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### Long Laying Intervals: A Possible Mechanism and its Implications

LEE B. ASTHEIMER<sup>1</sup>

Department of Avian Sciences, University of California, Davis, California 95616 USA

The time interval between oviposition of consecutive eggs within a clutch is longer than 24 h in many species. This phenomenon has a broad phylogenetic occurrence and does not appear to be restricted to ecologically or developmentally defined assemblages (see Appendix). Laying intervals longer than one day seem the rule among the Sphenisciformes, Pelecaniformes, Psittaciformes, Falconiformes, Strigiformes, and many tropical suboscine passerine families, but are conspicuously rare in the Galliformes, Anseriformes, and the oscine Passeriformes. The laying interval is of fixed length in most species, although exceptions include the Harpy Eagle (*Harpia harpyja*, 4-9 days), the Australian Malleefowl (*Leipoa ocellata*, 2-17 days), and members of the Cuculiformes that have irregular laying frequencies (see Appendix). Lack (1968) implied that these patterns may reflect underlying differences in the abilities of these animals to obtain energy for egg synthesis. However, the relatively fixed nature of laying intervals for many species suggests that such phenomena may reflect evolutionary selection and thus increases the difficulty in demonstrating proximate causes. I describe here a general mechanism, staggered yolk initiation, by which long laying intervals may develop, and explore some of the energetic consequences implied. Before considering these relations, I will address an alternative interpretation of the factors underlying long laying intervals proposed by Williams (1981).

Williams suggests that "the time required for mo-

bilization and deposition of . . . calcium [and] possibly phosphorus for the formation of the relatively heavy shell [of penguin eggs] is the main cause of the long laying interval [3-4 days] in the penguins." This statement is supported by the fact that penguin eggshells comprise a larger percentage of total fresh egg mass (13-15%) than shells of other species [precocial birds: 10% ( $n = 55$ ), altricial birds: 7.7% ( $n = 51$ ); Ar and Yom-Tov 1978], with the implication that this represents a proportionate demand for calcium that cannot be met in a single day. The rationale for considering phosphorus as a factor restricting shell formation is that penguin eggshells contain 2-6% more phosphorus/g than shells of other seabird species (Siegfried et al. 1978). However, that avian shell mass increases disproportionately relative to total egg mass is demonstrated by the relation (Paganelli et al. 1974):

$$S_m = 0.0485 E_m^{1.132},$$

where  $S_m$  is shell mass and  $E_m$  is total egg mass. This relation is derived from data for 368 species [after Schonwetter (see Paganelli et al. 1974)] with egg masses varying by over 5 orders of magnitude. The relative shell masses range from 6% of total egg mass in hummingbird (*Chlorostilbon canivetii*) to 17% of eggs of the extinct elephant bird (*Aepyornis*). Although the estimates of penguin shell mass predicted from this equation are lower than measured values (Williams et al. 1982), the latter fall within the 95% confidence limits provided by Paganelli et al. (1974). Table 1 presents the allometric relations of shell mass as a function of total egg mass for eggs from various avian taxa. It is apparent that the slope of these regressions ( $b$ ) changes little, while their intercept value

<sup>1</sup> Present address: Department of Biological Sciences, Douglass College, Rutgers University, New Brunswick, New Jersey 08901 USA.

TABLE 1. Allometric relations between shell mass and whole egg mass.

Group	n	r	S = aE <sup>b</sup>		SEE <sup>a</sup>	Source
			a	b		
Sphenisciformes	14	0.98	0.0824	1.103	0.052	Williams et al. (1982)
Pelecaniformes	14	0.95	0.0918	1.076	0.096	Williams et al. (1982)
Anatidae	26	0.96	0.0543	1.144	0.070	Ar and Yom-Tov (1978)
Charadriiformes	30	0.96	0.0324	1.230	0.104	Williams et al. (1982)
Procellariiformes	21	0.98	0.0899	1.013	0.112	Williams et al. (1982)
Phasianidae	16	0.96	0.1448	0.933	0.101	Carey et al. (1980)
Falconiformes	6	0.98	0.1084	0.967	0.091	Carey et al. (1980)
Altricial	43	0.96	0.0687	1.023	0.217	Ar and Yom-Tov (1978)
Precocial	24	0.99	0.0567	1.120	0.073	Ar and Yom-Tov (1978)
All groups above	188	0.97	0.0650	1.098	0.142	
Schonwetter data	368	0.99	0.0482	1.132	0.081	Paganelli et al. (1974)

<sup>a</sup> Standard error of the estimate of the log of shell mass in the log-normal regression equation.

(a) shows great variation. Although allometric relations often obscure intriguing anomalies that may have biological significance, the scaling principle should not be ignored in comparative analyses.

Examination of clutch size and relative shell mass also suggests skepticism regarding shell deposition as a limiting process in egg formation. Members of the Anatidae typically produce large clutches (6–12 eggs) with eggs laid on consecutive days. Eggs of this family represent a mean of 7.2% of the adult body mass (range = 3.3–11.8%, n = 144; Lack 1968), while penguin eggs average 3.6% of adult mass (range = 2.3–5.7%, n = 8 species; Williams 1980). In comparing egg data for two penguins, a goose, and a duck (Table 2), it is evident that high daily shell deposition can be maintained over long periods, even in a fasting bird (e.g. *Branta canadensis*), and that calcium demand in penguins cannot be considered extraordinary.

While admitting that conclusions drawn from such comparisons are simplistic, the compelling point is that, in the Anatidae, there is both sufficient calcium storage and a mechanism for its rapid deposition. Prior

to and during laying, female chickens show a complex suite of hormone-regulated responses that serve to increase stored calcium (Simkiss 1967, 1975; Dacke 1979). Although the extensive medullary ossification that occurs in the long bones of Cackling Geese (*B. c. minima*) during yolk development is depleted after the clutch is laid, the calcium content of cortical bone remains constant, a fact that prompted Raveling et al. (1978) to conclude that a calcium deficiency during laying is not indicated. Penguins, which feed on marine organisms with relatively high calcium and phosphorus contents, should have ample opportunity to lay down sufficient medullary or cortical bone for egg formation. However, the dynamics of mineral turnover in these tissues have not been examined in a fasting bird. It is noteworthy that female Cassin's Auklets (*Ptychoramphus aleuticus*) have serum calcium levels 60% higher than their mates several weeks before laying (Astheimer and Fry unpubl. data).

Many other species exhibit a long laying interval but do not have unusually heavy shells. In each instance there are undoubtedly a unique array of nu-

TABLE 2. Comparison of egg-laying statistics.

	<i>Anas platyrhynchos</i>	<i>Branta c. canadensis</i>	<i>Pygoscelis adeliae</i>	<i>Spheniscus demersus</i>
Adult body mass (ABM) (g)	1,000 <sup>a</sup>	5,000 <sup>a</sup>	3,400 <sup>b</sup>	2,300 <sup>b</sup>
Egg mass (g)	55 <sup>c</sup>	163 <sup>c</sup>	122 <sup>d</sup>	105 <sup>d</sup>
% ABM	5.4	3.3	3.6	4.6
Shell mass (g)	7.3	18.0	15.7	14.8
% ABM	13.3	11.0	12.8	14.4
Clutch size	11	6	2	2
Total shell mass in clutch (g)	80.3	108.0	31.4	28.8

<sup>a</sup> Data from Lack (1968).

<sup>b</sup> Data from Williams (1980).

<sup>c</sup> Data from Carey et al. (1980).

<sup>d</sup> Data from Astheimer and Grau (1983).

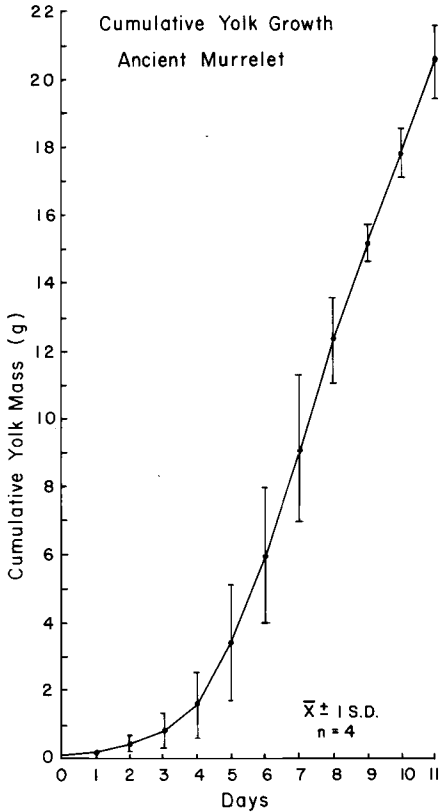


Fig. 1. Cumulative growth of Ancient Murrelet yolks.

trititional, environmental, and hormonal factors that may regulate the timing of egg formation. However, a common mechanism may be responsible for long laying intervals. Our studies of egg formation in nondomestic birds suggest that initiation of yolk deposition is delayed for a period equivalent to the laying interval. For example, rapid yolk deposition in Adélie Penguins (*Pygoscelis adeliae*) usually occurs on three follicles during a breeding season, with each yolk requiring 14–16 days for completion (Astheimer et al. 1982, Astheimer and Grau 1983). By examining distinctive natural and experimentally pigmented yolk layers, we discovered that the initiation of rapid yolk deposition on each follicle within a clutch was staggered by 3-day intervals, i.e. deposition on the second follicle (C-2) began 3 days after the first (C-1;  $n = 18$ ), and C-3 began approximately 3 days after C-2. The time required for egg formation was virtually the same for all eggs laid by the same female (Astheimer and Grau MS). Therefore, the staggering of yolk initiation is translated to the 3-day laying interval reported by many researchers (e.g. Sladen 1958).

This hiatus in yolk initiation will extend the pe-

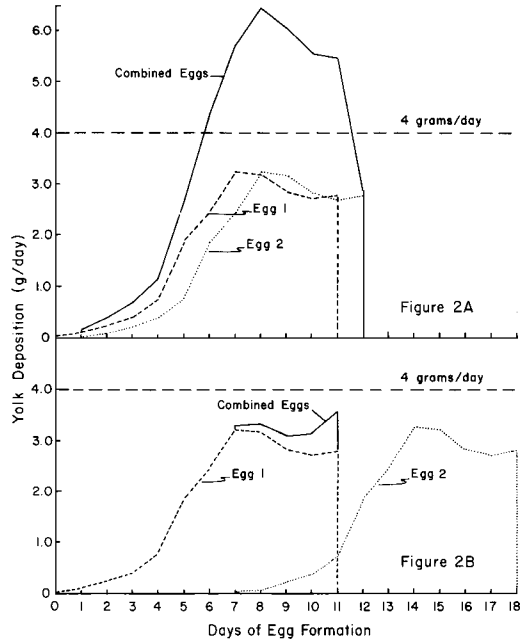


Fig. 2. Daily mass of yolk deposited on the yolks of an Ancient Murrelet clutch, where yolk initiation occurs on consecutive days (A) and where yolk initiation is staggered by a 7-day interval (B).

riod of yolk deposition on the clutch over a longer time, and consequently less yolk will be deposited daily. This mechanism, presented conceptually by King (1973), would reduce rapid depletion of lipid and protein reserves, particularly in a species forming large yolks over a short time period. For example, the Ancient Murrelet (*Synthliboramphus antioquus*), a Pacific alcid, lays a 2-egg clutch with a 7-day interval (range = 6–9 days), each egg representing 20–23% of the adult body mass (Sealy 1976). Each murrelet yolk requires 11 days to form (for methods see Grau 1976, Roudybush et al. 1979). Sealy (1976) reports dissection of a female murrelet containing a shelled egg in her uterus and a 14.3-mm yolk in a follicle. The growth curve for Ancient Murrelet yolk (determined by methods given in Astheimer and Grau MS) presented in Fig. 1 shows that the follicular yolk (estimated to be 1.85 g) represents 3–5 days of deposition. Although inferential, the large difference in egg development between the follicular yolk and the shelled egg strongly implies staggered yolk initiation.

When daily yolk deposition is plotted for conditions of 1-day vs. 7-day yolk initiation intervals in the formation of an Ancient Murrelet clutch (Fig. 2), a difference in the rate of energy incorporation is clearly evident. Although the longer interval appears to mitigate the peak demand between days 6 and 11 that would occur if eggs were laid daily, the

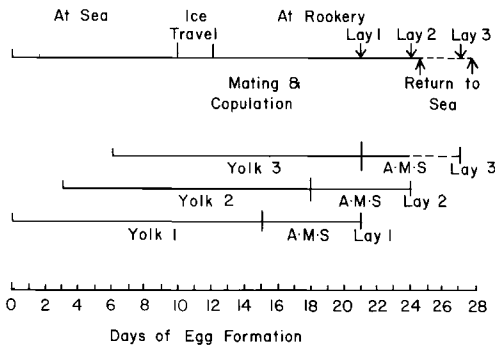


Fig. 3. Schematic diagram of the timing of egg formation for both eggs in an Adélie Penguin clutch. Day 1 represents the beginning of rapid yolk deposition on the first yolk.

cumulative energy expenditures associated with carrying extra mass for a longer time may negate some of the apparent energy savings. Nevertheless, this example does illustrate the potential for energy conservation in staggering yolk formation.

In addition to protracting the period of yolk deposition, staggered yolk initiation may also allow a longer period for albumen protein synthesis. In the chicken, albumen is necessarily produced over a 24-h period, with deposition occurring as the fertilized ovum descends the oviduct (Romanoff and Romanoff 1949). A longer interval between yolk completions would extend the period of albumen synthesis, possibly reducing the daily protein requirement for egg production in a manner similar to that described for yolk. There is some evidence that albumen is synthesized for several days prior to oviposition in Adélie Penguins (Astheimer and Grau 1983). The process is complicated in Adélie Penguins as, in addition to the 3-day hiatus in yolk development, there is also a 5-7-day lag between the completion of each yolk and oviposition of that egg (Fig. 3). Because this lag period is of almost equal length for each egg, the laying interval is still equivalent to the interval between yolk initiations. Our preliminary evidence suggests that the yolk is held in the follicle until approximately 24 h prior to laying, whereupon albumen, shell membranes, and shell are deposited over a time course similar to that observed in domestic galliforms. If albumen is produced several days prior to ovulation, the cells of the magnum, the site of albumen protein synthesis, would have to store albumen until the ovum passes through the oviduct. Though lacking histological evidence, gross anatomical studies indicate such storage occurs in the oviduct of Cassin's Auklets (Astheimer MS).

There is presently no certainty that laying intervals in all or most species are produced by staggered yolk initiations. However, persuasive argument can

be made for energy limitations promoting long laying intervals for those species where this interval is markedly variable [e.g. Snowy (*Nyctea scandiaca*) and Great Gray (*Strix nebulosa*) owls, Harpy Eagles]. The greatest lability in the laying interval appears in the Cuculiformes and may be a factor contributing to the success of brood parasitism as a reproductive pattern. Interestingly, residual lability is maintained in the nonparasitic roadrunner and the North American cuckoos, which are facultative brood parasites.

I do not wish to imply that energy limitations during egg formation exist for all species exhibiting long laying intervals. Evolutionary incentives for long intervals have probably derived from very diverse circumstances. Certainly the female's need and/or ability to restore adequate levels of essential amino acids and fatty acids, vitamins, or other nutrients to produce each successive egg could contribute to the evolution of staggered yolk production. A long laying interval would enhance any advantage accrued by asynchronous hatching where the age and size differences of nestlings within a clutch would be exaggerated. Brood reduction in eagles, for example, appears to be obligate in those species with the longest intervals between hatching (3-4 days, which corresponds to their laying interval) and facultative in species with shorter hatching intervals (1-3 days; Edwards and Collopy 1983).

Another, less obvious benefit is that longer intervals between ovulations result in longer egg-free periods in the oviduct. The 1- to 2-day egg-free period in such small insectivorous birds as swifts and many tropical tyrannids may be significant as nutrient replenishing periods. In the absence of an oviducal egg, these aerial feeders are likely to have greater agility, which could increase foraging success. An egg-free oviduct would also allow movement of sperm to the proximal fertilization location, without the necessity of sperm storage sites. In the absence of sperm storage, however, reinsemination would be necessary by the original consort or a different male. Although the ability to store sperm in the uterovaginal glands has been demonstrated in the six species studied (Hatch 1983), this adaptation may not be universal, or even desirable, in polygamous mating systems or those in which males have almost constant access to females.

Staggered yolk formation is simply a manifestation of the apparent flexibility of endocrine control of the follicular hierarchy, i.e. the sequence of yolk initiation within the ovary. In chickens (Gilbert et al. 1983) the hierarchy develops via a priming cycle of limited growth and stria in groups of small follicles. Eventually a clutch is initiated with selection of a single small follicle that enters the hierarchy each day, while others of the same size become atretic. The underlying cause for selection of one follicle over another is unknown. Presumably, in a wild bird, the priming cycle could continue without establishment of a fol-

licular hierarchy until appropriate environmental and nutritional requirements are met. It is beyond the scope of this paper to speculate on the regulation of this hierarchy, although FSH and LH probably play important roles (Opel and Nalbandov 1961, Mitchell 1967). However, it seems that all birds possess the hormonal apparatus necessary for hierarchical sequencing of yolk development, and minor adjustments conceivably could result in a wide range of patterns in egg formation and laying. It should be expected that long laying intervals could evolve independently in vastly different avian families, in some species as a response to the universal problem of allocating nutrients for egg production.

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APPENDIX. Laying intervals in selected species.\*

Species	Laying interval (days)	Clutch size	Source
<i>Struthio camelus</i>	2	—	Lack (1968)
<i>Casuaris casuaris</i>	3	3-8	Weidmann (1964)
<i>Rhea americana</i>	2	—	Weidmann (1964)
<b>Gaviiformes</b>			
<i>Gavia immer</i>	2+	2	Cramp (1977)
<i>G. arctica</i>	1-2	2	Cramp (1977)
<i>G. stellata</i>	2	2 (3)	Cramp (1977)
<b>Podicipediformes</b>			
<i>Podiceps cristatus</i>	2	4	Harrison (1978)
<i>P. griseogen</i>	2	4-5	Harrison (1978)
<b>Sphenisciformes</b>			
<i>Eudyptes</i> spp. (5)	4	2	Williams (1981)
<i>Pygoscelis</i> spp. (3)	3	2	Williams (1981)
<i>Spheniscus</i> spp. (4)	3.5	2	Williams (1981)
<b>Pelecaniformes</b>			
<i>Sula</i> spp. (3)	4-5	2	Nelson (1978)
<i>Phalacrocorax penicillatus</i>	3	3-4	Astheimer (pers. obs.)
<i>P. carbo</i>	3-4	2	Harrison (1978)
<i>Anhinga anhinga</i>	1-2	3-5	Harrison (1978)
<i>Pelecanus occidentalis</i>	2-3	2-3	Harrison (1978)
<b>Ciconiiformes</b>			
<i>Butorides striatus virescens</i>	2	4-5	Harrison (1978)
<i>Egretta caerulea</i>	2	3-5	Harrison (1978)
<i>Egretta thula</i>	2	3-4	Harrison (1978)
<i>Nycticorax nycticorax</i>	2	3-4	Harrison (1978)
<i>Ajaia ajaja</i>	2-3	2-3	Harrison (1978)
<i>Ardea cinerea</i>	2	3-5	Harrison (1975)
<i>A. purpurea</i>	3	4-5	Harrison (1975)
<i>Botaurus stellaris</i>	2-3	2-3	Harrison (1975)
<i>Geronticus eremita</i>	1-3	2-4	Cramp (1977)
<i>Platalea leucorodia</i>	2-3	3-4	Cramp (1977)

## APPENDIX. Continued.

Species	Laying interval (days)	Clutch size	Source
<i>Ciconia ciconia</i>	1-4	2-5	Brown et al. (1982)
<i>C. episcopus</i>	2-5	3-4	Brown et al. (1982)
<i>Leptoptilos crumeniferus</i>	1-3	2-3	Brown et al. (1982)
<i>Balaeniceps rex</i>	1-5	1-3	Brown et al. (1982)
<b>Anseriformes</b>			
<i>Cygnus olor</i>	2	5-7	Harrison (1978)
<i>C. buccinator</i>	2	5	Harrison (1978)
<i>C. cygnus</i>	2	3-5	Cramp (1977)
<i>C. columbianus</i>	2	3-5	Cramp (1977)
<b>Falconiformes</b>			
<i>Coragyps atratus</i>	2	2	Cramp (1980)
<i>Neophron percnopterus</i>	3-4	2	Cramp (1980)
<i>Gypaetus barbatus</i>	4-5	1-2	Cramp (1980)
<i>Aquila heliaca</i>	2+	2	Cramp (1980)
<i>A. pomarina</i>	3	2	Cramp (1980)
<i>A. chrysaetos</i>	3-4	2	Harrison (1978)
<i>A. rapax</i>	3	2	Brown et al. (1982)
<i>A. verreauxi</i>	3	2	Brown et al. (1982)
<i>Hieraaetus pennatus</i>	2-3	1-3	Brown et al. (1982)
<i>H. spilogaster</i>	2+	1-3	Brown et al. (1982)
<i>H. fasciatus</i>	3	1-3	Brown et al. (1982)
<i>Lophaaetus occipitalis</i>	2-3	1-2	Brown et al. (1982)
<i>Stephanoaetus coronatus</i>	3	1-2	Brown et al. (1982)
<i>Haliaeetus albicilla</i>	2-4	2	Harrison (1978)
<i>H. leucocephalus</i>	2+	2	Harrison (1978)
<i>Harpia harpyja</i>	6, 9, 14	1-2	Rettig (1978)
<i>Circus circus</i>	2+	4-6	Harrison (1978)
<i>C. cyaneus</i>	2	4-6	Harrison (1975)
<i>C. macrourus</i>	2	4-5	Harrison (1975)
<i>C. pygargus</i>	1.5-3	4-5	Harrison (1975)
<i>Pernis apivorus</i>	3-5	1-3	Harrison (1975)
<i>Milvus milvus</i>	3	2-3	Brown et al. (1982)
<i>M. migrans</i>	2-3	2-3	Harrison (1975)
<i>Accipiter cooperii</i>	2-3	4	Harrison (1978)
<i>A. gentilis</i>	3	2-3	Harrison (1978)
<i>A. tachiro</i>	3	2-3	Brown et al. (1982)
<i>A. badius</i>	2-3	2	Brown et al. (1982)
<i>A. nisus</i>	2-3	2-5	Brown et al. (1982)
<i>Melierax gabar</i>	3-4	2	Brown et al. (1982)
<i>Sagittarius serpentarius</i>	2-3	1-3	Brown et al. (1982)
<i>Falco eleonorae</i>	1-4	2+	Brown et al. (1982)
<i>F. peregrinus</i>	2-3	3-4	Harrison (1978)
<i>F. columbarius</i>	2	5-6	Harrison (1978)
<i>F. sparverius</i>	2-3	4-5	Harrison (1978)
<i>F. rusticolus</i>	3	3-4	Harrison (1978)
<b>Galliformes</b>			
<i>Leipoa ocellata</i>	2-17	—	Lack (1968)
<i>Lagopus lagopus</i>	1.5-2	6-11	Harrison (1978)
<i>L. mutus</i>	1-2	5-10	Harrison (1978)
<i>Bonasa umbellus</i>	1-2	9-12	Harrison (1978)
<b>Gruiformes</b>			
<i>Grus</i> spp. (4)	2	2	Walkinshaw (1973)
<i>Balearica regulorum</i>	3-4	3	Walkinshaw (1973)
<i>B. pavonina</i>	2	3	Walkinshaw (1973)
<i>Anthropoides paradisea</i>	1-3	2	Walkinshaw (1973)

## APPENDIX. Continued.

Species	Laying interval (days)	Clutch size	Source
<b>Charadriiformes</b>			
<i>Vanellus vanellus</i>	1.5-2	4	Johnsgard (1981)
<i>Pluvialis apricaria</i>	2-2.5	3-4	Johnsgard (1981)
<i>P. squatarola</i>	2	4	Johnsgard (1981)
<i>Charadrius montanus</i>	1-4	3	Johnsgard (1981)
<i>C. vociferus</i>	3.7	4	Johnsgard (1981)
<i>C. pecuarius</i>	2-4	2	Johnsgard (1981)
<i>Anarhynchus frontalis</i>	2	2	Johnsgard (1981)
<i>Stercorarius longicaudus</i>	1-3	2	Cramp (1982)
<i>Catharacta skua</i>	2.6	2 (1)	Cramp (1982)
<i>Chionis alba</i>	5	2-4	Murphy (1936)
<i>Larus argentatus</i>	2-3	2-3	Harrison (1978)
<i>L. occidentalis</i>	2-3	3 (2)	Harrison (1978)
<i>L. hyperboreus</i>	2	2-3	Harrison (1978)
<i>L. marinus</i>	2	2-3	Harrison (1978)
<i>Rissa tridactyla</i>	2	2	Harrison (1978)
<i>Sterna dougallii</i>	2-3	2	Harrison (1978)
<i>S. sandvicensis</i>	2	2	Harrison (1978)
<i>S. hirundo</i>	1-2	2-3	Harrison (1978)
<i>Synthliboramphus antiquus</i>	7	2	Sealy (1976)
<i>S. hypoleucus</i>	8	2	Murray et al. (1983)
<b>Psittaciformes</b>			
<i>Ara ararauna</i>	2	2	Forshaw (1973)
<i>A. nobilis</i>	2	4	Forshaw (1973)
<i>Aratinga solstitialis</i>	2	4	Forshaw (1973)
<i>A. canicularis</i>	2	3-5	Forshaw (1973)
<i>Pyrrhura leucotis</i>	2	5-9	Forshaw (1973)
<i>Forpus coelestis</i>	1.5-2	4-6	Forshaw (1973)
<i>Amazona guildingii</i>	3-4	2	Forshaw (1973)
<i>Agapornis cana</i>	2	3-4	Forshaw (1973)
<i>Poicephalus senegalus</i>	2	3	Forshaw (1973)
<i>Nestor notabilis</i>	3-5	3-4	Forshaw (1973)
<i>Strigops habroptilus</i>	long	1-2	Forshaw (1973)
<i>Rhynchopsitta pachyrhyncha</i>	2-3	2-3	Lanning and Shiflett (1983)
<b>Cuculiformes</b>			
<i>Coccyzus erythrophthalmus</i>	irreg.	2-3	Harrison (1978)
<i>C. americanus</i>	irreg.	3-4?	Harrison (1978)
<i>Geococcyx californianus</i>	irreg.	3-6	Harrison (1978)
<i>Crotophaga ani</i>	2	4-7	Harrison (1978)
<i>C. sulcirostris</i>	2-3	4	Harrison (1978)
<i>Cuculus canorus</i>	2	8-12	Harrison (1975)
<b>Strigiformes</b>			
<i>Tyto alba</i>	2+	4-7	Harrison (1975)
<i>Otus asio</i>	2-3	4-5	Harrison (1975)
<i>Glaucidium gnoma</i>	3-4	4-6	Harrison (1975)
<i>Strix nebulosa</i>	2-12	3-5	Harrison (1975)
<i>Nyctea scandiaca</i>	irreg.	3-13	Harrison (1975)
<i>Asio otus</i>	2	4-5	Harrison (1975)
<i>Aegolius acadicus</i>	2	5-6	Harrison (1975)
<b>Caprimulgiformes</b>			
<i>Steatornis caripensis</i>	2-4	2-9	Snow (1961)
<i>Nyctidromus albicollis</i>	2	2	Lack (1968)
<i>Caprimulgus europaeus</i>	1.5	2	Lack (1968)



## APPENDIX. Continued.

Species	Laying interval (days)	Clutch size	Source
<b>Apodiformes</b>			
<i>Apus apus</i>	2-3	3	O'Connor (1979)
<i>A. caffer</i>	1.5-2	2	Harrison (1975)
<i>A. affinis</i>	2	2-3	Harrison (1975)
<i>Calypte anna</i>	2	2	Johnsgard (1983)
<i>C. costae</i>	2	2	Johnsgard (1983)
<i>Selasphorus sasin</i>	2	2	Johnsgard (1983)
<i>S. rufus</i>	2	2	Johnsgard (1983)
<i>Helimaster constantii</i>	2	2	Johnsgard (1983)
<i>Lampornis clemenciae</i>	2	2	Johnsgard (1983)
<i>Orthorhynchus cristatus</i>	2	2	Johnsgard (1983)
<i>Glaucis hirsuta</i>	2	2	Snow and Snow (1973)
<i>Trogon rufus</i>	2	2	Lack (1968)
<i>Dacelo novaeguineae</i>	2-3	2-4	Lack (1968)
<b>Suboscine Passeriformes</b>			
<i>Pipra coronata</i>	2	2	Skutch (1969)
<i>P. mentalis</i>	2	2 (3)	Skutch (1969)
<i>Manacus vitellinus aurantiacus</i>	2	2	Skutch (1969)
<i>Schiffornis turdinus</i>	2	2	Skutch (1969)
<i>Thamnophilus bridgesi</i>	2	2	Skutch (1969)
<i>Myrmotherula axillaris</i>	2	2	Skutch (1969)
<i>M. fulviventris</i>	2	2	Skutch (1969)
<i>Dysithamnus mentalis</i>	2	2	Skutch (1969)
<i>Cercomacra tyrannina</i>	2	2	Skutch (1969)
<i>Synallaxis albescens</i>	2	2 (3)	Skutch (1969)
<i>Dendrocincla anabatina</i>	2	2	Skutch (1969)
<b>Tyrannidae (22 spp., listed below)</b>	2 (3)	2-3	
<i>Contopus cinereus</i>	2	2	Skutch (1960)
<i>Platyrinchus coronatus</i>	2	2	Skutch (1960)
<i>Myiophobus fasciatus</i>	2	2	Skutch (1960)
<i>Tyrannus melancholicus</i>	1-3	3	Skutch (1960)
<i>Megarhynchus pitangua</i>	2-3	2-3	Skutch (1960)
<i>Serpophaga cinerea</i>	2 (1)	2	Skutch (1960)
<i>Sayornis nigricans</i>	2	2+	Skutch (1960)
<i>Myiodynastes maculatus</i>	2	3	Skutch (1960)
<i>Myiozetetes granadensis</i>	2	3	Skutch (1960)
<i>Legatus leucophaeus</i>	2	2 (3)	Skutch (1960)
<i>Zimmerius vilissimus</i>	2 (3)	2	Skutch (1960)
<i>Todirostrum cinereum</i>	2	2 (3)	Skutch (1960)
<i>T. sylvia</i>	2	2	Skutch (1960)
<i>Tolmomyias sulphurescens</i>	2	2-3	Skutch (1960)
<i>Onychorhynchus coronatus mexicanus</i>	2	2-3	Skutch (1960)
<i>Myiobius sulphureipygius</i>	2	2	Skutch (1960)
<i>Oncostoma olivaceum</i>	2	2	Skutch (1960)
<i>Mionectes oleagineus</i>	2	3	Skutch (1960)
<i>Elaenia flavogaster</i>	2	2	Skutch (1960)
<i>E. chiriquensis</i>	2	2 (1)	Skutch (1960)
<i>Myiozetes inornata</i>	2	4-6	Thomas (1979)
<i>Pipromorpha macconnelli</i>	2	3	Willis et al. (1978)
<b>Oscine Passeriformes</b>			
<i>Gerygone igata</i>	2	4	Gill (1982)
<i>Corvus corax</i>	1-2	4-6	Harrison (1978)
<i>Cyanopica cyana</i>	2	5-7	Harrison (1975)

<sup>a</sup> This list does not presume to include all reports of laying intervals longer than 1 day, but rather gives an indication of how widespread the phenomenon is.