Egg-laying intervals in shorebirds

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The interval between consecutive eggs laid in a clutch by female birds is highly variable, ranging from one day to several weeks. I summarize data for 71 species of shorebird and examine relationships between minimum egg-laying intervals and constraints imposed by: 1) time, represented by breeding latitude and length of breeding season; 2) energy, as gauged by relationship between egg mass and female mass; and 3) risk of losing a clutch, measured by whether a species conceals eggs in a nest amidst vegetation or nests in the open. Among shorebirds, the interval is either one (e.g., most sandpipers) or two days (principally plovers, thick-knees and oystercatchers). There was no evidence that longer intervals correlate with greater female investment in egg (or clutch) mass. However, species breeding in more northerly latitudes (with shorter breeding seasons) are more likely to lay at daily intervals than species occupying temperate or tropical environs. A greater percentage of species that nest in vegetation that conceal eggs and incubating adults laid eggs at daily intervals compared with species nesting in open habitats. These latter two relationships are, however, confounded by taxonomy because sandpipers, which have a northerly breeding distribution and conceal nests, differ from plovers, thick-knees and oystercatchers, which principally breed in open habitats of temperate and tropical latitudes. Nevertheless, it is plausible that in addition to long breeding seasons, longer laying intervals in open-nesting species have evolved as a response to frequent clutch loss owing to predators or the environment.

INTRODUCTION

Among vertebrates, birds are the most uniform in reproductive biology: all species are oviparous. Despite this uniformity, remarkable variation exists across taxa and among individuals within species in various facets of oviparity (Carey 1996). A relatively unexplored facet of egg-laying is the interval between successive eggs in a clutch. The rate at which females lay consecutive eggs varies among species, and tends to be slower in larger taxa (Lack 1968, Winkler 2004) and those with smaller clutches (Johnson 2000, Lack 1968). Although egg-laying intervals are well known in commercially exploited taxa, they remain relatively poorly understood in wild birds, probably owing to the difficulty of recording precisely the timing of oviposition (Shubert 1990).

In the domestic chicken *Gallus domesticus*, a single functional left ovary ovulates at approximately 24-h intervals and oviposition occurs at slightly greater than this interval (Johnson 2000). However, even in the chicken, where a sequence (synonymous with clutch) may vary from 2–9 eggs, the rate of egg production (laying) ranges from 25–28.5 h, and this correlates negatively with number of eggs laid (Johnson 2000).

For wild birds, even those taxa with two functional oviducts (e.g. some Falconiformes, Apterygiformes), females never lay eggs at shorter than 24 h intervals (Winkler 2004). Many species lay eggs daily, including most passerines, waterfowl, and many shorebirds (Lack 1968). By contrast, other species lay consecutive eggs at periods exceeding 24 h, ranging upwards from 2–3 days (e.g., plovers, seabirds), and 4–8 days (e.g., megapodes, penguins) to 14–30 days (kiwis) (Carey 1996, Lack 1968). Interestingly, egg-laying intervals for these taxa are never as short as 24 h. Consequently, it appears that virtually all birds can be categorized into one of two groups based on the shortest (hereafter minimum) laying interval, species that: 1) regularly lay at intervals of one day, or 2) rarely or never lay at intervals of one day. It is true, however, that within both groups energy (or nutrient) shortages can lengthen egg laying beyond this minimum interval (Carey 1996, Lack 1968).

Variation in egg-laying intervals among and within species may be related to three principal ecological factors (Carey 1996, Lack 1968): 1) time constraints associated with length of breeding season, 2) energy costs of forming eggs, and 3) risk of clutch loss to predators. Species that breed at high latitudes (or elevations) lay eggs quicker owing to the need to complete breeding in a shorter season, compared to taxa at southerly latitudes (Morton 1976). The availability of food (energy) or nutrients (e.g. calcium) serve as proximate controls of egg laying, as evidenced by experimentally lengthened intervals in female Mallards *Anas platyrhynchos* denied food during the period of rapid follicular growth (Johnson 2000). And, in wild species that rely on exogenous energy sources to form eggs, egg-laying intervals commonly exceed the minimum during periods of inclement weather (Carey 1996, Lack 1968, Wiebe & Martin 1995). Food also may be an ultimate factor, interacting with mode of development (precocial vs altricial) to shape egg-laying intervals. Species that lay disproportionately large eggs (relative to female body size; e.g., megapodes, penguins) lay at longer intervals. Lack (1968), however, noted that among seabirds, which lay disproportionately small eggs relative to female body size, egg-laying intervals are long (2–5 days); he suggested that this was evidence for food limitation at the time of egg laying. Lastly, predation may shape egg-laying intervals via the risk of losing a clutch of eggs during the laying process (Lack 1968). This reasoning, however, addresses the energetics of replacing failed clutches rather than danger to a laying female.

Here, I examine variation in minimum egg-laying intervals in shorebirds in relation to time, energy and risk of clutch failure. Shorebirds are an intriguing group in which to study egg-laying intervals because they: 1) are diverse and well-studied; 2) breed from the high arctic to tropical latitudes; 3) mostly rely on exogenous food resources (see Lenington 1984) to lay small clutches; 4) often experience high, but variable, rates of clutch failure (Evans & Pienkowski 1984); and 5) either conceal their clutches in vegetation (e.g., sandpipers) or nest in open habitats (e.g., plovers, avocets, thick-knees), which correlates with the behaviour of adults disturbed from incubation (Gochfeld 1984).

METHODS

I reviewed species accounts (in, for example, *Birds of North America*, *Birds of the Western Palearctic*, *The Birds of Africa*) and original scientific literature summarizing details on breeding biology to compile information (Appendix) on the following variables. I summarized egg-laying intervals to the nearest hour when available. However, owing to the difficulty in accurately determining egg-laying intervals (Shubert 1990), many authors described the time between successive eggs in a clutch based on daily intervals. So, I categorized the interval between successive eggs as daily or longer. Clutch size was the modal number of eggs laid by a female. Fresh mass (g) of eggs and females came from species accounts or Dunning (1993).

To evaluate time constraints, I compared the frequency with which species laid at one day or longer intervals across four latitudinal categories (tropical, temperate, boreal and arctic) corresponding to decreasing length of the breeding season. Specifically, if time constrained laying, then a greater percentage of northerly taxa should have daily egg-laying intervals compared to those breeding at temperate or tropical latitudes. As another measure of time constraints, I characterized length of breeding season (number of weeks) over which a population initiated clutches. Since the distribution of some species spanned a wide latitudinal range and multiple studies occasionally existed from different locations in the species' range, I used the midpoint of the range of weeks spanning the interval of clutch initiation for the species. I used a chi-square test to compare the association between latitude and laying interval, and a t-test to compare length of breeding season between species laying at daily or longer intervals.

To evaluate energy constraints, I regressed egg (and clutch) mass (g) on female mass (g). If energy (or nutrients) limited egg-laying, then females that laid larger eggs (or clutches) relative to their body size should have longer egg-laying intervals. I used a t-test to compare the residuals from the regression for species laying at daily vs longer intervals.

Finally, if risk of clutch loss to predators or the environment (e.g., flooding, drifting sand) was high, then species breeding in habitats where clutch loss is common should lay at longer intervals because they could re-nest more readily (with less energy wasted in partial clutch loss) when clutches failed during the laying interval. I categorized each species as nesting in one of two categories (open vs concealed) based on a composite of habitat features and the behavioural response of adults to danger posed by potential nest predators (Gochfeld 1984). Briefly, open-nesting species (e.g., plovers, avocets and stilts, oystercatchers, and thick-knees) are those that did not use vegetation to conceal eggs in the nest or incubating adults. In the presence of potential egg predators, incubating adults typically slip off the nest quietly and rely on egg crypsis to evade predators; some species mob predators. By contrast, concealed nesters (e.g., sandpipers) are those that nest in vegetation that hides cryptically-plumaged adults and eggs. Concealed nesters typically react at closer distances to the approach of a predator by performing distraction displays (e.g. "mouse run"; Gochfeld 1984). Specifically, I predicted that species occupying open habitats (where clutches are at greater risk of loss) would have longer laying intervals than taxa nesting in vegetated habitats. I used chi-square tests to compare the frequencies of species in different categories.

RESULTS

Summary of egg-laying intervals

Nearly all shorebirds could be categorized into one of two categories. The first group, primarily sandpipers (40), avocets (4), some plovers (11), and an oystercatcher, consisted of 55 species in which females regularly laid eggs at daily intervals. A second group, comprised of thick-knees (2), plovers (12) and oystercatchers (2), included 16 species in which females rarely or never laid a clutch at intervals shorter than two days; for most of these species, the egg-laying intervals often exceeded 2 days. For both groups, however, egg-laying intervals occasionally exceeded the minimum, especially during periods of food shortage or inclement weather. For example, Nethersole-Thompson & Nethersole-Thompson (1979) recorded precisely Greenshank laying intervals (h) at 26 nests and noted that the usual 2-day (*c.*44 hour) interval often lengthened during cool, wet weather. This was true for other species that laid at longer intervals. For example, the time between consecutive eggs laid by female Snowy (Kentish) Plovers often lengthened from 2 to 3–5 days during periods of cool, wet weather of March and April in coastal northern California (Page *et al.* 1995, Colwell, unpubl. data).

When egg intervals exceeded the norm for a species, it was often (but not always) the case that long intervals occurred after the penultimate egg had been laid. For example, in 3 of 4 species of large arctic-breeding plover (*Pluvialis*), egg intervals early in a clutch approximated 2 days, but intervals between eggs 3 and 4 averaged 2.5 days (Byrkjedal & Thompson 1998). This was also true for other taxa (e.g. *Arenaria interpres*, *Calidris maritima*, *Tringa nebularia*).

Time constraints on egg laying

There was a tendency for species breeding at higher latitudes to lay at shorter intervals ($\chi^2 = 3.60$, d.f. = 1, p = 0.06), with 86% of 37 arctic or boreal species laying at daily intervals. Conversely, more (32% of 34) species breeding in temperate or tropical regions laid eggs at intervals greater than one day. Viewed another way, species that laid at one-day intervals tended (t = 1.50, d.f. = 59, p = 0.07) to have shorter breeding seasons (5.5±3.3 weeks) than species that laid at longer intervals (7.0±3.3 weeks); this pattern became stronger

Table 1. Summary for 71 shorebird species of modal clutch size and laying interval of consecutive eggs in a clutch.

Modal clutch size	**Minimum egg-laying interval**	
	1 day	**Longer than 1 day**
Four eggs	• *Recurvirostra avosetta, R. americana, Himantopus himantopus, H. mexicanus* • *Jacana spinosus* • *Vanellus vanellus, V. senegallus, V. coronatus* • *Charadrius dubius, Ch. semipalmatus, Ch. vociferus* • *Xenus cinereus, Actitis macularius, Tringa hypoleucos, T. glareola, T. melanoleuca, T. flavipes, T. totanus, Catoptrophorus semipalmatus* • *Numenius phaeopus, N. tahitiensis, N. arquata, Bartramia longicauda* • *Limosa lapponica, L. fedoa* • *Arenaria interpres, A. melanocephala* • *Calidris canutus, C. alba, C. pusilla, C. mauri, C. minuta, C. bairdii, C. melanotos, C. maritima, C. ptilocnemis, C. alpina, C. himantopus, Tryngites subruficollis, Philomachus pugnax* • *Limnodromus griseus, L. scolopaceus* • *Gallinago gallinago, G. delicata* • *Scolopax rusticola, S. minor* • *Phalaropus fulicaria, P. lobatus, P. tricolor*	• *Vanellus spinosus* • *Charadrius hiaticula, Ch. melodus* • *Pluvialis squatarola, P. apricaria, P. dominicus, P. fulva* • *Tringa nebularia* • *Numenius americanus*
Three eggs	• *Charadrius. morinellus* • *Haematopus ostralegus* • *Glareola pratincola* • *Pluvianus aegyptius*	• *Haematopus bachmani, H. palliatus* • *Charadrius alexandrinus, Ch. wilsonia, Ch. montanus*
Two eggs		• *Burhinus oedicnemus, B. capensis* • *Charadrius pecuarius* • *Anarhynchus frontalis*

(t = 2.28, d.f. = 58, p = 0.01) when I removed one outlier (*Charadrius vociferus*) from the group of species that laid at daily intervals. In both analyses, however, taxonomy confounded these relationships because a greater percentage of species breeding at high latitudes were sandpipers (which tend to lay daily), whereas plovers, thick-knees and avocets (which lay at longer intervals) are mostly distributed at low latitudes.

Energy constraints on egg laying

Of the 71 species of shorebird (Appendix 1), most (59) species had a modal clutch size of four; 8 laid three-egg clutches, and 4 laid two-egg clutches (Table 1). There was a significant relationship between clutch size and laying interval (Table 1; $\chi^2 = 20.8$, d.f. = 2, $p < 0.0001$), but not in the direction expected if large clutches required more energy. Rather, species laying smaller clutches (mostly plovers, oystercatchers, and thick-knees) had longer egg-laying intervals; conversely, most (85%) species (predominantly sandpipers) with a four-egg clutch laid at daily intervals. For species with three-egg clutches, the proportion of species laying at daily intervals was 38%. By contrast, all (4) species laying two-egg clutches did so at intervals longer than 1 day.

There was a significant (negative exponential) relationship between female mass and egg mass (Fig. 1; $R^2 = 0.60$, d.f. = 66, $p < 0.0001$). If energy constrained egg-laying, then females with disproportionately large eggs should have longer laying intervals between consecutive eggs in a clutch. However, there was no significant difference in the relative size of eggs between females that laid at daily or longer intervals (t = 0.81, d.f. = 65, p = 0.21). I obtained virtually

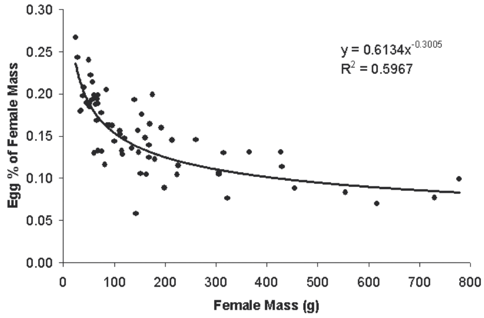

Fig. 1. The relationship between female body mass (g) and fresh egg mass (g) as a percentage of female body mass for 71 species of shorebird. I used the standardized residuals of this relationship to compare the energetic investment of females in their eggs, reasoning that species with daily laying intervals would have proportionately smaller eggs than species that laid at intervals greater than one day.

the same result when I used total clutch mass as a function of female mass.

Risk of clutch loss

Minimum laying intervals were correlated with nest type ($\chi^2 = 21.1$, d.f. = 1, $p < 0.0001$). Most (98%) species with minimum laying intervals of one day concealed their nests in vegetation; by contrast, 48% of species with longer laying intervals nested in open, unvegetated habitats.

DISCUSSION

Laying intervals are highly variable among birds (Carey 1996, Johnson 2000, Lack 1968, Winkler 2004). Most passerines lay consecutive eggs at daily intervals. Seabirds lay clutches of 1–4 eggs and laying intervals are typically 2–3 days, sometimes longer (Grau 1984). Among cursorial species (sensu Lack 1968), laying intervals typically span 1–2 days, with taxa laying larger clutches ovipositing at daily intervals; the latter is also true for waterfowl and grebes. As a group, shorebirds lay eggs at either daily intervals (sandpipers, avocets, stilts, jacanas, and some plovers) or slightly longer (many plovers, thick-knees, and some oystercatchers). And, shorebirds laying four-egg clutches typically lay at shorter intervals than those with two- or three-egg clutches. These patterns generally corroborate those reported by Lack (1968), although he classified sandpipers as having a two-day laying interval.

In his treatment of life history traits of birds, Lack (1968) addressed the ecological circumstances leading to interspecific differences in clutch size, egg size and incubation period; only occasionally did he specifically address the laying interval between consecutive eggs. As one of several co-evolved life history traits related to oviparity, laying intervals may be influenced by time constraints on breeding, energy (or nutrients) available to females to form eggs (and shells), and risk of clutch loss to predators and vagaries of the environment.

Time constraints

Minimum egg-laying intervals appear to be influenced by time constraints. Daily laying intervals typified species breeding at higher latitudes and/or over shorter periods, a pattern noted by Lack (1968). Time constraints of a short breeding season also influence other facets of shorebird breeding biology. For example, young of arctic-breeding species develop faster than their counterparts breeding at more southerly latitudes (Beintema & Visser 1989).

Energy

Shorebirds are precocial and females invest considerable energy in eggs that hatch nidifugous young (Rahn *et al.* 1975, Ross 1979). As most shorebirds are characterized as exogenous layers (see Lenington 1984), laying intervals often lengthen during periods of food shortage (or inclement weather). In this regard, food availability acts as a proximate mechanism influencing oviposition. Interestingly, however, the tendency for shorebird species laying two- or three-egg clutches to lay at longer than daily intervals, and the absence of a difference in egg (or clutch) mass between species with daily vs longer laying intervals, suggest that the evolutionary relationships between food and minimum laying intervals are complex.

Risk of clutch loss

Lack (1968) stated that "…one would expect the successive eggs in a clutch to be laid as rapidly as possible, i.e., one day apart, unless the laying female cannot find enough food to do this. She is more likely to find it hard if her eggs are relatively large, hence one minor disadvantage of a larger egg might be an increase in the laying interval and consequently heavier predation".

While this logic may apply to some groups, such as waterfowl that conceal their eggs in nests in vegetation and rely on camouflage of incubating females to enhance clutch survival, it is not clear that long laying intervals are a disadvantage in areas where high risk of nest failure exists. Perhaps the most intriguing result of this review was the association between minimum laying interval and nest type. Sandpipers, which lay eggs in concealed nests, laid at daily intervals whereas open-nesting plovers, thick-knees and most oystercatchers oviposited at longer intervals. In this analysis, nest type (concealed vs open) served as a surrogate for risk of clutch loss. A better test of this hypothesis would be to compare nest survival rates between species that lay at daily or longer intervals, with the prediction that long laying intervals would be associated with higher clutch failure, especially during the laying period. But, these data are extraordinarily difficult to extract from the literature owing to substantial variation in nesting success among locations and over time (see Evans & Pienkowski 1984), as well as differences in the methodologies used to characterize nest success (i.e., comparing apparent vs Mayfield nest survival).

Predation (and other facets of the environment that cause frequent clutch failure during laying) may select for short (Lack 1968) or long laying intervals. I speculate that by laying a single egg, and returning at a longer interval to complete the clutch, females can conserve energy and time under conditions of frequent clutch failure. Specifically, longer (than daily) laying intervals may have evolved to allow a female to effectively "sample" the risk of clutch loss by laying a single egg and returning at a later time to either lay a second egg, or, if the partial clutch has failed, establish a new nest elsewhere. In some species, the vagaries of the environment contribute to frequent clutch loss. In the population of Snowy Plovers that I study, predation is the most significant source of clutch failure, but losses to drifting sand, tidal over-wash and river flooding are the next most common natural (i.e. not anthropogenic) causes of clutch failure (Colwell, unpubl. data).

Among shorebirds, other facets of breeding biology, such as egg mass (Ross 1979), indeterminacy of egg-laying (Yogev & Yom-Tov 1994, 1996), nest scraping behaviour (Cramp & Simmons 1983), and altering the lining of the nest (Szentirmai & Szekely 2004), may be interpreted as a response to clutch-loss to predators. For example, most shorebirds are categorized as determinate layers (Kennedy 1991), although this distinction is not always clear. When a clutch fails during laying, a female initiates a new clutch typically in a new nest, where she lays the modal clutch size for a species. However, in the Spur-winged Plover *Vanellus spinosus* observational and experimental evidence shows that females act as indeterminate layers when the first-laid egg disappears from an incomplete (one-egg) clutch. That is, they lay either three or four additional eggs summing to an average clutch size of 4.5. But, when the second, third or fourth egg in a clutch disappears from a nest during laying, females continue to lay in a determinate manner, and finish the 4-egg clutch (Yogev & Yom-Tov 1994, 1996). Similar findings have been reported for other plovers (Klomp 1951, Rinkel 1940). In the Snowy Plover, females that lose the first egg of a three-egg clutch to a predator sometimes continue laying in another scrape and add 3 eggs for a total clutch of 4 (modal clutch size is 3; Colwell unpubl.). I am not aware of similar observations for sandpipers.

Courtship scraping may also be related to the risk of clutch loss, and correlated with nesting habitat (open vs concealed). As a part of courtship, all shorebirds build scrapes, one of which the female eventually selects as the nest where she will lay the first egg of a clutch. Although difficult to extract from literature, my review indicated that species varied greatly in number of courtship scrapes. I suggest that scraping behaviour, in addition to synchronizing the reproductive physiology of mates, has evolved in response to the higher risk of clutch loss in open vs concealed habitats. Others have conjectured similarly. For instance, Cramp & Simmons (1983, p. 88) noted that for the Egyptian Plover *Pluvianus aegyptius*, one possible function of the "dozens of scrapes made"… "for at least 30 days" was "deception of potential nest predators". The Snowy Plover often makes scrapes in sandy substrates where plover footprints are quite visible and may lead predators (e.g., *Corvus corax*) to nests. Pairs may scrape for a few days to weeks before the female initiates a clutch, resulting in many scrapes that tend to be clustered in particular areas but sometimes scattered over distances of several kilometers (Colwell, unpubl. data). In summary, species occupying open habitats, where clutch loss is likely, may make more scrapes to provide "false leads" to visual predators searching for nests.

Finally, although time and risk of clutch loss appear to be correlated with laying intervals in shorebirds, these results are confounded by taxonomy. Specifically, sandpipers are mostly northerly in their distribution and they conceal their nests; by contrast, plovers, thick-knees and oystercatchers have more southerly distributions and nest in the open. Consequently, it is difficult to draw firm conclusions from the results presented here. Nevertheless, I urge shorebird biologists to consider risk of clutch failure (to predators or the environment) when interpreting other facets of shorebird behaviour and biology.

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(Appendix . . .)

Appendix 1

Summary of clutch size and laying interval, in relation to constraints of energy, time and danger of clutch loss for 71 species of shorebird.

Species	Clutch size	Laying intervals (d)		Female mass (g)	Egg mass (g)	Egg as % of ♀ mass	Clutch as % of ♀ mass	Breeding season		Nest site	Source
		Total time	Between eggs					Latitude	Weeks		
Burhinidae											
Spotted Thick-knee *Burhinus capensis*	2	4	2	441.5	–	–	–	Tr	–	O	Urban *et al.* 1986
Stone-Curlew *B. oedicnemus*	2	4	2	455	40	0.09	0.18	Tr	7	O	Cramp & Simmons 1983, Urban *et al.* 1986
Charadriidae											
Senegal Wattled Plover *Vanellus senegallus*	3	4	1	224	23.3	0.1	0.31	Tr	–	O	Urban *et al.* 1986
Crowned Lapwing *V. coronatus*	4	2.5	1	163	17	0.1	0.42	Tr	–	O	Urban *et al.* 1986
Spur-winged Plover *V. spinosus*	4	5.5	2	152	16	0.11	0.42	Tr	11	O	Cramp & Simmons 1983, Yogev *et al.* 1996, Urban *et al.* 1986
Northern Lapwing *V. vanellus*	4	5.5	1	226	26	0.12	0.46	Te	9	O	Cramp & Simmons 1983, Johnsgard 1981
Black-bellied Plover *Pluvialis squatarola*	4	6	2	214	31	0.14	0.58	A	3.5	O	Cramp & Simmons 1983, Paulson 1995, Byrkjedal & Thompson 1998
Eurasian Golden-Plover *P. apricaria*	4	6	2	176	35	0.2	0.8	B	6	O	Cramp & Simmons 1983, Byrkjedal & Thompson 1998
American Golden-Plover *P. dominica*	4	5	2	154	27	0.18	0.7	A	3.5	O	Johnson & Connors 1996, Byrkjedal & Thompson 1998
Pacific Golden-Plover *P. fulva*	4	6	2	140	27	0.19	0.77	A	3.5	O	Johnson & Connors 1996, Byrkjedal & Thompson 1999
Snowy Plover *Charadrius alexandrinus*	3	5	2	41	8.5	0.21	0.62	Te	15.5	O	Page *et al.* 1995, Colwell unpubl. data
Wilson's Plover *Ch. wilsonia*	3	5.5	2	68	12.8	0.19	0.56	Te	8.5	O	Corbat & Bergstrom 2000
Great Ringed Plover *Ch. hiaticula*	4	5.5	2	64	12	0.19	0.75	A	7	O	Cramp & Simmons 1983, Wallander & Andersson 2003
Semipalmated Plover *Ch. semipalmatus*	4	4.5	1	46	8.7	0.19	0.76	B	4.5	O	Nol & Blanken 1999
Little Ringed Plover *Ch. dubius*	4	5	1	39	7.7	0.2	0.79	Te/B	10	O	Cramp & Simmons 1983
Piping Plover *Ch. melodus*	4	6	2	52	9.8	0.19	0.75	Te	10	O	Haig & Elliot-Smith 2004
Killdeer *Ch. vociferous*	4	4.5	1	101	14.5	0.14	0.57	Te	20.5	O	Jackson & Jackson 2000
Mountain Plover *Ch. montanus*	3	6	2	96	15.6	0.16	0.49	Te	8	O	Knopf 1996
Eurasian Dotterel *Ch. morinellus*	3	4	1	117	15	0.13	0.38	B	5	O	Cramp & Simmons 1983

(Appendix 1 continued)

Summary of clutch size and laying interval, in relation to constraints of energy, time and danger of clutch loss for 71 species of shorebird.

Species	Clutch size	Laying intervals (d)		Female mass (g)	Egg mass (g)	Egg as % of ♀ mass	Clutch as % of ♀ mass	Breeding season		Nest site	Source
		Total time	Between eggs					Latitude	Weeks		
(Charadriidae continued)											
Kittlitz's Plover *Ch. pecuarius*	2	3	2	34	6.1	0.18	0.36	Tr	10	O	Cramp & Simmons 1983
Wrybill *Anarhynchus frontalis*	2	3	2	58	12.4	0.21	0.43	Te	–	O	Johnsgard 1981
Haematopodidae											
Eurasian Oystercatcher *Haematopus*	3	3	1	616	43	0.07	0.21	Te	10	O	Cramp & Simmons 1983
American Black Oystercatcher *H. bachmani*	3	5	2	555	46	0.08	0.25	Te	6	O	Cramp & Simmons 1983, Andres & Falxa 1995, L'Hyver & Miller 1991
American Oystercatcher *H. palliatus*	3	5	2	730	55.8	0.08	0.23	Te	4.5	O	Nol & Humphrey 1994
Recurvirostridae											
Black-winged Stilt *Himantopus himantopus*	4	4	1	161	23.8	0.15	0.59	Tr	–	O	Johnsgard 1981, Urban *et al.* 1986
Black-necked Stilt *H. mexicanus*	4	4	1	169	21	0.12	0.5	Te	9.5	O	Robinson *et al.* 1999
Pied Avocet *Recurvirostra avosetta*	4	4.5	1	306	32	0.1	0.42	Te	–	O	Cramp & Simmons 1983, Johnsgard 1981, Urban *et al.* 1986
American Avocet *R. americana*	4	4.5	1	306	32.4	0.11	0.42	Te	7	O	Robinson *et al.* 1997
Jacanidae											
Northern Jacana *Jacana spinosa*	4	4	1	143	8.3	0.06	0.23	Tr	–	O	Johnsgard 1981
Scolopacidae											
Greenshank *Tringa nebularia*	4	6	2	193	30.8	0.16	0.64	B	3.5	C	Nethersole-Thompson & Nethersole-Thompson 1979
Greater Yellowlegs *T. melanoleuca*	4	5	1	170	27.9	0.16	0.66	B	4.5	C	Elphick & Tibbitts 1998
Lesser Yellowlegs *T. flavipes*	4	4	1	85	17.4	0.2	0.82	B	3.5	C	Tibbitts & Moskoff 1999
Redshank *T. totanus*	4	5.5	1	147	23	0.16	0.63	B	5	C	Cramp & Simmons 1983
Wood Sandpiper *T. glareola*	4	5.5	1	68	13.5	0.2	0.79	B	5	C	Cramp & Simmons 1983, Johnsgard 1981
Willet *Catoptrophorus semipalmatus*	4	5	1	261	38	0.15	0.58	Te	8	C	Lowther *et al.* 2001
Common Sandpiper *T. hypoleucos*	4	4.5	1	50	12	0.24	0.96	B	5	C	Cramp 1983, Johnsgard 1981

(Appendix 1 continued)

Summary of clutch size and laying interval, in relation to constraints of energy, time and danger of clutch loss for 71 species of shorebird.

Species	Clutch size	Laying intervals (d)		Female mass (g)	Egg mass (g)	Egg as % of ♀ mass	Clutch as % of ♀ mass	Breeding season		Nest site	Source
		Total time	Between eggs					Latitude	Weeks		
(Scolopacidae continued)											
Spotted Sandpiper *T. macularia*	4	4	1	52	9.6	0.18	0.74	Te	7	C	Oring *et al.* 1997
Terek's Sandpiper *T. cinerea*	4	4.5	1	75	13.3	0.18	0.71	B	5	C	Cramp & Simmons 1983, Johnsgard 1981
Upland Sandpiper *Bartramia longicauda*	4	4.5	1	169	23.5	0.14	0.56	Te	6	C	Houston & Bowen 2001
Whimbrel *Numenius phaeopus*	4	5	1	430	48.7	0.11	0.45	A	2.5	C	Skeel & Mallory 1996
Bristle-thighed Curlew *N. tahitiensis*	4	4.5	1	428	55.9	0.13	0.52	A	3.5	C	Marks *et al.* 2002
Eurasian Curlew *N. arquata*	4	4.5	1	778	77	0.1	0.4	B	5.5	C	Cramp & Simmons 1983
Long-billed Curlew *N. americanus*	4	6	2	759	–	–	–	Te	5	C	Dugger & Dugger 2002
Bar-tailed Godwit *Limosa laponnica*	4	5	1	315	41	0.13	0.52	Te	4	C	McCaffery & Gill 2001
Marbled Godwit *L. fedoa*	4	5	1	366	48	0.13	0.52	Te	4.5	C	Gratto-Trevor 2000
Ruddy Turnstone *Arenaria interpres*	4	4.5	1	111	17.3	0.16	0.62	A	2.5	C	Cramp & Simmons 1983, Nettleship 2000
Black Turnstone *A. melanocephala*	4	4.5	1	135	18.3	0.14	0.54	A	2.5	C	Handel & Gill 2001
Red Knot *Calidris canutus*	4	4.5	1	148	19.3	0.13	0.52	A	1	C	Cramp & Simmons 1983, Harrington 2001, Johnsgard 1981
Sanderling *C. alba*	4	4	1	57	11	0.19	0.77	A	3.5	C	Cramp & Simmons 1983, Johnsgard 1981
Semipalmated Sandpiper *C. pusilla*	4	4.5	1	28	6.8	0.24	0.97	A/B	3.5	C	Gratto-Trevor 1992, Sandercock 1998
Western Sandpiper *C. mauri*	4	4	1	28	–	–	–	A	4.5	C	Wilson 1994, Sandercock 1998
Little Stint *C. minuta*	4	4	1	24	6.4	0.27	1.07	A	2.5	C	Cramp 1983, Johnsgard 1981
Baird's Sandpiper *C. bairdii*	4	4.5	1	50	9.3	0.19	0.74	A	2.5	C	Moskoff & Montgomerie 2002
Pectoral Sandpiper *C. melanotos*	4	4.5	1	66	12.8	0.19	0.78	A	4.5	C	Holmes & Pitelka 1998
Purple Sandpiper *C. maritima*	4	5	1	86	14	0.16	0.65	A	5	C	Cramp & Simmons 1983, Payne & Pierce 2002

(Appendix 1 continued)

Summary of clutch size and laying interval, in relation to constraints of energy, time and danger of clutch loss for 71 species of shorebird.

Species	**Clutch size**	**Laying intervals (d)**		**Female mass (g)**	**Egg mass (g)**	**Egg as % of ♀ mass**	**Clutch as % of ♀ mass**	**Breeding season**		**Nest site**	**Source**
		Total time	**Between eggs**					**Latitude**	**Weeks**		
(Scolopacidae continued)											
Rock Sandpiper *C. ptilocnemis*	4	4.5	1	91	14.8	0.16	0.65	A	4.5	C	Gill *et al.* 2002
Dunlin *C. alpina*	4	4	1	66	11.1	0.17	0.67	A/B	4.5	C	Cramp 1983, Warnock & Gill 1996
Stilt Standpiper *Micropalama himantopus*	4	4.5	1	61	12.1	0.2	0.79	A/B	5.5	C	Klima & Jehl 1998
Buff-breasted Sandpiper *Tryngites subruficollis*	4	5.5	1	54	12	0.22	0.89	A	6.5	C	Lanctot & Laredo 1994
Ruff *Philomachus pugnax*	4	4.5	1	180	22	0.12	0.49	A	5	C	Cramp & Simmons 1983
Short-billed Dowitcher *Limnodromus griseus*	4	4	1	120	17.7	0.15	0.59	B	3.5	C	Jehl *et al.* 2001
Long-billed Dowitcher *L. scolopaceus*	4	4	1	109	–	–	–	A	3.5	C	Takekawa & Warnock 2000
Wilson’s Snipe *Gallinago delicata*	4	4	1	112	17	0.15	0.61	Te	7	C	Tuck 1972, Mueller 1999
Common Snipe *G. gallinago*	4	4	1	115	15.2	0.13	0.53	Te	–	C	Cramp & Simmons 1983, Johnsgard 1981
Eurasian Woodcock *Scolopax rusticola*	4	4	1	323	24.5	0.08	0.3	Te	–	C	Cramp & Simmons 1983, Johnsgard 1981
American Woodcock *S. minor*	4	4	1	199	17.6	0.09	0.35	Te	–	C	Keppie & Whiting 1994
Wilson’s Phalarope *Steganopus tricolor*	4	4	1	68	9	0.13	0.53	Te	5	C	Colwell & Jehl 1994, Colwell & Oring 1988, Howe 1975
Red-necked Phalarope Phalaropus lobatus	4	4	1	35	6.3	0.18	0.72	A	3.5	C	Cramp & Simmons 1983, Tinbergen 1935, Rubega *et al.* 2000
Red Phalarope P. fulicaria	4	4	1	61	7.9	0.13	0.52	A	3.5	C	Kistchinski 1975, Tracy *et al.* 2002
Glareolidae											
Egyptian Plover *Pluvianus aegyptius*	3	3	1	82	9.5	0.12	0.35	Tr	11	O	Cramp & Simmons 1983, Urban *et al.* 1986
Collared Pratincole *Glareola pratincola*	3	3	1	76	10	0.13	0.39	Tr	5	O	Cramp & Simmons 1983

Female weights (g) are from Dunning (1993) or the sources listed.
Egg weights are fresh mass (g).
Breeding latitude: A = Arctic; B = Boreal; Te = Temperate; Tr = Tropical.
Season length is the number of weeks over which clutches are initiated.
Nest site: O = open, unvegetated; C = eggs and adults concealed by vegetation.