TIME OF DAY OF OVULATION BY THREE DUCK SPECIES IN SUBARCTIC ALASKA[1]

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Abstract. I examined variation in ovulation times of Northern Pintails (*Anas acuta*), American Wigeon (*A. americana*), and Lesser Scaup (*Aythya affinis*) breeding in subarctic Alaskan wetlands. Ovulation times and, by extension, egg-laying times were highly variable in all three species, with ovulations occurring during all hours of the day. Only Lesser Scaup demonstrated a morning peak in ovulations, within a broad range of ovulation times. Lack of a distinct time of day of ovulation suggests that fitness is not related to egg-laying time for these species, particularly at subarctic latitudes with nearly perpetual daylight. Egg-laying interval may have more adaptive significance than egg-laying time for these species. Ovulation intervals were estimated to be approximately 24 hr, which is short relative to the range of intervals documented in birds, despite high energetic and nutritional costs of egg formation in these species. Evidence of approximately 24-hr ovulation intervals, particularly in the absence of a distinct time of day for egg laying, supports hypotheses that a shortened period of egg production in waterfowl may have selective advantage due to reduction in the period of nest exposure to predation, earlier hatch dates, reduced hatch asynchrony, or improved viability of early-laid eggs.

Key words: Anas, Aythya, ducks, egg laying, ovulation times, waterfowl.

The time of day of ovulation and egg laying by birds varies by species (Skutch 1952, Scott 1991, Oppenheimer et al. 1996). Furthermore, considerable variation in egg-laying time among individuals exists within some species (Weatherhead et al. 1991, Schubert and Cooke 1993) but not others (Meijer 1992, Meek and Robertson 1995). Watson et al. (1993) posited that low variability in egg-laying time within a species reflects adaptation to selective pressure, with fitness maximized by egg laying at a particular time. For example, many passerines lay eggs close to sunrise, which has been hypothesized to reduce the likelihood of damage to oviducal eggs when the female is active and to reduce energetic costs to the female incurred by carrying the weight of an oviducal egg (Oppenheimer et al. 1996). Conversely, a lack of a relationship between fitness and time of day of egg laying is implied for species with indistinct ovulation or egg-laying times (Oppenheimer et al. 1996), although other aspects of egg formation, such as egg-laying interval (Astheimer

1985, Wiebe and Martin 1995), may have adaptive significance.

In mid-continent prairies and parklands of North America, most ducks (*Anas, Aythya,* and *Oxyura*) are assumed to lay eggs in the morning (Gloutney et al. 1993) at 24-hr intervals (Alisauskas and Ankney 1992, 1994). I examined variation in ovulation times (and, by extension, egg-laying times) of Northern Pintails (*Anas acuta*), American Wigeon (*A. americana*), and Lesser Scaup (*Aythya affinis*) breeding in subarctic Alaskan wetlands to determine if they fit the paradigm described for ducks in mid-continent regions and to assess the adaptive significance of egg-laying time for ducks breeding at high latitudes. Assessing variation in egg-laying times based on ovulation times requires an assumption of a consistent period between ovulation and laying; this is supported by the finding of Alisauskas and Ankney (1994) that ovulation and laying times were strongly correlated. Estimating ovulation times is advantageous over examining nest contents to estimate laying times, because nest studies may be subject to undetected egg depredation or intraspecific nest parasitism (Watson et al. 1993).

METHODS

Alisauskas and Ankney (1994) presented a method by which time of day of ovulation for a sample of collected, laying females was estimated by regressing mass or nutrient level of the largest ovarian follicle by time of collection. A significant positive regression suggests that individuals lay at a similar time of day and also that intervals are 24 hr. The point at which the regression intersects the dry mass or nutrient level of fully-grown follicles estimates average time of ovulation. If the regression is nonsignificant, either ovulation intervals are not 24 hr or females are asynchronous in ovulation times (Alisauskas and Ankney 1994).

I used methods of Alisauskas and Ankney (1994) to assess time of day of ovulation by Northern Pintails collected on Yukon Delta (61°26′N, 165°27′W) and Yukon Flats (64°24′N, 149°59′W) National Wildlife Refuges (NWR) during 1990 and 1991, and American Wigeon and Lesser Scaup collected on Yukon Flats NWR in 1991. Study areas are in subarctic Alaska and were described by Esler and Grand (1994). Collection times ranged from 08:30 to 21:15 (all times are reported in Alaska standard time). I used only females whose largest ovarian follicle was >4.56, 5.63, and 7.27 g dry mass for Northern Pintails, American Wigeon, and Lesser Scaup, respectively; these included only laying females and those in rapid follicle growth within one laying interval of ovulation (Esler 1994). Largest follicle dry mass was regressed against time
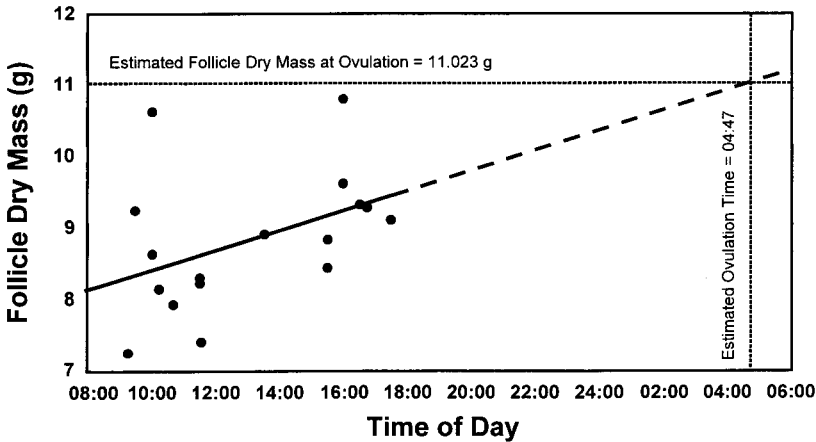
FIGURE 1. Regression of time of day of collection by ovarian follicle dry mass of Lesser Scaup used to estimate average time of ovulation in subarctic Alaska.

of collection for each species. Ovulation times were estimated (± 95% prediction intervals) (Sokal and Rohlf 1981) based on final follicle dry masses (Esler 1994).

To further examine within-species variation in time of day of ovulation, I estimated ovulation times for individual females using their largest follicle dry mass, collection time, and predictive models of ovarian follicle growth (Esler 1994). I used Rayleigh tests of uniformity for circular data to test a null hypothesis of random distribution of ovulation times within each species, with an alternative hypothesis of a unimodal distribution (Fisher 1993).

To determine whether observed patterns of time of day of ovulation could be influenced by laying intervals longer than 24 hr, I calculated the proportion of collected, laying females that had an egg in the oviduct. Scott and Ankney (1979) determined that this figure approximated daily laying rates. Assuming that ovulation, accretion of albumen and shell, and laying requires approximately 24 hr, nearly all individuals should have an egg in the oviduct if egg-laying intervals are 24 hr; if intervals average 36 hr, then approximately 66% should have an egg in the oviduct, and so forth.

RESULTS

Largest follicle dry mass was not linearly related to collection time for Northern Pintails ($r^2 < 0.01$, $n = 49$, $P = 0.68$); this also was true when study sites were considered separately ($r^2 < 0.01$, $P > 0.60$). This relationship also did not exist for American Wigeon ($r^2 = 0.15$, $n = 14$, $P = 0.18$). For Lesser Scaup, follicle dry mass was marginally linearly related to collection time ($r^2 = 0.18$, $n = 17$, $P = 0.09$), and average ovulation time of day was estimated to be 04:47 (Fig. 1), based on a final follicle dry mass of 11.023 g (Esler 1994). However, the data were highly variable (Fig. 1) and 95% prediction intervals around this estimate encompassed all hours of the day.

Estimated ovulation times of individual females were highly variable for all three species, with ovulations occurring at all times of day (Fig. 2). Ovulation times were uniform, rather than unimodal, for Northern Pintails ($P = 0.24$) and American Wigeon ($P = 0.95$). However, analyses for Lesser Scaup suggested a unimodal distribution of ovulation times ($P = 0.02$). Average ovulation time of day for Lesser Scaup was 05:43 (95% confidence intervals = 03:13–08:14), which is comparable to the estimate derived from regression analysis.

For Northern Pintails, 67 of 70 (95.7%) laying females had oviducal eggs. This estimate was 92.9% (13 of 14) for American Wigeon and 94.4% (17 of 18) for Lesser Scaup. These figures suggest that average laying rates are approximately 1 egg day^{-1}. For Ruddy Ducks, with a confirmed 24 hr egg-laying interval, the proportion of laying females with an oviducal egg was 87.0% (Alisauskas and Ankney 1994). Although these estimates are <1.0, that may be a result of the delay, of unknown duration, of ovulation after the previous egg was laid (Alisauskas and Ankney 1994); a small number of birds could be expected to be collected during that period.

DISCUSSION

Ovulation times were highly variable for Northern Pintails, American Wigeon, and Lesser Scaup on my subarctic Alaska study sites. Of these ducks, only Lesser Scaup demonstrated a morning peak in ovulations, although estimates of ovulation times for this species were broadly distributed, including occurrences throughout the day (Fig. 2). Variable ovulation times could result from ovulation intervals > 24 hr or asynchronous ovulation times among individuals (Alisauskas and Ankney 1994). Data from my study suggested that ovulation intervals were approximately 24 hr, thus observed variability in ovulation times of these three species presumably reflects individual variation.
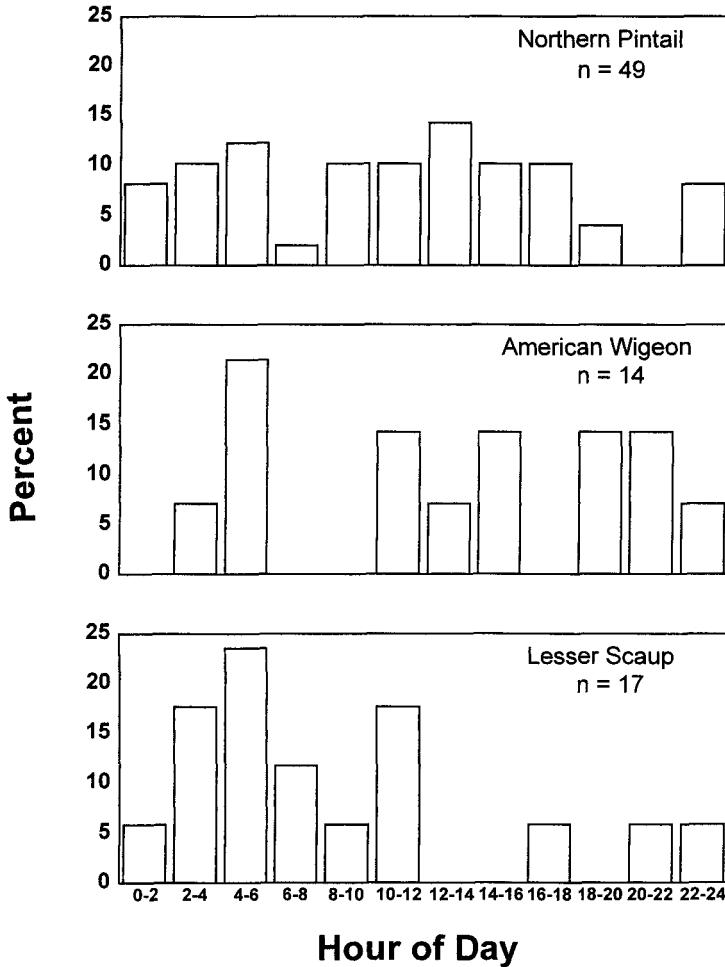
FIGURE 2.   Proportions of estimated ovulation times by 2-hr blocks for three duck species collected in subarctic Alaska.

These results, particularly for Northern Pintails and American Wigeon, contrast with patterns reported for ducks in mid-continent regions, where morning peaks in egg-laying have been described (Gloutney et al. 1993). Asynchrony in ovulation by subarctic ducks may be a result of nearly perpetual daylight at high latitudes, which in turn may result in indistinct times for behavioral events. However, even in mid-continent regions, ovulation and egg-laying times may have unimodal distributions but relatively high variation (Gloutney et al. 1993, Alisauskas and Ankney 1994). Following the logic of Watson et al. (1993) and Oppenheimer et al. (1996) that distinct egg-laying times should evolve if a particular time of day for this event enhances fitness, there is little evidence for strong selection pressure on time of day of ovulation or egg laying in these species, particularly at subarctic latitudes.

Egg-laying intervals vary considerably among species, and adaptive significance of this trait has been described for some birds (Astheimer 1985, Wiebe and Martin 1995). Despite relatively high energetic costs of egg formation compared to other avian taxa (King 1973), *Anas* and *Aythya* ducks ubiquitously lay at 24-hr intervals (Alisauskas and Ankney 1992), which is short relative to the range of intervals documented in birds (Astheimer 1985). Selective advantages of short laying intervals in waterfowl have been hypothesized (Watson et al. 1993). First, short intervals reduce the duration of nest exposure to predation (Clark and Wilson 1981). Second, shortened intervals result in earlier hatch dates, which has been linked to increased fecundity in many studies (Rohwer 1992). Third, short egg-laying intervals require less adjustment of incubation times of individual eggs to facilitate hatch synchrony (Flint et al. 1994). Finally, egg

viability declines over time (Arnold et al. 1987), so reducing the period of egg laying improves hatchability of early-laid eggs. Some or all of these selective pressures likely act on the three duck species in the sites addressed in this study. I conclude that my data support a hypothesis of selection for short ovulation and egg-laying intervals but that there is little adaptive significance to the time of day of these events.

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