Estimating the stage of incubation for nests of greater prairie-chickens using egg flotation: a float curve for grousers

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Introduction

Researchers often require accurate estimates of incubation stage for back-calculating the timing of nest initiation or predicting the date of hatching to capture young, to determine the durations of egg-laying, incubation and the construction of breeding phenologies, and to calculate nest productivity. Estimates of nest age are also critical for assessment of the influence of temporal variation in nest survival, and to model daily nest survival as a function of individual- or time-specific covariates (Dinsmore et al. 2002). For example, the timing of nest losses is often related to nest success and the probability of renesting (Schroeder 1997, Pitman et al. 2006, McNew et al. in press). Egg flotation is one of the most common methods employed for estimating stage of embryo development with egg flotation-development relationships documented for many species of birds (Hays & LeCroy 1971, Dunn et al. 1979, Fisher and Sengel 1991, Custer et al. 1992, Brua & Machin 2000, Liebezeit et al. 2007). To our knowledge, there are no published techniques to estimate stage of incubation for nests of grouse. Field biologists estimating stage of incubation for eggs of grouse nests have often used a modified version of an egg flotation technique developed for captive ring-neck pheasants *Phasianus colchicus* and gray partridges *Perdix perdix* (Westerskov 1950, Martin & Cooke 1987). It is unknown whether egg flotation can be used to accurately assess age of grouse nests under field conditions. As part of a larger study on the breeding ecology of greater prairie-chickens *Tympanuchus cupido;* (hereafter 'prairie-chickens'), McNew et al. (in press) developed a regression model to accurately predict the stage of incubation for nests from egg flotation angles and egg buoyancy.

Methods

Prairie-chickens were captured with walk-in traps and drop-nets at leks during March–May of 2006–2008 at three study sites in eastern Kansas, USA (Schroeder & Braun 1991, Silvy et al. 1990). Females were fitted with radio transmitters and located via triangulation $\geq$4 times/week during the nesting period (April–July), and daily once it was determined from movement patterns that a female was nesting. Once a female had localized in an area for 3 successive days, we located and flushed the bird so that the eggs could be counted and the nest location recorded with a GPS unit. Females with nests were monitored daily from a distance of >100 m. Nest sites were revisited during incubation to assess clutch size and incubation stage.

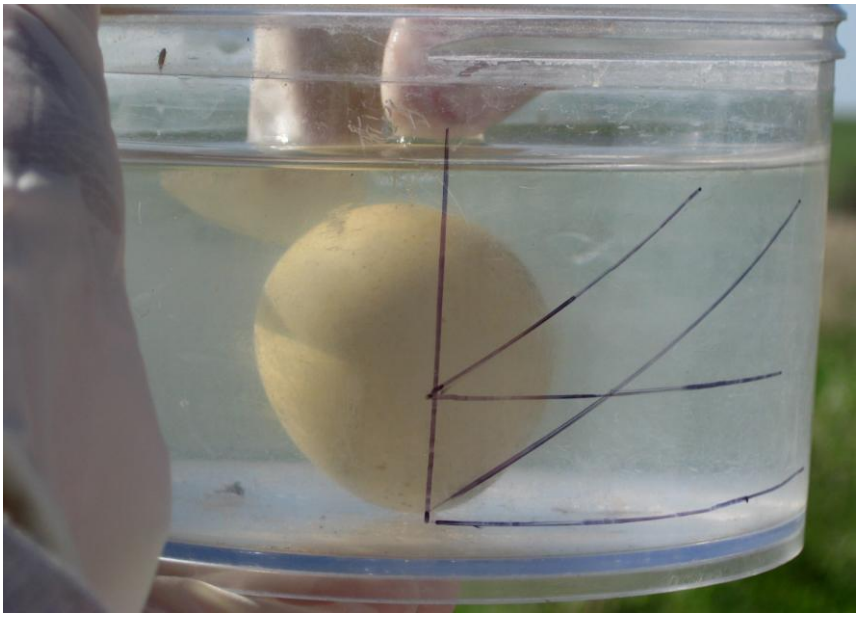

Figure 1. Estimating the float angle or height of a greater prairie-chicken egg. This egg is floating at ~90° and is not yet buoyant.

To evaluate the relationship between egg buoyancy and stage of incubation, we restricted our analysis to nests of known age. Known-age nests included nests discovered during egg-laying and nests that successfully hatched. We collected the clutch from the nestbowl and retreated to a distance of >100 m to float the eggs in a small, clear container of lukewarm water (Figure 1). If an egg touched the bottom of the container, the angle between the bottom of the container and the center axis of the egg was measured. If the eggs floated freely in the water, the distance between the top of the egg and the surface of the water was measured. We used linear regression to evaluate the relationship between float angle and the age of the clutch in days (after Liebezeit et al. 2007). We converted egg angles to proportions (P = angle/90°) before transforming them to the logit scale. Values of 0 and 1 cannot be logit transformed, and we set angles of 0° and 90° to 1° and 89°, respectively, before transformation. Proportional angles were transformed to logits by:

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

We then used linear regression to assess the relationship between the logit-transformed proportional float angles and days of incubation. For nests where eggs floated above the bottom of the cup, linear egression was used to predict the day of incubation from float height; measured as the distance between the surface of the water and the top of the egg (in mm). The predictive ability of regression equations was assessed by subtracting the nest age in days of incubation from the predicted age for each nest on a given day. The absolute mean deviation $\pm$ SE was used as the statistic of model error. Deviations were plotted against embryo age to illustrate model precision. Finally, interspecific error was compared between float curves developed for prairie-chickens and curves developed for Ringed-neck Pheasants by Westerskov (1950). All statistical analyses were conducted using Program SAS (ver. 9.1, SAS Institute Inc., Cary, NC).

Results

We collected float data from 68 clutches of known age. Mean float angle was estimated for eggs of 62 clutches found early in incubation. Average float height between the top of the egg and the water surface was measured for six clutches where eggs were floated above the cup bottom. Logit-transformed egg angle was a significant predictor of embryo age in early incubation (< 14-d old; $r^2 = 0.56$, $P < 0.001$; Figure 2):

$$\textit{Day of Incubation} = 3.25 + 1.19\ (\textit{logit } P).$$

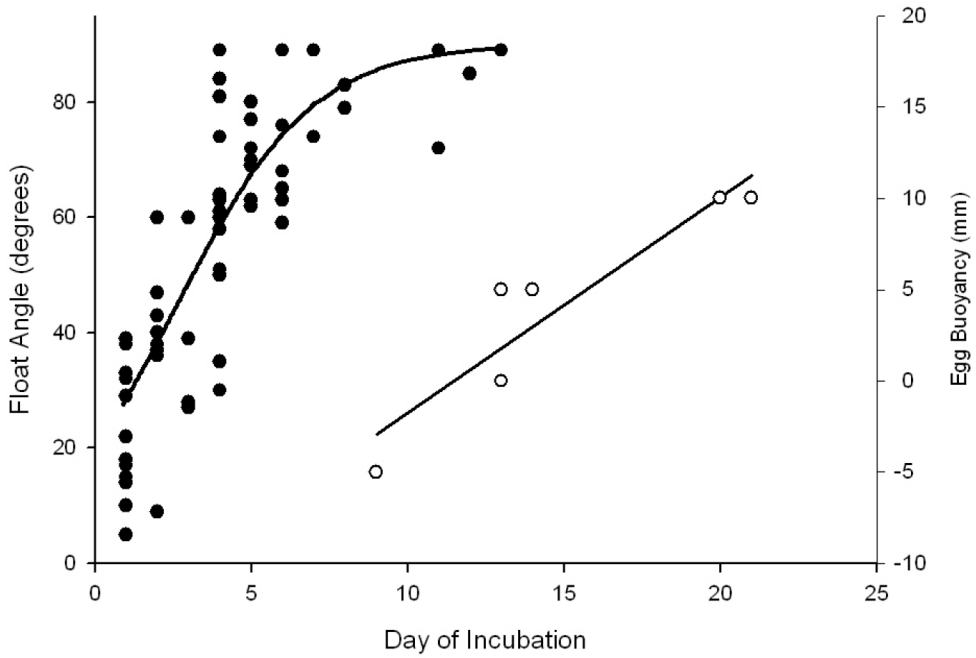

Figure 2. Egg angle (filled circles) and egg buoyancy (open circles) for prairie-chicken nests of known age that were floated during incubation. Egg buoyancy refers to distance from the top of the egg to the surface of the water (in mm).

The mean deviation (± SE) between actual embryo age and predicted embryo age was 0 ± 0.24 days and the 90th percentile of the predicted error for the early-mid incubation period was <9% (± 2 days). Model error was greater for clutches floated during mid-incubation (10-14 days) and was ± 4 days from predicted values. For clutches floated late in incubation (>14 d), linear regression analysis revealed a significant relationship between egg buoyancy and stage of incubation ($r^2 = 0.86$, $P = 0.007$; Figure 2):

Day of Incubation = 12.0 + 0.73 (*Float Height*)

Mean deviation of model predictions for the late incubation period was ± 1 day.

Discussion

Egg floatation was an accurate indicator of stage of incubation for prairie-chicken clutches and had good levels of predictive power. Using data on egg angle and egg buoyancy and regression techniques described by Liebezeit et al. (2007), we found that 90% of prairie-chicken nests could be aged to ±1-2 days if the clutch was floated early or late in incubation (<10 or >14 d). Error was greater (± 4 d) for clutches floated during mid-incubation (10-14 d), due to greater variability in egg buoyancy in a smaller sample of clutches. This study is the first evaluation of egg floatation as a means to estimate the stage of nest incubation for prairie grouse, and extends float curves developed for other species of upland gamebirds (Westerskov 1950). Use of float curves developed for pheasants and partridge consistently overestimated the age of clutches of Greater Prairie-Chickens by an average of ~2 days and the magnitude of the error increased with stage of incubation. We expect that our float curves should provide improved estimates of incubation stage for the nests of other grouse. However, grousers would be prudent to calibrate these float curves by collecting egg flotation data from their own known-age nests to account for potential interspecific variation the effects of egg size on buoyancy and rates of embryonic development.

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