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EGG DATA SLIPS—ARE THEY USEFUL FOR INFORMATION ON EGG-LAYING DATES AND CLUTCH SIZE?[1]

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Abstract. Egg data slips from museum collections were used to examine their reliability, especially bias in their seasonal distribution of egg-laying dates and clutch size and in overall mean clutch size of nidicolous altricial birds in North America. In general, egg data slips are useful. Suspect data, whether apparently falsified or not, are rare and usually detectable. Mean clutch sizes from egg data slips are usually not seriously biased upward, and are comparable with other nonoological sources. Thus, with some exceptions, Lack's (1946) criticism that mean clutch sizes may be inflated is greatly exaggerated. Similarly, Lack's criticism that the largest complete clutches in the middle of the nesting season are overrepresented lacks support. Lack's remaining criticism is generally true; early dates from egg data slips are overrepresented. For a further review of the value of egg data slips, see McNair (1985).

Key words: Clutch size; egg data slips; egg-laying dates; incubation; nidicolous altricial birds; oology.

INTRODUCTION

Egg data slips from museum collections have been used to examine temporal and geographic patterns of the reproductive biology of birds in the Holarctic region (Johnston 1954; von Haartman 1963; Anderson and Hickey 1970; Murray 1976; Austin 1977; Svensson 1978; Crowell and Rothstein 1981; Koenig 1984a, 1984b; McNair 1984, 1985; Moore and Koenig 1986; and others). Nevertheless, the reliability of egg data slips has been questioned by many ornithologists (pers. comm.), perhaps fueled by Storer's (1930) skepticism and Lack's (1946) criticism. Storer stated that oologists may have included suspect data for many collected egg sets. Lack cautioned that egg data slips suffered from three major shortcomings: (1) early dates were overrepresented, (2) the largest complete clutches in the middle of the nesting season were overrepresented, and (3) mean clutch sizes might be inflated because oologists would prefer to collect the largest clutch possible. Svensson (1978), Kiff (1979), and others have stated these problems, i.e., bias in the seasonal distribution of egg-laying dates and clutch size and in overall mean clutch size, are minimal and that egg data slips are underused.

No previous study in North America has explicitly used egg data slips for any species to investigate the methodological problems outlined above, except for Lark Sparrow, *Chondestes grammacus* (McNair 1985). In this paper, I also use egg data slips for 12 other nidicolous, altricial birds, i.e., Hairy Woodpecker (*Picoides villosus*), Northern Rough-winged Swallow (*Stelgidopteryx serripennis*), Tufted Titmouse (*Parus bicolor*), Brown-headed Nuthatch (*Sitta pusilla*), Yellow-throated (*Dendroica dominica*) and Pine (*D. pinus*) warblers, Summer Tanager (*Piranga rubra*), Blue Grosbeak (*Guiraca caerulea*), Painted Bunting (*Passerina ciris*), Bachman's (*Aimophila aestivalis*) and Grasshopper (*Ammodramus savannarum*) sparrows, and Rusty Blackbird (*Euphagus carolinus*).

MATERIALS AND METHODS

Using information on egg data slips, I generated the following data: (1) latitude (to the nearest degree), (2) longitude (to the nearest degree), (3) date of clutch initiation, (4) clutch size, and (5) incubation stage. For three species, Brown-headed Nuthatch, and Yellow-throated and Pine warblers, I omitted recording the incubation stage when transcribing the data for these analyses. Total sample size for each of the 13 species is: Hairy Woodpecker (474), Northern Rough-winged Swallow (430), Tufted Titmouse (263), Brown-headed Nuthatch (372), Yellow-throated Warbler (126), Pine Warbler (226), Summer Tanager (289), Blue Grosbeak (307), Painted Bunting (421), Bachman's Sparrow (205), Lark Sparrow (945), Grasshopper Sparrow (438), and

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Rusty Blackbird (226). I excluded nest records that recorded Brown-headed Cowbird (*Molothrus ater*) brood parasitism, nest records without clutch size data or with inadequate clutch size data, and contradictory or suspect data that precluded reliable calculation of date of clutch initiation and clutch size (sensu Anderson and Hickey 1970; Svensson 1978; McNair 1984, 1985). I included some egg sets that had missing data for one or more variables if other information appeared correct (e.g., exact date unknown). Thus, some sample sizes are unequal. For 11 of 13 species, only 2.0 to 4.9% of the egg data slips were excluded. Ten percent each of egg data slips were excluded for Bachman's Sparrow and Rusty Blackbird.

I determined the date of clutch initiation from egg data slips by using the procedure described in McNair (1985). In brief, the egg data slips were divided into six groups according to stage of incubation. The estimated date of clutch initiation was equal to the date the egg set was collected minus clutch size plus one day. Additional days were subtracted from this date according to the collector's estimation of incubation time elapsed. For species with an estimated incubation period of 12 days, I used the incubation time elapsed as thus: fresh—0 day, slight—2 days, halfway—6 days, advanced—10 days, unknown—6 days (half of estimated incubation period). For species with an estimated incubation period of 14 or 16 days, I increased the estimates of incubation time elapsed for advanced, and halfway and unknown incubation stages one day each for a 14-day incubation period and 2 days each for a 16-day incubation period. If the number of days of incubation were estimated and stated explicitly, I used that number. This sixth group overlaps groups one through five. Only three incubation stages were used for Bachman's Sparrow, fresh (0 day), not fresh (1 to 14 days), and unknown (7 days).

Mean clutch size was calculated from clutches containing no fewer than three or four eggs, depending on the species. Smaller clutches were assumed to be incomplete because of Brown-headed Cowbird parasitism or other forms of disturbance, and these small clutches were not used in the analyses.

I used untransformed values of my data because the variables of interest, especially clutch size and date of clutch initiation, were either normally distributed or approximated a normal distribution. An analysis of covariance (ANCOVA) was performed using clutch size as the dependent variable, date of clutch initiation, latitude, and longitude as the covariates, and incubation stage as the qualitative treatment variable. Nonsignificant covariates were deleted from the final models. The analysis of covariance was used to examine the ability of oologists to reliably determine clutch size on the basis of their ability to estimate incubation stage. Resolution of this problem is necessary before addressing the three criticisms of Lack (1946). Partial linear regression (PLR) was performed using clutch size as the dependent variable and date of clutch initiation as the independent variable, adjusted for the effects of latitude and longitude. Nonsignificant independent variables, except for date of clutch initiation, were deleted from the final models. The partial linear regression analyses were used to examine the second of Lack's criticisms, i.e., the largest complete clutches in the middle of the nesting season were overrepresented.

RESULTS

Oologists collected fresh clutches most frequently for all 10 species, and egg sets of slight and unknown incubation stages were also heavily collected (Table 1). Comparisons of the groups of incubation stage of each species for clutch size indicate no significant differences exist among any of the comparisons except for Northern Rough-winged Swallow and Rusty Blackbird (ANCOVA, Student Neuman-Keuls test, $P < 0.05$, Table 1). For each of these two species, only one pair-wise comparison was significant; each case involved the estimated incubation stage. Overall, no incubation stage shows any trend of larger or smaller mean clutch sizes when compared to other incubation stages for all 10 species.

Clutch size declined with date of clutch initiation for all 13 species, and for nine species the decline was significant (PLR, Table 2). All R^2 values were low; the highest was 0.16. Modeling polynomial terms for date of clutch initiation in the partial linear regression equations increased the maximum R^2 values only a few percent for only three species. For two species, Brown-headed Nuthatch and Rusty Blackbird, clutch size declined with date of clutch initiation. Only Summer Tanager showed a difference in the regression relationship; clutch size peaked in the middle of the breeding season.

The mean dates of clutch initiation for all 13 species are the same or very similar to the median dates (Table 3). Except for Northern Rough-winged Swallow, distributions of egg-laying dates are skewed toward earlier dates, despite the breadth of latitudinal and longitudinal range sampled for all species.

Mean clutch size and clutch range, and range of clutch initiation dates from egg data slips for each species provide an estimate of clutch size and egg-laying dates over the years (Table 3). I also provide values for the same variables from the literature, not based primarily on egg data slips, for six of the 13 nidicolous altricial species, Table 4 (see McNair 1984, 1985, for data on Brown-headed Nuthatch and Lark Sparrow). There is general agreement between egg data slips and the literature on these variables for these species. However, the majority of accounts are inadequate and it is difficult to assess the significance of comparisons within species because of the scarcity of detailed material from the literature. Other literature which contains material based to a varying degree on egg data slips, e.g., Bent's volumes, Johnston (1964), Graber et al. (1972, 1977, 1983), many state bird books, etc., does not alter the above results and have not been tabulated in Table 4.

DISCUSSION

This study suggests that one of Storer's (1930) contentions, that oologists may have included suspect data for many collected egg sets, is largely unfounded. While examining the data, I rejected less than 5% of egg data slips for all but two of the 13 species. Lloyd Kiff (pers. comm.) has also found that 5% or less of egg data slips are suspect for most species. Suspect data cannot be proven to be deliberately falsified unless the exact circumstances are known. From my data, apparent falsification occurred for four-egg sets of the Grasshopper Sparrow (*A. s. floridanus*) in Florida where the species is rare and local (McNair 1986), but was more common for Bachman's Sparrow which is a geographically-restricted species and whose nests are also difficult to find. These valuable egg sets were either exchanged from collector to collector or brought a high price in the market. Any attempt to deceive collectors or purchasers, though, was not based only on market factors as many species whose highly valued egg sets were exchanged or which brought high prices on the market were not falsified, e.g., Yellow-

TABLE 1. Estimates of mean clutch size of different incubation stages for 10 species of nidicolous altricial birds.

Species	Incubation stage (*n* = no. of clutches)						ANCOVA[a]	*F*-test (for I)	*P*[b] (for I)
	Fresh	Slight	Halfway	Advanced	Estimated	Unknown[c]			
Hairy Woodpecker	4.20 (138)	4.02 (114)	4.13 (23)	3.97 (33)	3.69 (16)	4.10 (118)	LAT	1.91	0.09, ns
Northern Rough-winged Swallow	5.48 (164)[d]	5.84 (74)	5.80 (20)	5.55 (11)	6.09 (11)[d]	5.56 (131)	LAT, D	2.66	0.02, s
Tufted Titmouse	5.70 (108)	5.75 (57)	5.86 (14)	5.56 (9)	5.53 (19)	5.37 (52)	LAT, D	1.13	0.34, ns
Summer Tanager	3.74 (129)	3.70 (46)	3.86 (7)	3.63 (16)	3.43 (7)	3.68 (78)	none	0.89	0.49, ns
Blue Grosbeak	3.68 (133)	3.57 (61)	3.64 (14)	3.58 (12)	3.63 (8)	3.56 (70)	LONG, D	0.58	0.72, ns
Painted Bunting	3.88 (211)	3.88 (64)	3.86 (7)	3.60 (10)	3.88 (8)	3.87 (89)	LONG	0.94	0.46, ns
Bachman's Sparrow	4.06 (93)		4.13 (69)[e]			3.88 (26)[e]	LAT	0.22	0.80, ns
Lark Sparrow	4.12 (408)	4.10 (230)	4.03 (60)	4.16 (43)	4.17 (23)	3.97 (100)	LONG, D	1.05	0.39, ns
Grasshopper Sparrow	4.22 (138)	4.29 (113)	4.08 (60)	4.52 (25)	4.36 (14)	4.45 (77)	LAT, D	2.08	0.07, ns
Rusty Blackbird	4.59 (64)	4.65 (40)	4.61 (23)	4.68 (19)	4.82 (17)[d]	4.27 (59)[d]	D	3.60	0.01, s

[a] ANCOVA: significant covariables in C on I model. See explanation in text; C = clutch size, I = incubation stage, LAT = latitude, LONG = longitude, D = date of clutch initiation.
[b] Probability value for significance of I in ANCOVA.
[c] U = unknown incubation stage.
[d] Significant pair-wise comparison, Student Neuman-Keuls test.
[e] See explanation in text.

TABLE 2. Partial linear regression (PLR) of clutch size on date of clutch initiation, adjusted for latitude and longitude, for 13 species of nidicolous altricial birds.

Species	PLR[a]	*F*-test (for D)	*P*[b] (for D)
Hairy Woodpecker	LAT	0.01	0.90, ns
Northern Rough-winged Swallow	LAT	14.07	0.0002, s
Tufted Titmouse	LAT	38.42	0.0001, s
Brown-headed Nuthatch	LAT	38.03	0.0001, s
Yellow-throated Warbler	none	12.36	0.0006, s
Pine Warbler	LAT	10.17	0.0016, s
Summer Tanager	none	0.82	0.37, ns
Blue Grosbeak	LONG	17.57	0.0001, s
Painted Bunting	LONG	1.63	0.20, ns
Bachman's Sparrow	LAT	1.59	0.21, ns
Lark Sparrow	LONG	12.59	0.0004, s
Grasshopper Sparrow	LAT, LONG	40.30	0.0001, s
Rusty Blackbird	none	25.84	0.0001, s

[a] PLR: significant covariables in C on D model. See explanation in text; C = clutch size, LAT = latitude, LONG = longitude, D = date of clutch initiation.
[b] Probability value for significance of D in PLR.

throated Warbler (pers. observ.; Lloyd Kiff, pers. comm.). Fortunately, apparent fake data are less frequent than honest mistakes and purported oologists who falsified data were not clever liars and most of these individuals are known (Lloyd Kiff, pers. comm.; pers. observ.). For any type of suspect data, the egg data slips can be checked by an examination of the eggs themselves which may confirm that the data are questionable. For many species, some error or apparent error is evident on the egg data slips, and this problem is usually detectable by individuals who are knowledgeable about species' breeding biology and their distribution. For example, Brewer's Blackbird (*E. cyanocephalus*) nests mistaken for Rusty Blackbird nests in the Canadian Prairies were recognized as Brewer's based on information for collecting locality, nest placement, nest materials, habitat, and additional collector remarks. P. A. Taverner even misidentified museum specimens of these two species which he relabeled one year later (C. Stuart Houston, pers. comm.). Even experts made misidentifications because of the lack of good field guides, binoculars, rudimentary knowledge of the distribution and breeding biology of many species, and other factors. Furthermore, oologists were both residents and itinerants on expeditions to geographical areas beyond their home base. The frequency of suspect data is very low in South Carolina, for these 13 and other species, where four resident oologists collected a preponderance of the egg sets. In the Prairie provinces of Canada, however, the frequency of suspect data is higher because a greater number of itinerant oologists collected egg sets of species not well known to them from previous experience. Rarely, honest mistakes in identification of a species nests and eggs from egg data slips may be more difficult to resolve (Bechard and Houston 1984a). Regardless of the type of suspect data, no data set is perfect, and it is sufficient for scientific purposes to say that over 95% of egg data slips for the majority of species are useable, i.e., valid.

Egg data slips also offer an opportunity to document changes in distribution and occasionally in abundance of many species (Houston and Bechard 1982; Bechard and Houston 1984a, 1984b; McNair 1986, in press a, in press b).

This study also suggests that oologists' ability to reliably determine clutch size on the basis of their ability to estimate incubation stage is consistent and that incubation stage terminology is adequate (Table 1). The estimated incubation stage, which was one of the pairs in each of the two pair-wise comparisons that were significantly different, overlaps the other five incubation stages. Therefore, I interpret the significance tests as a statistical artifact and of minimal biological significance. In general, fresh and unknown sets were not smaller or larger than other incubation stages, nor were more advanced sets smaller or larger than others. Thus, it is unnecessary to exclude clutches of fresh or unknown incubation stages *a priori* because these clutches should not be potentially incomplete. Apparently, oologists checked nests often enough to ascertain that clutches were complete and they were experienced in detecting if eggs were removed by predators, cowbirds, etc., from clutches more advanced than the fresh incubation stage. Many egg sets were collected as a result of single visits by itinerant oologists, who evidently were able to estimate the extent of incubation correctly.

The partial linear regression analyses suggest larger complete clutches in the middle of the nesting season are not overrepresented from egg data slips except for possibly Summer Tanager, contrary to Lack's assertion. The range of egg-laying dates from egg data slips for all 13 species is the best data available, though the end of the breeding seasons may be poorly defined. Though few of the 13 species have adequate nonoological nesting data to compare with egg data slips, the egg data slips follow the usual decline in clutch size with egg-laying date for nidicolous altricial species when first, replacement, and later clutches are combined (Berndt and Winkel 1967, von Haartman 1967, Lack 1968, Fuller and Glue 1977, Nolan 1978, Garson 1980, O'Conner and Morgan 1982, Orell and Ojanen 1983, Schmidt and Steinbach 1985, and many others), though some species may show an initial rise then decline in clutch size (Klomp 1970), or even a continual rise with egg-laying dates (Delius 1965, Cannings and Threlfall 1981). Regression analyses may mask some relationships between clutch size and date of clutch initiation when applied to continent-wide areas because clutch size may vary over such a large region and latitudinal range or because of uneven sample sizes among different geographical areas. Nevertheless, regression analyses are the best tool available for these egg data slips though interpretation of the significant polynomial terms for date of clutch initiation and their effect on clutch size is difficult (see Orell and Ojanen 1983 for curvilinear regression analyses of clutch size on date of clutch initiation).

Overall, overrepresentation of early dates of clutch initiation was a bias from egg data slips, though several species did not show this bias. This overrepresentation of early dates of clutch initiation is the most common bias in egg data slips (McNair 1985). Unfortunately, lack of adequate independent estimates of the pattern of date of clutch initiation for these 13 species are not available except for Northern Rough-winged Swallow, Brown-headed Nuthatch, Lark and Grasshopper sparrows, and Rusty Blackbird, Table 4 (McNair 1984, 1985).

This study and others indicate the bias of a

TABLE 3. Estimates of clutch size and date of clutch initiation for 13 species of nidicolous altricial birds.

Species	Clutch size		Date of clutch initiation			Latitudinal range (°N)	Longitudinal range (°W)
	$\bar{x} \pm SD$ (n)	Range	$\bar{x} \pm SD$ (n)	Median	Range (days)		
Hairy Woodpecker	4.09 ± 0.77 (461)	3–7	5 May ± 18 days (452)	5 May	21 March–30 July (131)	26°–62°	60°–149°
Northern Rough-winged Swallow	5.61 ± 0.93 (428)	4–9	21 May ± 16 days (424)	21 May	2 April–14 July (103)	28°–53°	71°–124°
Tufted Titmouse	5.64 ± 1.00 (263)	4–8	21 April ± 19 days (261)	21 April	3 March–23 June (112)	25°–42°	73°–99°
Brown-headed Nuthatch	5.08 ± 0.91 (365)	3–7 (9)	2 April ± 20 days (361)	1 April	21 February–8 July (137)	27°–38°	76°–96°
Yellow-throated Warbler	4.14 ± 0.70 (126)	3–5	20 April ± 18 days (126)	16 April	26 March–22 June (88)	28°–39°	76°–97°
Pine Warbler	3.73 ± 0.50 (226)	3–5	20 April ± 25 days (226)	12 April	7 March–3 July (118)	28°–46°	71°–95°
Summer Tanager	3.71 ± 0.49 (287)	3–5	19 May ± 14 days (279)	19 May	27 March–17 July (112)	25°–39°	95°–111°
Blue Grosbeak	3.62 ± 0.52 (306)	3–5	3 June ± 22 days (301)	30 May	6 April–12 August (128)	25°–40°	76°–123°
Painted Bunting	3.86 ± 0.42 (420)	3–5	27 May ± 19 days (401)	23 May	19 March–30 July (133)	22°–37°	79°–103°
Bachman's Sparrow	4.06 ± 0.62 (196)	3–5	13 May ± 24 days (190)	8 May	21 March–23 July (124)	26°–39°	77°–95°
Lark Sparrow	4.09 ± 0.66 (933)	3–6	14 May ± 21 days (924)	13 May	22 March–25 July (125)	25°–49°	78°–123°
Grasshopper Sparrow	4.30 ± 0.69 (438)	3–6	31 May ± 27 days (437)	26 May	18 March–20 August (155)	27°–49°	70°–122°
Rusty Blackbird	4.54 ± 0.65 (226)	3–6	20 May ± 11 days (222)	20 May	22 April–16 June (55)	43°–68°	57°–162°

TABLE 4. Mean clutch size, clutch range, and range of egg-laying dates from the literature not based on oology data for six species of nidicolous altricial birds.

Species	Mean clutch size (n)	Clutch range	Egg-laying dates (range)	Latitude (°N)	Reference
Northern Rough-winged Swallow	6.25 (61)	5–8	10 May–25 June	42°	Lunk 1962
Tufted Titmouse	6.0 (9)	5–7	—	36°	Laskey 1957
Painted Bunting	3.44 (16)	—	Mid-June–July	34°	Parmelee 1959
Lark Sparrow	4.1–4.3 (28–41)	3–5	1 May–20 July	37°–40°	Johnston 1964 Rising 1974
	—	—	18 May–17 July	49°–51°	Walley 1985
Grasshopper Sparrow	4.1–4.5 (44)	—	—	39°–40°	Wray et al. 1982
	4.4 (7)	4–5	21 May–22 July	42°	Walkinshaw 1940
	4.4 (13)	4–5	20 May–1 July	43°	Wiens 1969
Rusty Blackbird	4.58 (67)	3–6	6 May–19 June	42°–68°	NRS[a]

[a] Breeding data from various North American nest record schemes, primarily Canadian. Egg-laying dates determined by using the bracketing method of Myres (1955). Difference in mean clutch size compared with egg data slips was not significant ($t = 0.49$, $P > 0.05$).

larger mean clutch size from egg data slips compared to other sources is usually minimal or absent. Indeed, the opposite risk exists of including egg sets that were not yet complete. Inclusion of the few clutches from egg data slips of one egg less than the accepted minimum for each species would slightly lower mean clutch size, of course. It is better to exclude than include these data, however, because these low clutch sizes have not been proven to be complete.

Nevertheless, individual oologists may have selectively collected larger clutches of particular species (cf. Lack 1946). Large clutches of colonial breeding species whose nests are easily accessible were collected by many oologists, e.g., Royal Tern (*Sterna maxima*) in South Carolina (McNair, unpubl.), because oologists can easily choose the larger sets.

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