migration, feeding habits, and breeding of waterfowl. Recent censuses of anatids in Britain and Ireland, plus activities of the Wildfowl Trust are reported. Waterfowl biologists should be sure to keep up with this annual and, therefore, to subscribe to the next volume before 15 September 1985.

A dictionary of ecology, evolution and systematics.—R. J. Lincoln, G. A. Boxshall, and P. F. Clark. 1982. Cambridge University Press, Cambridge. 298 p. Hard/paper cover. No price given. Specialized dictionaries are regularly needed by all scientific and scholarly disciplines because new terms are created and familiar words have their meaning altered faster than general dictionaries can keep up with them. This one covers the terminology (10,000+ terms) of evolutionary biology, giving special attention to principles, processes, and classifications. It provides short, working definitions that indicate current usage, rather than encyclopedic essays. Separate definitions are given for terms that have widely differing meanings. A random sample shows the entries to have been well chosen and their definitions to be clear, sensible, and non-tautological. Twenty-one appendices give the geological time scale, biogeographic regions, taxonomic hierarchy, and much other basic information that is often hard to find. Altogether, an immensely useful reference work.

John Abbot in Georgia: the vision of a naturalist artist (1751-ca. 1840).—Vivian Rogers-Price. 1983. Madison-Morgan Cultural Center, Madison, Georgia. 149 p. Paper cover. $15.00 plus $2.00 postage and handling. Source: Madison-Morgan Cultural Center, 434 South Main Street, Madison, GA 30605. Born in London, Abbot came to this country at the age of 22, and, after three years in Virginia, remained in Georgia for the rest of his life. He observed, collected, and drew the spiders and lepidoptera, the plants upon which they fed, and the birds of his adopted region. Thus, he worked half a century after Bartram, contemporaneously with Wilson, and a generation before Audubon. Although as productive as they, he has been neglected because few of his watercolors were published. Fitting recognition finally came in a 1983 exhibition devoted to his life and work, plus this companion book. Rogers-Price, an art historian, gives first a biography that well puts Abbot into context, and then a complete, illustrated catalogue of the exhibition. Fully annotated, the illustrations are reduced, monochrome reproductions of Abbot's watercolors and etchings or lithographs based on them. This scholarly work shines new light onto the early history of ornithology and entomology in America. Index.