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Incubation Temperature Influences Locomotor Performance in Young Wood Ducks (*Aix sponsa*)

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ABSTRACT

Incubation temperature is an important maternal effect in birds that can influence numerous offspring traits. For example, ducklings from eggs incubated at lower temperatures have lower growth rates, protein content, and are in poorer body condition than ducklings from eggs incubated at higher temperatures. Based on these observations, we predicted that incubation temperature would indirectly influence performance through its direct effects on body size. Wood duck (*Aix sponsa*) eggs were incubated at three ecologically relevant temperatures (35, 35.9, 37°C). After hatching, all ducklings were housed under identical conditions and were subjected to aquatic and terrestrial racing trials at 15 and 20 days posthatch (dph). Contrary to our prediction, incubation temperature did not influence most duckling body size parameters at 15 or 20 dph. However, incubation temperature did have a strong influence on locomotor performance independent of body size and body condition. Ducklings hatched from eggs incubated at the lowest temperature had significantly reduced maximum aquatic swim velocity than ducklings from higher temperatures. Maximum terrestrial sprint velocity followed a similar pattern, but did not differ statistically among incubation treatments. To our knowledge, this is the first study to demonstrate that slight changes in incubation temperature can directly affect locomotor performance in avian offspring and thus provide a significant source of phenotypic variation in natural wood duck populations. *J. Exp. Zool. 315:274–279, 2011.* © 2011 Wiley-Liss, Inc.

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Maternal effects are defined as nongenomic female traits that influence offspring phenotype (Mousseau and Fox, '98; Wolf and Wade, 2009). In birds, common maternal effects include nest site selection, hormone and nutrient allocation to eggs, feeding behavior, and incubation behavior (Price, '98). These maternal traits contribute to variation in offspring development, phenotype, and fitness (Bernardo, '96; Price, '98; Badyaev and Uller, 2009).

Incubation temperature can strongly influence offspring phenotype and survivorship of ectothermic species, but has seldom been examined in endotherms (Gutzke and Packard, '87; Burger, '90; Van Damme et al., '92; Elphick and Shine, '98; Booth et al., 2000). Contrary to reptilian embryos that often develop under highly variable thermal conditions, most avian eggs are exposed to a narrower range of nest temperatures (Deeming and Ferguson, '91; Martin et al., 2007). Only recently have studies examined the relationships of slight variations in incubation temperature on the phenotype of birds (Goth and Booth, 2004; Eiby et al., 2008). However, despite the small variation in incubation temperatures typically observed in birds, it can play an important role in determining the phenotype of their

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hatchlings (Hepp et al., 2006; DuRant et al., 2010). For example, wood duck (*Aix sponsa*) ducklings from eggs incubated at lower temperatures hatched with lower body mass and less protein content than ducklings hatched from eggs incubated at higher temperatures (Hepp et al., 2006). In the days following hatching, ducklings hatched from eggs incubated at lower temperatures exhibited significantly lower growth rates and body condition than those hatched from eggs incubated at higher temperatures (DuRant et al., 2010). Reduced body size and poor body composition can have a variety of consequences for young animals, including reductions in locomotor performance, a trait important for survival (Gleeson and Harrison, '88; Miles et al., '95; Braña and Xiang, 2000; Du and Xiang, 2002). Such effects have been documented in reptiles, with eggs incubated at lower temperatures producing smaller individuals that were slower sprinters than those incubated at higher temperatures (Elphick and Shine, '98). Based on these results, we predicted a similar pattern should occur in birds, with incubation temperature having an indirect effect on performance through its influence on body size. Locomotor performance has many fitness implications because it directly influences predator avoidance, prey capture, and foraging efficiency (Pough, '89) and indeed several studies have demonstrated this relationship in reptiles (Garland and Losos, '94; Miles, 2004; Husak, 2006). Young waterfowl are incapable of flight until nearly 3 months of age (Bellrose and Holm, '94), but their locomotor performance on land and water could influence their ability to avoid predators and forage (Bellrose and Holm, '94).

In our experiment, we incubated wood duck eggs at three temperatures that fall within the range of naturally incubated wood duck nests (Hepp et al., 2006). We then raised ducklings for >2 weeks under common garden conditions before quantifying their swimming and sprinting performance. We predicted that ducklings that hatched from eggs incubated at the lowest temperature would be smaller in body size, and as a consequence, would exhibit reduced performance compared with those hatched from higher temperatures.

METHODS

Study Species

The wood duck (*A. sponsa*) is a widely distributed dabbling duck whose breeding range extends across most of the eastern and along the northwestern coast of the United States (Hepp and Bellrose, '95). Wood ducks are cavity nesters and readily use nest boxes which allows eggs to be collected throughout the breeding season. Female wood ducks reach sexual maturity as early as 1 year of age and are capable of producing multiple clutches during a single breeding season (Bellrose and Holm, '94). At our study site, nesting begins in February and continues through most of July. The average clutch size for wood ducks is approximately 12 eggs, with 1 egg laid daily. Nest temperature variation in wood ducks is likely attributable to a variety of variables influenced by parental behavior, including nest initiation date, nest-site selection, incubation constancy, and female body condition. In a southern population of wood ducks natural average incubation temperatures can range from 34.8 to 37.8°C among clutches, resulting in incubation periods ranging from 30 to 37 days (Hepp et al., 2006). Longer incubation periods are associated with lower incubation temperatures.

Egg Collection and Incubation

Eggs were collected from the Department of Energy's Savannah River Site in South Carolina. Nest boxes were located on several wetlands and ponds within the site and have been occupied by wood ducks for over 25 years, producing $>2{,}500$ eggs each season. Nest boxes were checked every 4 days until a nest was initiated, then the active nests were checked daily for new eggs. Upon collection, eggs were individually marked and replaced with wooden eggs to prevent the female from abandoning the nest. All eggs were held at 20°C (physiological zero) for <5 days until they could be placed in an incubator (Grumbach, Asslar, Germany) at Virginia Tech. Eggs were randomly assigned to one of three mean incubation temperature treatments: low (35°C; $n = 14$), medium (35.9°C; $n = 16$), and high (37°C; $n = 15$). Using frequency plots, we verified that lay sequences and number of days eggs were held before being placed within the incubators were evenly dispersed among the three incubation treatment groups. We accounted for clutch effects by only including one egg per nest per incubation treatment. All incubators maintained a relative humidity of 60–65% and were programmed to experience two 3°C temperature reductions from the mean incubation temperature for 75 min per day to simulate a naturally incubated nest in which the female leaves the nest twice a day to forage (Manlove and Hepp, 2000).

Duckling Husbandry

After hatching, all ducklings from the three incubation treatments were housed under identical conditions in an environmental chamber set on a 14L:10D photoperiod and maintained at 28°C. Ducklings were housed in groups of two to three usually according to treatment in $46 \times 32 \times 24.5$ cm plastic cages that were arranged in a rack system. A thermal gradient (28–35°C) was created in each cage by suspending a heat lamp (50 watts) 32.5 cm above each cage. Throughout the experiment, all ducks had constant access to food (ground-up Dumor Chick Starter/Grower 20%) and water. Every morning, ducklings were weighed and tarsus (tarsometatarsus) lengths were measured. Growth rate was calculated by subtracting the hatch mass of a duckling from its mass at 20 days posthatch (dph) then dividing by 20 (number of days since hatched). At the end of the experiment, all ducklings were sacrificed according to Virginia Tech IACUC protocol ♯ 08–067-FIW.

Ducklings used in our study were part of a broader study which focused on the influence of incubation temperature on immunocompetence in young birds (DuRant et al., unpublished data). Although an ideal experiment would be conducted independently from our other immunological studies, our approach allowed us to maximize the use of all animals before euthanasia as required under Virginia Tech animal use policies. Regardless of incubation treatment, all ducklings used in our study were subjected to an identical immune protocol before the performance experiments. Specifically, a blood sample was taken from all ducklings once they reached 6 dph and again at 12 dph. After the initial blood sample was taken at 6 dph, all ducklings were injected with 200 μL of 10% sheep red blood cell which elicits an antibody response commonly used to quantify humoral immunocompetence (Hay and Hudson, '89). This immune assay is commonly used in ecoimmunology because it stimulates antibody production but has no pathology associated with it (Hay and Hudson, '89).

Locomotor Performance

Maximum terrestrial velocity (MTV) of ducklings incubated at the three temperatures was measured when ducklings were 15 and 20 dph. After measuring body mass and tarsus length, individuals were prodded by hand on their tail feathers to initiate running down a 2.3 m linear track. The track was lined with pairs of photocells projecting infrared beams at 10 cm intervals which were interfaced with a laptop computer (Columbus instruments, Columbus, OH). Individuals were raced down the track three consecutive times at both age points. We calculated a duckling's MTV as the fastest 0.5 m segment of the three laps (Holem et al., 2006; Huey and Dunham, '87; Irschick and Losos, '98).

Swimming performance was quantified for the same ducklings immediately following the completion of the terrestrial trials at each age point. Ducklings were raced down a 2.2 m × 0.12 m × 0.18 m plywood swim track filled with water for a total of three consecutive trials. Aquatic trials were videotaped and later analyzed using Adobe Premiere Pro Video editing software (Adobe Systems Inc.). A large metal ruler was attached to the side of the swimming track so that velocity could be calculated during video analysis. The fastest 0.5 m increment was used to calculate an individual's maximum aquatic velocity (MAV).

Statistical Analyses

No significant deviations from normality (Ryan-Joiners) and homoscedasticity (Bartlett's tests) were found; therefore, data were not transformed before statistical analysis. All analyses assessed statistical significance at $\alpha < 0.05$.

We tested for effects of incubation temperature on body size (mass and tarsometatarsus) and growth rate at 15 and 20 dph using an analysis of covariance (ANCOVA; SAS proc glm) with incubation temperature as the main effect and egg mass as a covariate. Egg mass was included in the model because it often has a strong influence on hatchling size (Hepp et al., '87, Galbraith, '88). The interaction between incubation temperature and egg mass was included in all initial models, but was only retained in models where it was statistically significant. The effect of incubation temperature on body condition was tested using an ANCOVA (SAS proc glm) with incubation temperature as the main effect, mass as a dependent variable and tarsus length as a covariate.

MTV and MAV of ducklings recorded at 15 and 20 dph were analyzed separately using two repeated measures analysis of variance (SAS proc mixed). Incubation treatment and age were main effects in both models. Initial models also included tarsus length, mass, and body condition as individual covariates, but these terms were dropped in subsequent models because they did not influence MTV or MAV (in all cases $P > 0.26$). Additionally, regression analyses were used to test for relationships between duckling swim and sprint performance at 15 and 20 dph.

RESULTS

In most cases, incubation temperature did not influence body size, growth rate, or body condition in young wood duck ducklings at 15 dph and 20 dph (Table 1; in all but one case $P > 0.11$), with the exception of duckling tarsus length at 20 dph (temp: $F_{2,44} = 4.50$, $P = 0.017$; egg mass: $F_{1,44} = 10.13$, $P = 0.003$; egg mass × temp: $F_{2,44} = 4.67$, $P = 0.015$). Ducklings from the medium temperature group (35.9°C) were on average 0.38% and 1.7% structurally larger than ducklings from the low (35°C) and high (37°C) temperature treatments, respectively. As expected, there was a significant positive effect of egg mass on mass and tarsus at 15 dph ($F_{1,44} = 4.91$, $P = 0.03$; $F_{1,44} = 9.67$, $P = 0.003$, respectively), and tarsus at 20 dph ($F_{1,44} = 9.22$, $P = 0.004$), but there was less evidence that egg mass influenced growth rate and mass at 20 dph ($F_{1,44} = 2.00$, $P = 0.16$; $F_{1,44} = 2.31$, $P = 0.14$, respectively).

Incubation temperature significantly influenced MAV of ducklings (temp: $F_{2,42} = 4.49$, $P = 0.01$) and this effect was independent of body size or condition (mass: $F_{1,41} = 0.00$, $P = 0.95$; tarsus: $F_{1,41} = 0.03$, $P = 0.87$; body condition: $F_{1,41} = 0.11$, $P = 0.74$). Despite the similar size of ducklings among incubation temperature treatments, ducklings from the lowest temperature group (35°C) were on average 34% slower than ducklings incubated at the highest temperature (37°C) and 18% slower than ducklings from the medium incubation temperature (35.9°C) at 15 dph (Fig. 1A). We did not detect a significant effect of age on aquatic velocity ($F_{1,42} = 0.23$, $P = 0.63$); however, there was a marginally significant incubation temperature × age interaction ($F_{2,42} = 2.97$, $P = 0.06$) which was driven by a trend toward convergence in aquatic velocities among treatments at day 20.

Although velocity patterns were similar in the terrestrial and aquatic environments, incubation temperature did not significantly influence terrestrial velocity (temp: $F_{2,42} = 2.06$, $P = 0.14$; temperature × age interaction dropped because $P = 0.38$). Ducklings incubated at the lowest temperature group (35°C) were on average 31% slower than those incubated at the highest temperature (37°C) and 21% slower than ducklings incubated at the medium temperature (35.9°C) at day 15, and relative convergence in velocities occurred at day 20 (Fig. 1B). Similar to our results on MAV, there was not a significant influence of tarsus length, body size, or body condition on MTV at 15 or 20 dph (in all cases $P > 0.26$). Age

Table 1. Body size and condition for wood duck (*Aix sponsa*) ducklings according to incubation temperature.[1]

Incubation temperature	Mass 15 dph (g)	Mass 20 dph (g)	Tarsus 15 dph (mm)	Tarsus 20 dph (mm)	Body condition 15 dph	Body condition 20 dph	Growth rate (g/day)
35.0°C	95.61 ± 4.26	142.9 ± 6.45	28.14 ± 0.35	31.54 ± 0.34	98.70 ± 3.29	143.7 ± 5.15	5.91 ± 0.32
35.9°C	106.4 ± 3.95	146.45 ± 5.98	28.69 ± 0.32	32.09 ± 0.31	105.1 ± 3.05	143.9 ± 4.85	6.13 ± 0.30
37.0°C	106.2 ± 4.08	147.76 ± 6.18	28.75 ± 0.33	31.43 ± 0.32	104.3 ± 3.16	152.4 ± 5.21	6.16 ± 0.31
Test	$F = 2.14$	$F = 0.15$	$F = 0.97$	$F = 4.50$	$F = 2.37$	$F = 0.06$	$F = 0.17$
Statistic	$P = 0.13$	$P = 0.86$	$P = 0.39$	$P = 0.017$	$P = 0.11$	$P = 0.94$	$P = 0.84$

[1] LS mean values ±1 SE for mass, tarsus length, growth rates, and body condition for Wood duck (*Aix sponsa*) ducklings that hatched from eggs incubated at one of three experimental temperatures (35, 35.9, or 37°C). Values for mass, tarsus length, and growth rate are adjusted for egg mass. LS means for body condition are reported as duckling mass adjusted for tarsus length. Only ducklings who survived until 20 days posthatch were included in analyses. 35°C: $N = 14$, 35.9°C: $N = 16$, 37°C: $N = 15$.

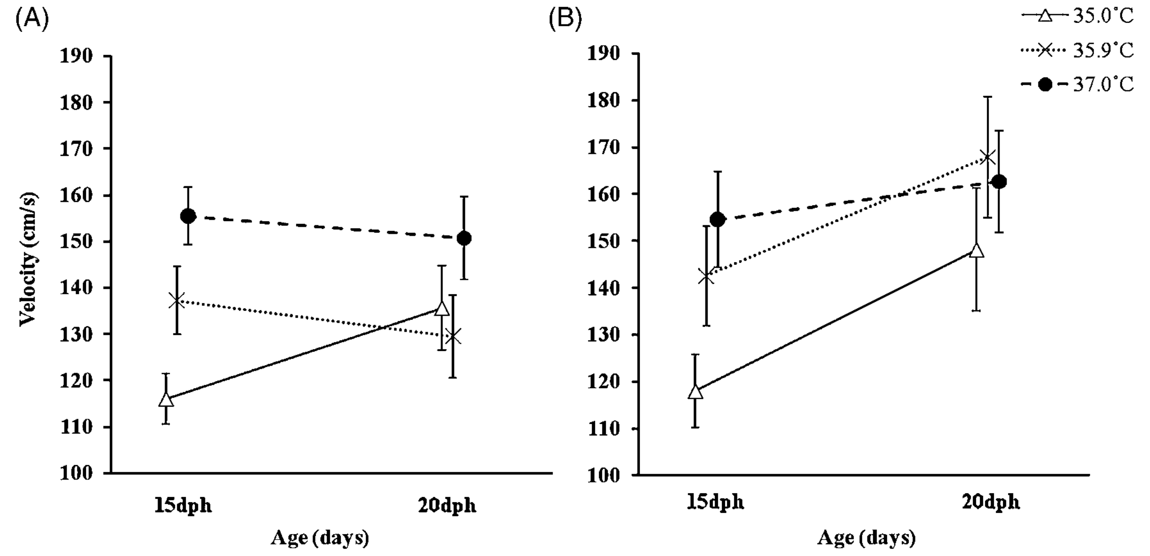

Figure 1. Maximum aquatic (A) and terrestrial (B) velocities of ducklings 15 and 20d after hatching from eggs incubated at one of three experimental temperatures (35.0, 35.9, or 37.0°C). 35.0°C: $N = 14$, 35.9°C: $N = 16$, 37°C: $N = 15$. Error bars are ±1 SE of the mean.

significantly influenced MTV of ducklings ($F_{1,42} = 9.88$, $P = 0.003$) independent of their incubation temperature treatment, with ducklings being on average 15% faster at 20 dph than at 15 dph. We found no significant correlation between swim and sprint speed of ducklings at 15 or 20 dph (in both cases $P > 0.09$).

DISCUSSION

This is the first study to demonstrate that incubation temperature can affect locomotor performance in birds. Similar variation in locomotor performance is most likely present in natural wood duck populations, as our experimental ducklings were incubated at environmentally relevant temperatures that also incorporated cool-down periods that mimicked female recesses for foraging. Our results suggest that small changes in developmental temperatures may have important fitness implications, as locomotor performance in water and on land may be essential for survival (Bellrose and Holm, '94). Because female incubation behavior has such a large influence on nest temperatures, maternal behavior may be a source of significant phenotypic variation among offspring, providing variability upon which selection can act.

Contrary to our prediction, the effect of incubation temperature on performance was not caused by changes in body size or condition. Body size, growth rate, and body condition of ducklings were not impaired in ducklings incubated at the lowest temperature at day 15 or 20. In contrast, DuRant et al. (2010) showed that ducklings incubated at 35°C were 15% smaller 9 dph than those incubated at higher temperatures (35.9 and 37.0°C). Although it is unclear why we did not detect an effect of incubation temperature on body size in our study, the results fortuitously enabled us to directly examine the possible effect of early developmental experiences on locomotion, independent of body size.

Maximum velocity of ducklings was highly dependent on incubation temperature. Ducklings hatched from eggs incubated at 35°C swam and ran 31–34% slower at 15 dph and 10–11% slower at 20 dph than those hatched from eggs incubated at 37°C. Because the effect was independent of body size, our results suggest that incubation temperature may affect other aspects of development related to performance that were not measured in our experiment, such as motor skills, muscle fiber morphology, and/or body composition. In fish, incubation temperature influences muscle morphology and growth (DeAssis et al., 2004; Carey et al., 2009). In addition, several studies have shown that muscle fiber morphology and body composition correlate with locomotor performance measures in various vertebrate species (Gleeson and Harrison, '88; Torrella et al., '98; Odell et al., 2003; Vervust et al., 2008). Based on these lines of evidence, it is plausible that locomotor performance in ducklings was influenced by the negative effects of low incubation temperature on body composition (Hepp et al., 2006), particularly reductions in protein content in skeletal muscle.

Age significantly affected terrestrial performance, with ducklings achieving higher velocities at 20 dph than 15 dph. Although age was not statistically significant in the aquatic setting, a similar pattern toward convergence of velocities at day 20 was exhibited in both performance experiments. Ducklings incubated at higher temperatures did not show much improvement in terrestrial or aquatic performance from day 15 to day 20 compared with those incubated at the lowest temperature. A possible explanation for this observation is that ducklings incubated at warmer temperatures mature muscles important for locomotor performance earlier in life compared with those incubated at lower temperatures. If so, achieving faster velocities earlier in life could be important to duckling survival as most prefledge brood mortality (86–91%) occurs within the first 2 weeks of nest exodus (McGilvrey, '69). Conducting performance trials at earlier ages (<14 dph) may provide a more comprehensive understanding of the influence of incubation temperature on development of locomotor skills in precocial birds.

Although the influence of incubation temperature on neonate phenotype has been well documented in several oviparous reptile species (Gutzke and Packard, '87; Booth et al., 2000; Du and Xiang, 2002), its effects on avian phenotype have long been overlooked. Only recently has the incubation environment, which is largely determined by adult incubation behavior, been studied as an important parental effect in wild birds. Our results support the idea that incubation conditions are an important determinant of avian phenotype as we demonstrated that slight changes in incubation temperature influence locomotor performance of ducklings. The fact that we detected this effect 2 weeks after hatching suggests that young birds do not quickly recuperate from developmental deficits caused by cooler incubation temperatures, a finding consistent with those reported by DuRant et al. (2010). Early effects on hatchling performance can have important survival implications, as many young birds depend on locomotor performance for predator escape. Incubation temperature influenced aquatic performance during a point in ontogeny when most ducklings are relying more heavily on aquatic, rather than terrestrial locomotion (Bellrose and Holm, '94). At this point in their development, it is common for prefledged ducklings to dive or rapidly swim across the surface of the water when threatened (Bellrose and Holm, '94). Such an effect on offspring locomotor performance may put selection pressure on incubating birds to maintain eggs within a very narrow range of optimal temperatures. Thus, adult birds in poor-breeding habitats, poor body condition, or nesting in areas with limited food resources may have difficulty meeting reproductive demands, ultimately presenting incubating parents with a trade-off between maintaining their own body condition vs. the quality of their offspring.

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