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ASSESSING THE DEVELOPMENT OF SHOREBIRD EGGS USING THE FLOTATION METHOD: SPECIES-SPECIFIC AND GENERALIZED REGRESSION MODELS

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Abstract. We modeled the relationship between egg flotation and age of a developing embryo for 24 species of shorebirds. For 21 species, we used regression analyses to estimate hatching date by modeling egg angle and float height, measured as continuous variables, against embryo age. For eggs early in incubation, we used linear regression analyses to predict hatching date from logit-transformed egg angles only. For late incubation, we used multiple regression analyses to predict hatching date from both egg angles and float heights. In 30 of 36 cases, these equations estimated hatching date to within four days of the true hatching date for each species. After controlling for incubation duration and egg size, flotation patterns did not differ between shorebirds grouped by mass ($\geq$100 g or <100 g) or taxonomy (Scolopacidae versus Charadriidae). Flotation progressed more rapidly in species in which both adults incubate the clutch versus species in which only one adult incubates the clutch, although this did not affect prediction accuracy. We also pooled all continuous data and created a generalized regression equation that can be applied to all shorebird species. For the remaining three species, we estimated hatching date using five float categories. Estimates of hatching date using categorical data were, overall, less accurate than those generated using continuous data (by 3%–5% of a given incubation period). Our equations were less accurate than results reported in similar studies; data collected by multiple observers and at multiple sites, as well as low sample sizes for some species, likely increased measurement error. To minimize flotation method prediction error, we recommend sampling in early incubation, collecting both egg angle and float height data in late incubation, and developing site- and species-specific regression models where possible.

Key words: Charadriidae, embryo age, hatching date, Scolopacidae.

Evaluación del Desarrollo de los Huevos de Aves Playeras Usando el Método de Flotación: Modelos de Regresión Especie-Específicos y Generalizados

Resumen. Modelamos la relación entre la flotación del huevo y la edad de un embrión en desarrollo para 24 especies de aves playeras. Para 21 especies, usamos análisis de

regresión para estimar la fecha de eclosión modelando el ángulo del huevo y la altura de flotación, medidos como variables continuas, contra la edad del embrión. Para huevos al inicio del período de incubación, usamos análisis de regresión lineal para predecir la fecha de eclosión sólo a partir de la transformación logit de los ángulos de los huevos. Para la parte final del período de incubación, usamos análisis de regresión múltiple para predecir la fecha de eclosión a partir de los ángulos de los huevos y de la altura de flotación. En 30 de los 36 casos, estas ecuaciones estimaron la fecha de eclosión con una exactitud de cuatro días alrededor de la verdadera fecha de eclosión para cada una de las especies consideradas. Luego de ajustar los modelos considerando la duración de la incubación y el tamaño del huevo, los patrones de flotación no difirieron entre las aves playeras agrupadas por peso ($\geq$100 g ó <100 g) o taxonomía (Scolopacidae versus Charadriidae). La flotación avanzó más rápidamente en las especies en las cuales ambos adultos incuban la nidada, que en las que sólo un adulto incubó la nidada, aunque esto no afectó la exactitud de la predicción. También combinamos todos los datos continuos y creamos una ecuación de regresión generalizada que puede ser aplicada a todas las especies de aves playeras. Para las tres especies restantes, estimamos la fecha de eclosión usando cinco categorías de flotación. En términos generales, las estimaciones de la fecha de eclosión usando datos categóricos fueron menos exactas que aquellas generadas usando datos continuos (de 3% a 5% para un período de incubación dado). Nuestras ecuaciones fueron menos exactas que los resultados presentados por otros estudios. Los datos recolectados por múltiples observadores y en múltiples sitios, y el tamaño de muestra reducido para algunas especies, probablemente incrementaron el error de medición. Para minimizar el error de predicción del método de flotación, recomendamos muestrear en el período temprano de incubación, recolectar datos del ángulo del huevo y de la altura de flotación al final de la incubación y desarrollar modelos de regresión específicos para los sitios y las especies cuando sea posible.

INTRODUCTION

Determining the stage of incubation of eggs in active nests is an important component in many avian studies where nest initiation or hatching dates are of interest. Knowledge of such dates can improve the accuracy of nest survival estimates, help to ascertain nest fate, and reduce the need for frequent nest visits. Minimizing disturbance to incubating adults can reduce the chance of observer-related nest failure. Estimates of embryo age are also useful in deciding when to capture incubating adults and nestlings (especially nidifugous young of shorebirds), establishing embryo age in toxicological and egg-swapping experiments, and scheduling management actions (e.g., mowing or tilling of fields) to avoid harm to nesting birds (Grant 1996, Brua and Machin 2000).

For more than half a century, biologists have used a variety of techniques to determine the age of developing embryos in eggs. Most of these methods rely on the fact that eggs tend to lose mass at a relatively constant rate during incubation, to evaporative water loss and respiration by the developing embryo (Westerskov 1950, Ar and Rahn 1980). In addition, evaporation rates per unit of egg surface are similar across different species with disparate egg sizes (Drent 1970). In some cases, variable environmental or biotic conditions may in-

fluence embryo development, making estimates of embryo age difficult (Nol and Blokpoel 1983). In general, however, rates of loss of egg mass are highly correlated with the developmental stage of the embryo.

Sacrificing eggs so that embryos can be viewed is clearly the most accurate method of determining incubation stage (Fant 1957), although this is not a practical alternative when studying threatened and endangered species or when there is a desire to estimate natural levels of hatching success. Estimating egg density can also be used to age embryos, although this technique requires very accurate measurement of weight, which can be difficult under field conditions (O'Malley and Evans 1980, Grant 1996, Morrison and Hobson 2004). A third method of aging eggs is to shine a strong light through the shell and observe the contents. With this method, the development of the embryo and the size of the air cell indicate embryo age (Hanson 1954, Weller 1956). However, this candling technique does not work well for aging embryos in all stages of development, or for observing contents when eggs are darkly colored, mottled, or thick-shelled (Wooler and Dunlop 1980, Brua and Machin 2000).

Flotation of eggs, one of the most common methods employed for estimating embryo de-

velopment, relies on the fact that as an embryo develops, the specific gravity of the egg changes from greater than to less than that of water (i.e., 1 g/1 ml). Newly laid eggs sink to the bottom of a column of water and, as the embryos develop, eggs tip upward and eventually float on the surface. One can quantify this development by measuring: (1) the angle between the horizontal plane and the longitudinal axis of the egg, (2) the location of the egg within the water column, and (3), if the egg breaks the surface, the height at which it floats. Of all the methods of aging eggs, flotation has been the most widely employed, with information available for at least seven families of birds (Hays and LeCroy 1971, Dunn et al. 1979, Carroll 1988, Fisher and Swengel 1991, Custer et al. 1992, Sandercock 1998, Brua and Machin 2000).

Within the shorebirds (Suborder Charadrii), egg flotation data have been published for relatively few species (van Paassen et al. 1984, Sandercock 1998, Mabee et al. 2006). Because of this paucity of information in the literature, we were motivated to combine our existing, individual flotation data sets to conduct comprehensive analyses that would not only provide embryo age estimates for additional shorebird species, but also evaluate the overall efficacy of this method in accurately determining hatching date. In this paper, we present species-specific and generalized equations that describe the relationship between embryo development and egg flotation by collating data from 24 shorebird species collected at 17 study sites. These equations can be used to predict nest initiation or hatching date based on the float characteristics of an egg.

Our specific objectives were to: (1) develop regression equations for estimating embryo development in eggs of a variety of shorebird species using the egg flotation technique, (2) compare embryo development among species with different taxonomy, incubation durations, and parental care, and (3) summarize the error associated with estimating hatching date using the flotation technique and recommend methods to minimize this error.

METHODS

STUDY SITES

We present egg flotation data from 24 shorebird species collected at 17 study sites located throughout the northern hemisphere (Fig. 1). Latitude and longitude coordinates for each study site are given in an Appendix published online at < http://www.wcs.org/media/file/ Liebezeitetal2007_Appendix.pdf > . Most sites (13 of 17) were located in arctic or subarctic tundra in habitats ranging from lowland marshes to drier uplands. The remaining sites were at temperate latitudes and consisted of rocky intertidal shorelines, prairie uplands, shallow alkaline wetlands, or mudflats.

FIELD METHODS

We determined the float characteristics of eggs by individually immersing them in water in a transparent, wide-mouthed container. We used lukewarm water from a thermos or water taken directly from ponds or lakes. We usually floated two or more eggs from each clutch, and we floated some clutches several times throughout the breeding season. Generally, observers used a protractor to measure the angle between the horizontal plane of the water and the longitudinal axis of the egg (hereafter "egg angle"; typically measured to within ±5°), although a few experienced observers estimated this angle visually. We also measured the vertical distance an egg floated above the surface of the water (hereafter "float height"; typically measured to ±1 mm) using a clear plastic ruler. For most species, egg angle and float height were measured as continuous data. However, for three species, observers classified egg flotation parameters into categories (Fig. 2). For eight species, egg angle measurements were collected as continuous data while float height measurements were collected as categorical data. We did not uniquely identify eggs or examine changes in flotation scores of individual eggs over time.

INDIVIDUAL SPECIES ANALYSES

To determine the relationship between egg flotation characteristics and embryo age, we used data from nests where the date of clutch completion or hatching was known. Nests were presumed to have hatched on the date when newly hatched chicks were observed either in or within a few meters of the nest, or within 24–72 hr after star-cracked and pipped eggs were observed in the nest (exact number of hours based on shell-breaking and emergence times reported in Poole et al. [2003]). For nests with
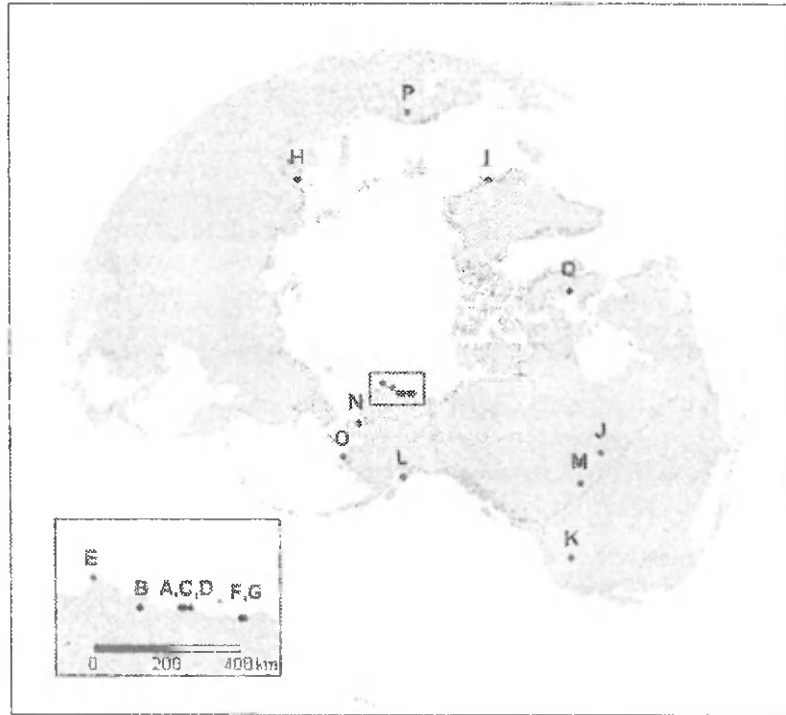
FIGURE 1.   Geographic locations of study sites where shorebird egg flotation data were collected between 1993 and 2006. A = Kuparuk Oilfield, Alaska, USA; B = Teshekpuk Lake, Alaska, USA; C, D = Prudhoe Bay, Alaska, USA; E = Barrow, Alaska, USA; F = Pt. Thomson, Alaska, USA; G = Arctic National Wildlife Refuge, Alaska, USA; H = Medusa Bay, Taimyr Peninsula, Siberia, Russia; I = Zackenberg, Greenland; J = Big Quill, Saskatchewan, Canada; K = Honey Lake, California, USA; L = Kenai Fjord National Park, Alaska, USA; M = Brooks, Alberta, Canada; N = Cape Espenberg, Alaska, USA; O = Yukon Delta National Wildlife Refuge, Alaska, USA; P = NE Enontekio, Finland; Q = Great Plain, West Baffin Is., Canada. Latitude and longitude coordinates for each study site are available at <http://www.wcs.org/media/file/Liebezeitetal2007_Appendix.pdf>.

a known hatching date, we estimated embryo age at the time the eggs were floated by back-calculating from the date of hatching (labelled as "days until hatching" in all figures). For nests with a known clutch completion date only, we estimated the days until hatching using site-specific incubation durations if available, or more generic incubation durations provided in the literature (Poole et al. 2003). We determined clutch completion dates for nests discovered during laying by revisiting them daily until clutches were complete, or by assuming birds laid one egg per day until the standard clutch size for that species was reached (typically four eggs). We defined the first day of incubation as the date the final egg of the clutch was laid. When more than one egg per clutch was floated on a given visit, we used the average angle and height as the sample unit. We did not use egg

angle data from nests with fewer than three eggs, as these nests could represent incomplete or partially depredated nests and thus bias our analyses. We discarded data from individual eggs within a clutch that had abnormal scores relative to the rest of the clutch (<1% of observations). In most cases, these eggs were either infertile or had a dead embryo inside.

We developed species-specific equations to predict embryo development and thus anticipate the day eggs would hatch. To do this, we first pooled data from different study populations for a given species; two study populations were pooled for three species, and between three and seven populations were pooled for nine species. The remaining 12 species had data from only one site (Appendix). Second, we pooled data across years (range: 2–13 years) for all species. For our analyses, we used float data
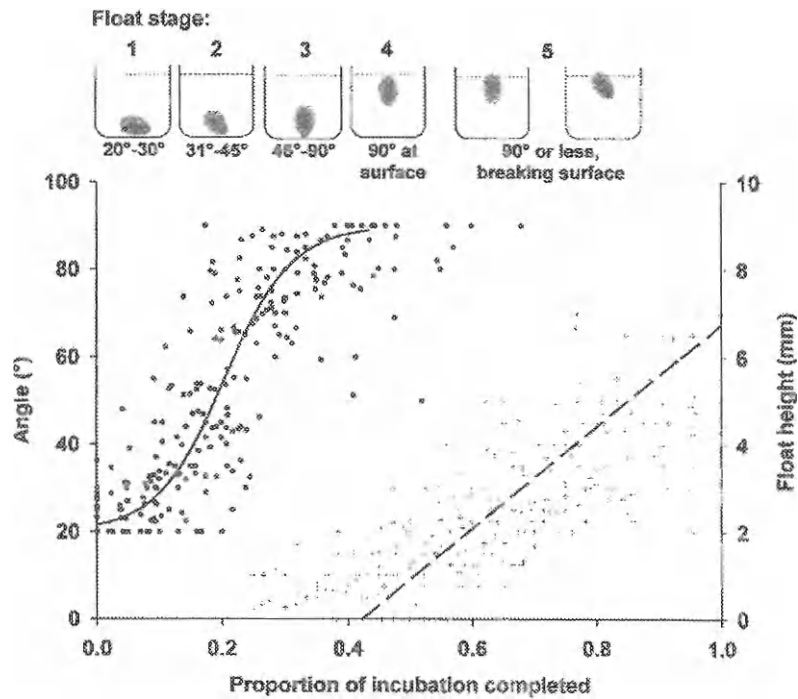
FIGURE 2.   Egg angle (solid line) and float height (dashed line) regressions using continuous data pooled from 21 (egg angle) and 20 (float height) shorebird species. Illustrations of how the position of an egg in a float container changes through time are presented above the graph. The numbers at the top of the figure refer to the five combined egg angle–float height categories.

from a single nest on a given day as our sample unit. Consequently, we did not restrict our data to a single observation per clutch per season. We accepted a low level of pseudoreplication because sample sizes of nests were sometimes small, and we wanted to explore general patterns in egg flotation across a large range of species.

Continuous data. We analyzed the data for early (i.e., sinking eggs) and late (i.e., floating eggs) incubation separately. When individual eggs in the same clutch both sank and floated, we classified the nest as being in late incubation. As we were interested in predicting hatching date (a measure of embryo development, or age), our models are based on regressions of embryo development on float characteristics, i.e., we treated embryo age as the dependent variable and float characteristics as the independent variables. Although this method essentially requires rotating the axes by 90°, the resulting regression parameters have standard errors describing variance in hatching date as opposed to flotation characteristics. More-

over, this avoids under- or overestimating the rate of development for individual nests in a data set where development may progress differently among nests (as seen in aging studies using molt scores; Pimm 1976, Ginn and Melville 1983).

We employed linear regression with logit-transformed egg angles to capture the relationship between embryo development and egg angle. We could not use logistic regression in these analyses because the relationship between variables was not sigmoidal when considering embryo age as the independent variable. Because of their pyriform profile, unincubated shorebird eggs lie at the bottom of the water container at a minimum angle of 20°. Similarly, an egg can only rotate to a vertical position, or 90°, as the embryo develops. Thus, 20° and 90° were the lowest and highest egg angles that could be measured during our study. To transform the egg angle measurements to logits, we first converted them to proportions (P) by assigning a value of 0 and 1 to 20° and 90°, respectively, and interpolating the values for

intermediate angles. Eggs with observed angles of 20° and 90° were first adjusted to 21° and 89° to avoid proportional angles of exactly 0 and 1, which cannot be logit-transformed. Proportional angles were transformed to logits using the formula:

$$\text{logit } P = \ln[P/(1 - P)].$$

We then employed linear regression to predict the number of days to hatching using these transformed egg angles.

For eggs in late incubation (i.e., eggs that floated above the water surface), we used multiple regression to predict the number of days to hatching using two factors, egg angle and float height. For these analyses we used untransformed data, as there was no evidence of a nonlinear relationship between embryo age and either egg angle or float height during the latter half of incubation. Six species were excluded from the late-incubation single species analyses because of low sample sizes ($n < 10$; Appendix).

Categorical data. For species for which float data were collected categorically, we first standardized the data into five egg angle and float height categories as described in Alberico (1995; Fig. 2). We related float category to embryo age graphically, and generated a mean age for each float category to be used in predictions.

GROUP COMPARISONS

To combine data across species, we first generated a mean egg angle or float height per species per "day" (based on days until hatching). Using mean values reduced the influence of measuring the same nest more than once without restricting our coverage of the incubation period. Because incubation duration varies widely within and among species due to factors such as egg size, breeding locale, and parental behavior (Nol 1986, Schamel and Tracy 1987), we standardized incubation duration by expressing embryo age as proportion of the incubation period completed. This allowed us to compare relative differences in the rate of embryonic development between groups of species that had different life history characteristics. We also attempted to standardize float height scores across species by dividing the float height of a given egg by that species' average egg dimensions (i.e., length + width/2;

species values reported by Schönwetter [1967], Schekkerman et al. [2004]). We found that this did not improve model fit, and consequently report only the results for the untransformed float heights.

We developed and compared regression models for species grouped by taxonomy (Scolopacidae vs. Charadriidae; after Thomas et al. [2004]), by whether both adults share incubation or only one adult incubates the eggs (hereafter "biparental" vs. "uniparental" species; after Larsen et al. [1996]), and by adult body mass (large vs. small). We categorized "small" shorebirds as <100 g and "large" shorebirds as ≥ 100 g because the mean mass of shorebirds is roughly 99 g (Larsen et al. 1996). We tested for significant differences among these regression models by determining whether the 95% confidence intervals of the regression coefficients overlapped.

PREDICTIVE ABILITY AND ERROR

We estimated the predictive ability of our regression equations by subtracting the actual embryo age from the predicted age for each nest on a given day. We generated the predicted days until hatching for each nest by inserting the transformed egg angle or float height data into the appropriate regression models. Because the regression equations represent an average of all data, there were a few instances where the predicted hatching date for nests were past hatching (i.e., days until hatching were -1). This occurred rarely and only when eggs floated unusually high. In these cases, we set the days until hatching as 0. For the categorical data, we assigned the predicted age of an egg in a given category as the average of all known-age eggs that were classified in that same category. Then, as with the continuous data, we subtracted the actual age from the predicted age to generate estimates of bias.

For both the continuous and categorical data sets, we generated the absolute mean deviation $\pm$ SE as a descriptive statistic for the error. The absolute value reflects the amount of uncertainty (i.e., both under- and overestimation) researchers will have to consider when deciding how confident they should be in using flotation scores. Similarly to (van Paassen et al. 1984), we report 90th percentiles of error to gauge the accuracy of our samples in age prediction. If our samples are representative of the total

TABLE 1. Sample size and coefficients for linear regressions (r^2) of embryo age versus egg angle (early incubation: age $= a + b$*logit of proportional egg angle) and multiple regressions (R^2) of embryo age versus egg angle and float height (late incubation: age $= a + b$*float height in mm $+ c$*egg angle in °) for 21 shorebird species for which continuous data were collected. Embryo age is measured as "days until hatching," which refers to the absolute number of days for single species analyses, and the proportion of the incubation period for all species combined.

Species	Early incubation (sinking eggs)				Late incubation (floating eggs)				
	n^a	r^2	a	b	n^a	R^2	a	b	c
Black-bellied Plover (*Pluvialis squatarola*)	15	0.76	−20.47	1.43	17	0.66	−4.60	2.25	−0.13
American Golden-Plover (*Pluvialis dominica*)	38	0.75	−20.17	1.41	51	0.69	−10.61	1.42	−0.04
Pacific Golden-Plover (*Pluvialis fulva*)[b]	11	0.79	−20.60	1.17	1	−	−	−	−
Common Ringed Plover (*Charadrius hiaticula*)[b]	14	0.51	−20.44	0.83	5	−	−	−	−
Piping Plover (*Charadrius melodus circumcinctus*)[b]	67	0.71	−22.47	1.13	0	−	−	−	−
Willet (*Tringa semipalmata inornatus*)[b]	44	0.72	−19.26	1.36	6	−	−	−	−
Marbled Godwit (*Limosa fedoa fedoa*)[b]	19	0.68	−18.78	1.13	2	−	−	−	−
Ruddy Turnstone (*Arenaria interpres interpres*)	14	0.73	−16.17	1.25	27	0.71	−16.45	3.36	0.03
Sanderling (*Calidris alba*)	17	0.80	−18.18	0.79	12	0.87	−15.69	3.64	0.01
Semipalmated Sandpiper (*Calidris pusilla*)	69	0.59	−16.50	0.84	187	0.63	−5.22	1.47	−0.08
Western Sandpiper (*Calidris mauri*)	24	0.77	−17.27	0.92	23	0.81	8.31	1.70	−0.27
Little Stint (*Calidris minuta*)	50	0.49	−18.29	0.74	52	0.68	−14.22	2.39	[c]
Temminck's Stint (*Calidris temminckii*)	42	0.59	−16.42	0.84	10	0.16	16.50	−31.50	−0.36
Pectoral Sandpiper (*Calidris melanotos*)	57	0.44	−17.47	0.82	92	0.41	−7.29	1.23	−0.06
Dunlin (*Calidris alpina*)	141	0.66	−17.50	0.88	45	0.56	0.28	1.32	−0.15
Curlew Sandpiper (*Calidris ferruginea*)[b]	32	0.42	−15.77	1.06	6	−	−	−	−
Stilt Sandpiper (*Calidris himantopus*)	10	0.50	−16.15	0.55	13	0.75	−6.16	1.19	−0.07
Buff-breasted Sandpiper (*Tryngites subruficollis*)	14	0.69	−19.96	1.68	32	0.80	−7.87	2.02	−0.08
Long-billed Dowitcher (*Limnodromus scolopaceus*)	36	0.61	−17.15	1.44	22	0.53	−4.66	1.06	−0.08
Red-necked Phalarope (*Phalaropus lobatus*)	76	0.59	−16.61	1.08	44	0.50	−12.99	2.51	0.02
Red Phalarope (*Phalaropus fulicaria*)	53	0.36	−15.29	0.73	54	0.56	−3.03	1.41	−0.10
All species	265	0.70	0.21	0.05	214	0.65	0.79	0.07	0.00

[a] For single species analyses, n equals the number of float values across all nests and days. A float value for each nest on a given day was obtained by calculating an average score for all eggs floated. All eggs in a nest, however, could be floated and scored on multiple occasions. For the "all species" group, n is the number of float values after generating a mean value for each day (day until hatching) for each species.

[b] Equations were not developed for these species during late incubation because of inadequate sample sizes.

[c] Equation for this species included only float height data, as egg angle information was not recorded.

population, researchers can expect 90% of their nests to be aged with error less than or equal to the reported values. For categorical data, we generated separate estimates of error for each of the five float categories.

For figures depicting regressions for individual species, we placed days until hatching on the *x*-axis for ease of use, even though the regression equations were calculated with embryo development as the dependent variable. Be-

TABLE 2.   Error statistics associated with aging eggs by floating them during early incubation for 21 shorebird species. Estimates of prediction error for days until hatching are for linear regressions of embryo age versus the angle an egg floated in water (logit-transformed).

Species	n^a	Range of error (days)[b]	Absolute mean deviation ± SE (days)	90th percentile of absolute error (days)
Black-bellied Plover	15	−2, 4	1.2 ± 0.3	2.0
American Golden-Plover	38	−5, 3	1.5 ± 0.2	2.6
Pacific Golden-Plover	11	−3, 2	1.2 ± 0.2	1.7
Common Ringed Plover	14	−4, 3	1.9 ± 0.2	2.7
Piping Plover	67	−4, 5	1.6 ± 0.1	3.4
Willet	44	−8, 6	2.3 ± 0.3	5.4
Marbled Godwit	19	−6, 4	2.3 ± 0.4	3.7
Ruddy Turnstone	14	−4, 3	1.4 ± 0.3	2.4
Sanderling	17	−2, 2	0.9 ± 0.1	1.5
Semipalmated Sandpiper	141	−7, 4	1.2 ± 0.1	2.5
Western Sandpiper	24	−2, 2	1.1 ± 0.1	1.7
Little Stint	50	−6, 5	1.5 ± 0.2	3.1
Temminck's Stint	42	−6, 3	1.4 ± 0.2	3.0
Pectoral Sandpiper	57	−7, 6	1.6 ± 0.2	3.7
Dunlin	141	−4, 3	1.2 ± 0.1	2.4
Curlew Sandpiper	32	−5, 4	1.8 ± 1.5	3.8
Stilt Sandpiper	10	−2, 3	1.3 ± 0.3	2.5
Buff-breasted Sandpiper	14	−2, 4	1.2 ± 0.3	2.0
Long-billed Dowitcher	36	−3, 6	1.3 ± 0.2	3.1
Red-necked Phalarope	76	−5, 4	1.9 ± 0.1	3.8
Red Phalarope	53	−5, 5	1.7 ± 0.2	3.5
All species[c]	265	−0.25, 0.26	0.07 ± 0.00	0.15

[a] For single species analyses, n is the number of float values across all nests and days. A float value for each nest was obtained on a given day by calculating an average score for all eggs floated. All eggs in a nest, however, could be floated and scored on multiple occasions. For the "all species" group, n is the number of float values after generating a mean value for each day (day until hatching) for each species.

[b] A negative value indicates an underestimate of age.

[c] The unit of error for the "all species" group is "proportion of the incubation period."

cause multiple regression equations are difficult to display graphically, we illustrate only the relationship between hatching date and float height (i.e., egg angle is not used). Both parameters were used, however, in the equations (Table 1), because doing so increased the predictive power of the equations in seven of 14 species that were analyzed using both methods. For all figures, the scale of the x-axis corresponds to the maximum incubation period for a given species, based on mean literature values (Poole et al. 2003) and the range of our data.

SPSS 10.7 (SPSS 1999) was used for all analyses. Results are reported as $\bar{x}$ ± SE, and P-values < 0.05 were considered significant, unless otherwise noted.

RESULTS

INDIVIDUAL SPECIES: CONTINUOUS DATA

Early incubation. Linear regressions describing the relationship between embryo development

and logit-transformed egg angle for nests in early incubation were generated for 21 species. Regression coefficients (r^2) were ≥0.80 for one species, between 0.60 and 0.79 for 11 species, and below 0.60 for the remaining nine species (Table 1). Of the 21 species, three had 90th percentile error values within ±2 days, and all other species had values of ±2–4 days, except the Willet (*Tringa semipalmata*; ±5.4 days; Table 2). When all species were analyzed together, the 90th percentile of the predictive error was equal to 15% of the incubation period (i.e., within three days of the actual nest age 90% of the time if a species had a 20-day incubation period; Table 2).

Late incubation. Multiple regression analyses relating embryo development to egg angle and float height for nests in late incubation were generated for 14 species (Fig. 3). For one additional species (Little Stint [*Calidris minuta*]), we used linear rather than multiple regression to relate embryo development to
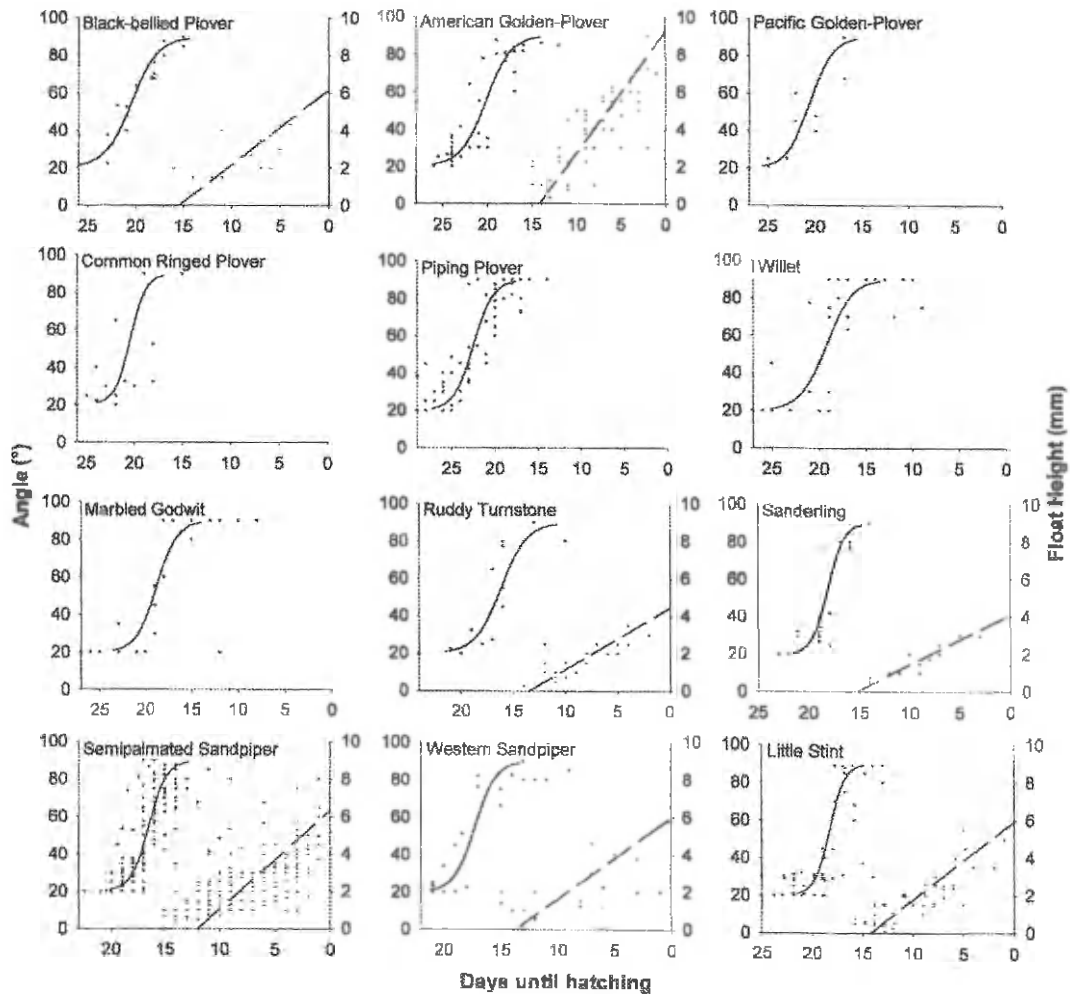
FIGURE 3.   Linear regressions depicting the relationship between (1) days to hatching and logit-transformed proportional egg angle for nests in early incubation (solid lines), and (2) days to hatching and float height for nests in late incubation (dashed lines). See Figure 1 for study area locations and Table 1 for regression equations for each species.

float height as egg angles were not collected for this species during late incubation. R^2 values were ≥0.80 for three species, between 0.60 and 0.79 for six species, and below 0.60 for the remaining six (Table 1). Of the 15 species, 10 had 90th percentile error values of ±2–4 days, and the remaining five species exceeded ±4 days (up to 6.6 days; Table 3). When all species were analyzed together, the 90th percentile of the predictive error was equal to 17% of the incubation period (i.e., within 3.4 days of the actual age 90% of the time if a species had a 20-day incubation period; Table 3).

INDIVIDUAL SPECIES: CATEGORICAL DATA

Of the three species for which categorical data were collected, all showed a strong positive relationship between float category and days to hatching (Fig. 4). Of the three species and five float stages, the 90th percentile of error for all predictions fell within ±2 days of the true age for four species and category combinations (27%, $n = 15$; Table 4). All but two of the remaining species and category combinations had 90% of their predictions within ±4 days of the true age. There was a significant difference
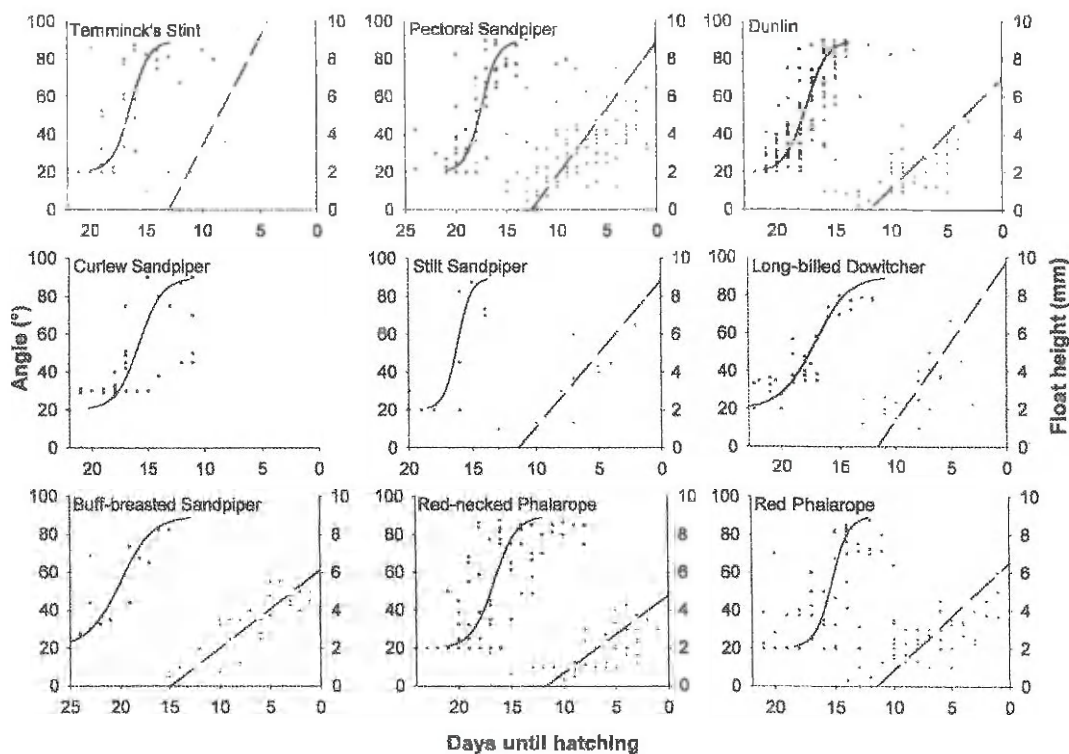
FIGURE 3. Continued.

among the five categories in the accuracy of our estimates ($\chi^2_4 = 16.0$, $P = 0.003$), with the error lowest in float categories 2 and 3, and highest in category 5. Category 5 likely had higher error because it covered the largest portion of the incubation period. When all species were analyzed together, the 90th percentile of the predictive error was equal to 20% of the incubation period (i.e., within 4 days of the actual age 90% of the time if a species had a 20-day incubation period; Table 4).

GROUP COMPARISONS

There was overlap between the confidence intervals of linear (i.e., early incubation) or multiple (i.e., late incubation) regression parameters for "large" and "small" shorebirds and species belonging to the Scolopacidae and Charadriidae families, indicating no significant differences between these groups. However, we found that the slope of the linear regression of embryo age versus the logit-transformed egg angles was steeper, and the multiple regression

float height coefficient of embryo age versus float height and egg angle was higher, for uniparental versus biparental species (angle coefficient: uniparental $= 0.07 \pm 0.01$; biparental $= 0.05 \pm 0.00$; slope coefficient: uniparental $= 0.10 \pm 0.01$; biparental $= 0.06 \pm 0.01$). After standardizing for incubation duration, these results suggest that both egg angle and float height change less rapidly with embryo age in uniparental versus biparental species. Despite these differences in the models, regression equations specific to uniparental and biparental species reduced the 90th percentiles of prediction error by a maximum of 2% of the incubation period, or about 0.4 days.

FACTORS AFFECTING HATCHING DATE ESTIMATION

Estimates of hatching date are affected by factors that increase measurement error or increase the variation in embryo development. In this study, measurement error was likely increased by collating data from different

TABLE 3. Error statistics associated with aging eggs by floating them during late incubation for 15 shorebird species. Estimates of prediction error for days to hatching are for multiple regressions of embryo age versus the height and angle an egg floated.

Species	n^a	Range of error (days)[b]	Absolute mean deviation ± SE (days)	90th percentile of absolute error (days)
Black-bellied Plover	17	−5, 6	1.9 ± 0.4	4.3
American Golden-Plover	51	−8, 4	1.8 ± 0.2	3.9
Ruddy Turnstone	27	−8, 5	1.7 ± 0.3	3.2
Sanderling	12	−3, 2	1.1 ± 0.2	2.1
Semipalmated Sandpiper	187	−7, 6	1.9 ± 0.1	3.8
Western Sandpiper	23	−3, 4	1.6 ± 0.2	3.0
Little Stint[c]	52	−6, 4	1.7 ± 0.2	3.3
Temminck's Stint	10	−4, 5	2.9 ± 0.5	4.2
Pectoral Sandpiper	92	−8, 9	2.4 ± 0.2	4.6
Dunlin	45	−5, 5	1.7 ± 0.2	3.4
Stilt Sandpiper	13	−2, 3	1.2 ± 0.3	2.4
Buff-breasted Sandpiper	32	−4, 4	1.7 ± 0.2	2.8
Long-billed Dowitcher	22	−5, 3	1.5 ± 0.3	3.1
Red-necked Phalarope	44	−6, 9	2.4 ± 0.3	4.5
Red Phalarope	54	−9, 10	3.8 ± 0.3	6.6
All species[d,e]	214	−0.28, 0.25	0.08 ± 0.00	0.17

[a] For single species analyses, n is the number of float values across all nests and days. A float value for each nest on a given day was obtained by calculating an average score for all eggs floated. All eggs in a nest, however, could be floated and scored on multiple occasions. For the "all species" group, n is the number of float values after generating a mean value for each day (day until hatching) for each species.

[b] A negative value indicates an underestimate of age.

[c] The equation for this species included only float height data as egg angle information was not recorded.

[d] The unit of error for the "all species" group is "proportion of the incubation period."

[e] In addition to the 15 species listed in the table, the "all species" group includes data from six species for which sample sizes were too small to generate individual species regression equations (Common Ringed Plover, Curlew Sandpiper, Marbled Godwit, Pacific Golden-Plover, Piping Plover, and Willet; see Table 1 and the Appendix [available online at <http://www.wcs.org/media/file/Liebezeitetal2007_Appendix.pdf>] for sample sizes).

locations, as each location had different observers and associated subtle differences in how eggs were floated. To assess this influence, we compared prediction error values for species sampled at a single site and species sampled at multiple sites. During early incubation, we did not see an increase in measurement error with the number of sites sampled (mean 90th percentile error values weighted by sample size were 3.5 vs. 2.9 for species sampled at single vs. multiple sites, respectively; Table 2, Appendix). However, in late incubation the mean 90th percentile error value (weighted by sample size) for prediction error was lower for species sampled at a single site (3.1) compared to that of species sampled at five or more sites (4.3; Table 3, Appendix). Some of this error may be attributed to lower sample sizes at the multiple sites ($\bar{x} \approx 12$ nests per species per site from multiple sites vs. ~30 nests per species at single sites). No such comparison is possible for the categorical data because all species were sampled at a single site.

To indirectly evaluate the effect of interannual variation in environmental conditions, we conducted an analysis to determine how the number of years that data were collected for a species affected our error estimates. The average 90th percentile error value for species sampled in multiple years at a single site was 3.1 for early incubation and 2.9 for late incubation. Because there was only one species sampled at a single year and site, we could not generate any values to directly compare these numbers. However, these two values are lower than the "all species" 90th percentile errors of 3.5 and 3.8 days for the early and late incubation periods, respectively (generated using the "all species" proportion errors of 15% and 17%, and assuming a mean incubation length of 23.7 days for species sampled during early incubation [i.e., sinking eggs] and 22.5 days

TABLE 4. Error statistics associated with aging eggs by assigning them to five float categories for three species for which categorical data were collected. Estimates of prediction error for days to hatching were generated by comparing the predicted age of an embryo in a given float category (calculated as the average of all known-age nests that were classified in that category) with the true age of the embryo based on nest initiation or hatching. See Figure 2 for illustrations of an egg's position during each float category.

Species[a]	Float category	n[b]	Range of error (days)[c]	Absolute mean deviation $\pm$ SE (days)	90th percentile of absolute error (days)
Black Oystercatcher	1	7	−2.0, 4.0	1.9 ± 0.5	2.8
(*Haematopus bachmani*)	2	10	−4.0, 3.0	1.6 ± 0.5	3.1
	3	9	−4.0, 2.0	1.8 ± 0.4	3.2
	4	2	−1.0, 1.0	1.0 ± 0.0	1.0
	5	10	−1.5, 2.5	1.1 ± 0.2	1.5
	All	38	−4.0, 4.0	1.5 ± 0.2	3.0
Black-necked Stilt	1	9	−1.0, 1.0	0.2 ± 0.2	1.0
(*Himantopus mexicanus*)[d]	2	6	−2.0, 4.0	1.5 ± 0.6	3.0
	3	4	−3.0, 2.0	1.5 ± 0.8	2.7
	4	3	−2.5, 1.5	1.8 ± 0.4	2.3
	5	—	—	—	—
	All	22	−3.0, 4.0	1.0 ± 0.3	2.5
American Avocet	1	42	−6.0, 2.0	0.8 ± 0.2	2.0
(*Recurvirostra americana*)	2	58	−4.5, 6.5	1.5 ± 0.2	4.5
	3	37	−6.0, 3.0	1.5 ± 0.2	3.0
	4	18	−9.5, 5.5	2.5 ± 0.5	4.8
	5	5	−3.0, 3.0	1.8 ± 0.6	3.0
	All	160	−9.5, 6.5	1.4 ± 0.1	3.1
All species	1	58	−0.20, 0.19	0.08 ± 0.01	0.15
	2	74	−0.25, 0.29	0.07 ± 0.01	0.20
	3	50	−0.38, 0.20	0.11 ± 0.01	0.20
	4	23	−0.30, 0.24	0.11 ± 0.02	0.19
	5	15	−0.10, 0.11	0.04 ± 0.01	0.09
	All	220	−0.38, 0.29	0.08 ± 0.00	0.20

[a] Data are listed as number of days for each species, and proportion of the incubation period for all species combined.

[b] For single species analyses, n is the number of float values across all nests and days. A float value for each nest on a given day was obtained by calculating an average score for all eggs floated. All eggs in a nest, however, could be floated and scored on multiple occasions. For the multispecies analyses, n is an average of the average float values for each species for each proportion of the incubation period.

[c] A negative value indicates an underestimate of age.

[d] There were no data available for Black-necked Stilt, category five.

for species sampled during late incubation [i.e., floating eggs]). This suggests that variation in environmental conditions among years has little effect on estimates of embryo age.

We also investigated how the presence of subspecies affected measurement error. We sampled four subspecies of Dunlin (*Calidris alpina*) and their 90th percentile error value was similar to that of other species with only a single race (early incubation: 2.4 versus an average of 2.9 for 20 other species; late incubation: 3.4 versus an average of 3.7 for 14 other species). This suggests that potential life history differences (e.g., incubation duration) among the four races of Dunlin did not increase the error associated with estimating hatching date.

DISCUSSION

Using continuous and categorical egg angle and float height data, we created species-specific flotation relationships that allowed us to predict days until hatching for early and late stages of incubation for 24 species of shorebirds. These relationships provided reasonable predictive power, with the most accurate predictions from continuous data for early incubation, followed by continuous data for late incubation, and finally, categorical data throughout incubation. Other studies have also found that egg angle tends to be more reliable at predicting hatching date during early compared to late incubation (van Paassen et al. 1984). This greater accuracy
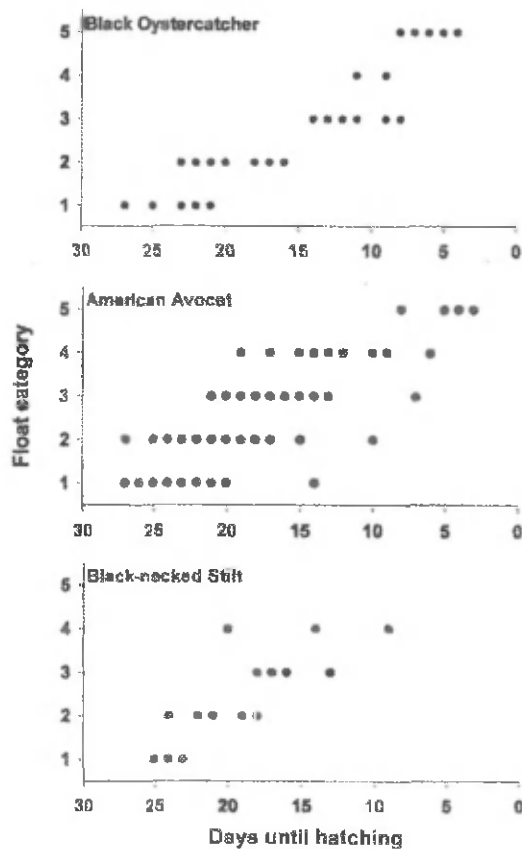
FIGURE 4.   Relationship between days to hatching and the combined egg angle and float height categories for three shorebird species. See Figure 1 for study area locations and Figure 2 for illustration of the five float categories.

may be due to rapid changes in the angle of the egg that occur early in incubation. Also, accurate float data can be collected more easily at this time because the egg touches the bottom of the float container and thus does not move around during measurement.

We also showed that taxonomy (Charadriidae versus Scolopacidae) and body mass of the shorebird (small versus large) had little effect on the relationship between hatching date and egg angle or float height. However, we did find that egg angle and float height changed more rapidly for species with biparental incubation compared to species with uniparental incubation after controlling for differences in incubation duration. This observation makes intuitive sense, since biparental incubation typically means that eggs are incubated more

per unit time (Larsen et al. 1996). Despite this difference, there was little benefit in applying separate regression models in terms of prediction accuracy. These results allowed us to generate a standardized equation to predict hatching date from egg angle and float height measurements that can be applied to almost any shorebird species. As an aid to predicting hatching date for shorebird species not included in our single-species analyses, an interactive version of Figure 2 is available at < http:// www2.dmu.dk/1_Viden/2_Miljoe-tilstand/3_ natur/biobasismanual.asp >. The availability of these equations is timely since the need to determine the incubation age of embryos will likely increase as researchers begin including embryo age (or "nest age") as a covariate in nest survivorship models (Dinsmore et al. 2002, Jehle et al. 2004, Nur et al. 2004).

INDIVIDUAL SPECIES: CONTINUOUS AND CATEGORICAL DATA

There were several advantages to using both linear and multiple regression to analyze the continuous egg angle and float height data. First, the approach allowed us to predict egg angles and float heights for periods of time when no raw data were available. This is in contrast to earlier studies that classified flotation data into categories or provided a scatter plot of egg angle and float height relative to embryo development (sometimes with confidence intervals around points with more than one observation; Dunn et al. 1979, Custer et al. 1992, Brua and Machin 2000). Second, the approach provided an objective method for predicting and estimating error around hatching dates; such statistical assessments of an embryo aging method have seldom been done (but see van Paassen et al. 1984, Sandercock 1998). Finally, this approach allowed us to assess how well regression equations might apply to other species based on the degree of overlap of their respective confidence intervals. We believe this is the first attempt to test for differences among species or species groupings with regard to flotation equations.

The categorical data provided a relatively low level of accuracy for estimating hatching dates compared to the continuous data. This result is not surprising, since categorical data divides a continuous process into subjective classes (Walter and Rusch 1997). However, in temper-

ate and tropical areas, where heat can cause asynchronous embryo development (Grant 1982), estimates of hatching date from categorical data using the flotation method may provide comparable accuracy to estimates using continuous data (JAR, unpubl. data). Categorical data may also be easier to replicate, especially when numerous observers are recording data.

PREDICTIVE POWER

Our hatching date estimates tended to be somewhat less accurate than those of other studies (typically within 2–3 days; van Paassen et al. 1984, Sandercock 1998). The greater accuracy of other studies might be partially explained by the fact that these researchers collected their data independently and studied incubation duration at one study site. As suggested above, we suspect that data collected from multiple study sites, and relatively low sample sizes for some species, likely increased the measurement error in this study. However, our analyses indicate it is unlikely that our error values were inflated by collecting data over many years (i.e., seasonal variation) or across subspecies. Schamel and Tracy (1987) found that both seasonal variation and latitude affected Red Phalarope (*Phalaropus fulicaria*) incubation duration. We did not evaluate whether data collected across large geographical areas affected prediction accuracy. However, the effect of geography is likely small, because information for each study species was collated from a relatively narrow (≤8°) latitudinal range and we used site-specific incubation durations when available.

In addition to sampling variation, species-specific sources of variation may affect prediction accuracy. Nol and Blokpoel (1983) found flotation measurements to be highly variable for Ring-billed Gulls (*Larus delawarensis*), whereas other researchers have found less variability in other study species (Carroll 1988, Walter and Rusch 1997, Brua and Machin 2000). Prediction accuracy may also be influenced by: (1) variability in egg size (Westerskov 1950), (2) behavioral differences in parental care that produce inconsistent incubation durations (Nol and Blokpoel 1983, Feldheim 1997), (3) physiological factors such as differences in egg pore area, shell thickness Ar

and Rahn (1980), and variability in gas conductance (Visser et al. 1995), and (4) environmental factors associated with nest microclimate (Romanoff 1934). The impact of these factors seems negligible, however, given our inability to differentiate flotation patterns based on shorebird body mass or taxonomy.

RECOMMENDATIONS

Researchers wishing to use the flotation method may implement additional measures to overcome some of the inaccuracy inherent in estimating the age of embryos. First, we recommend using information on both egg angle and float height when estimating hatching dates. Together, these measurements quickly indicate whether an egg has recently been laid or is near hatching. Second, eggs from the same nest should be floated multiple times to corroborate findings from the initial measurement. This will ameliorate the effects of inadvertently using misleading data from eggs that were not fertilized or had embryos that failed to develop. Third, we suggest floating eggs when the nest is initially found, as this increases the chances of floating eggs during early incubation when estimates are generally more accurate. Fourth, we advise visiting the nest on a daily basis starting 2–4 days prior to the expected hatching date to check for signs of hatching (i.e., star cracks or pip holes). This conservative approach will assist in confirming nest fates when hatching dates are overestimated. Fifth, when practical, we advise developing site-specific float regression equations for study species rather than using our general float equations; such site-specific equations remove the inaccuracies inherent in our data caused by multiple observers recording data at multiple sites, and account for geographic and seasonal variation. Finally, in situations where it is important to minimize disturbance time (e.g., for colonial birds where predators might take eggs after adults have been flushed), we advise collecting categorical data, as this method is quicker and, as we have shown, can provide a reasonable level of predictive accuracy.

ACKNOWLEDGMENTS

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