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Original Article

Incubation temperature and social context affect the nest exodus of precocial ducklings

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The environments that animals experience during development have important fitness consequences. In birds, parents influence the developmental environment of their offspring through incubation. Subtle changes in incubation temperature affect offspring morphology and physiology, such as growth, immune function, and thermoregulation, yet little is known about how it may affect critical early-life behaviors. Because expression of behavior can be influenced by the social environment, the effect of incubation temperature on behavior may be context-dependent. We investigated whether incubation temperature and social context influence a critical early-life task in wood ducks (*Aix sponsa*). Wood ducks nest in tree cavities and, shortly after hatching, ducklings must jump and climb out of the cavity. Failure to exit the nest is fatal. In 2 experiments, we incubated eggs at different mean temperatures and examined the nest exodus of ducklings individually and in mixed-incubation temperature pairs. When tested individually, ducklings incubated at 35.8 °C and 37.0 °C were ~2.5 times more successful at exiting the nest, and jumped and climbed more often, than those incubated at 35.0 °C. However, in an experiment conducted the following year, we found that social interactions mitigated these effects and there was no difference in nest exodus success when ducklings incubated at 35.0 °C and 36.0 °C were tested together in pairs. This may be because, when in pairs, ducklings incubated at the low-temperature experience social enhancement whereas those incubated at the high temperature maintain similar behaviors. These results advance our understanding of how parental effects influence offspring behaviors and performance within different social contexts.

Key words: ***Aix sponsa*****, early development, offspring behavior, parental effect, social environment, wood duck.**

INTRODUCTION

The environments that animals experience during development can have long-term fitness consequences (Lindström 1999). Parents can influence the early developmental environment of their offspring through various parental effects, such as nutrient or toxicant deposition to the propagule, alteration of the nest environment, grooming, and food provisioning (Bernardo 1996; Mousseau and Fox 1998a). Even small changes during development can have lasting effects on offspring morphology, physiology, behavior, reproductive success, and survival (Southwick 1955; Williams 1994; Mousseau and Fox 1998b; Lindström 1999; DuRant, Hopkins, Hepp, et al. 2013; Dixon et al. 2016).

In birds, the regulation of incubation temperature is one of the most important parental effects influencing offspring development (Webb 1987; Deeming and Ferguson 1991; DuRant, Hopkins, Hepp, et al. 2013; Hepp et al. 2015). Parents must maintain egg temperatures within a narrow range to ensure proper development. However, incubation is energetically costly for the parent and limits the amount of time available for foraging, which is especially demanding for uniparental incubators that do not receive food from their mates (Tinbergen and Williams 2002; Nord and Williams 2015). Thus, parents face trade-offs in time and energy investments between maintaining incubation temperatures and maintaining their own body condition (Monaghan and Nager 1997; Reid et al. 2002). Internal and external factors, such as weather or body mass, can shift this tradeoff and influence how much time and energy parents allocate towards incubation, as well as directly influence incubation temperature (Aldrich and Raveling 1983; Haftorn and Reinertsen 1985; Conway and Martin 2000; Coe et al. 2015). Thus, average incubation temperature can vary among clutches of eggs, among clutches from different breeding attempts of the same individual, and even within one clutch (Reid et al. 2000; Hepp et al. 2006; Boulton and Cassey 2012; Coe et al. 2015; Hope, DuRant, et al. 2018). Even if eggs hatch successfully, variation in incubation temperature may still influence offspring condition. Recent studies show that subtle changes in average incubation temperature can

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influence avian offspring growth rate, immune function, hormone levels, metabolic rate, thermoregulation, and long-term survival (DuRant et al. 2010; DuRant et al. 2011; Nord and Nilsson 2011; DuRant, Hopkins, Hawley, et al. 2012; DuRant, Hopkins, Wilson, et al. 2012; Hepp and Kennamer 2012; DuRant, Hopkins, Carter, et al. 2013; DuRant et al. 2014; Hepp et al. 2015; Berntsen and Bech 2016; Nord and Nilsson 2016).

Incubation temperature can also have considerable effects on behavior and performance metrics that are important for survival. Here, we use "behavior" to describe what an animal does, and "performance" to describe a quantifiable measure of how well (e.g., how quickly) the animal does it (Irschick and Higham 2015). In non-avian reptiles, many studies have shown that incubation temperature influences behavior, including activity level, foraging, aggression, and cognition, as well as locomotor performance (Deeming and Ferguson 1991; van Damme et al. 1992; Flores et al. 1994; Booth 2006; Burgess et al. 2006; Amiel and Shine 2012; Ballen et al. 2015). In birds, evidence is limited to 2 studies. One found that 15- to 20-day-old wood duck ducklings (*Aix sponsa*) incubated at a lower temperature had reduced running and swimming performance compared with those incubated at a higher temperature (Hopkins et al. 2011). More recently, others found that wood duck ducklings incubated at a low temperature displayed more proactive behaviors than those incubated at 2 higher temperatures (Hope, Kennamer, et al. 2018). However, much remains unknown about how incubation temperature influences other aspects of performance or behavior that are critical for early survival in birds. For many species, a large amount of mortality occurs during the transition between life in the nest and independence. Thus, behaviors and performance metrics associated with begging, fledging, and natal dispersal are particularly important because they can have major fitness implications (Godfray 1991; Leonard and Horn 1998; Visser and Verboven 1999; Forero et al. 2002).

Although incubation temperature is a key determinant of offspring phenotype, the post-hatching environmental context ultimately influences which phenotypes are advantageous or disadvantageous and thus, may further influence the expression of alternative phenotypes. The social environment may be a particularly important context for shaping offspring behavior because the fitness consequences of certain behaviors frequently depend on the actions of other individuals (Moore et al. 1997). For example, in altricial species, most broods fledge synchronously despite asynchronous hatching and individual differences in size (Nilsson and Svensson 1993; Bowers et al. 2013; Radersma et al. 2015). This suggests that, although it may be advantageous for each nestling to wait until they are optimally developed before fledging, it may be more advantageous for them to follow the actions of their siblings, so they are not abandoned by their parents. Similarly, an individual's behavior may change in relation to the phenotype or condition of other individuals in the group. For example, great tit (*Parus major*) nestlings beg more when they are paired with a food-limited sibling than when paired with a well-fed control sibling (Carere et al. 2005), suggesting that it is advantageous to beg more when there is increased competition from a hungry nestling. Indeed, this "social enhancement," where the behavior of one individual amplifies the same behavior in others, has been shown in multiple species (Leonard and Horn 1998; Rodríguez-Gironés et al. 2002; Carere et al. 2005), and may play a role in shaping offspring behaviors when individuals with different phenotypes are in the same nest. Because there is evidence that average incubation temperatures vary within avian nests of some species (Beatty 2015; Hope, DuRant, et al. 2018), incubation temperature and social context may interact to influence avian offspring behavior.

To investigate whether incubation temperature and the social environment influence critical early-life behavior and performance, we conducted 2 experiments using wood ducks (*A. sponsa*). In the wild, wood duck ducklings must climb out of the nest cavity and jump down to their mother shortly after hatching. This behavior is crucial because ducklings that do not exit quickly may be left behind by their mother and siblings, and those that fail to exit die in the nest (Bellrose and Holm 1994). Most nests exhibit synchronous hatching and nest exodus (Gottlieb 1963; Hepp and Bellrose 2013). However, in large clutches, substantial developmental asynchrony is common (Kennamer et al. 1990), which may result in single or multiple ducklings that must exit by themselves. In the wild, it is common to find nests in which 1–2 fully hatched ducklings are dead (S. Hope, R. Kennamer, and W. Hopkins, personal observation; nests with >2 dead ducklings occur, but are rare), suggesting that situations where 1–2 ducklings must exit the nest by themselves are common. Further, average incubation temperature varies among eggs within wood duck nests (Hope, DuRant, et al. 2018), suggesting that there are situations in which ducklings incubated at different temperatures must exit the nest singly, as well as together. We incubated eggs at different mean temperatures and tested nest exodus behavior and performance (i.e., speed) of ducklings individually (Individual Experiment) and in mixed-incubation temperature pairs (Pairs Experiment). Because wood duck ducklings incubated at a lower temperature have reduced locomotor performance compared with those incubated at a higher temperature (Hopkins et al. 2011), we predicted that, when tested individually, ducklings incubated at the low temperature would take more time to exit the nest and fewer ducklings would successfully exit the nest box compared with those incubated at the higher temperatures. When tested in pairs, we predicted that ducklings incubated at the higher temperature would more frequently exit the nest box before those incubated at the lower temperature. However, we also hypothesized that social interactions would amplify exodus behavior because, in the wild, it is advantageous for ducklings to leave at the same time as their siblings (Bellrose and Holm 1994). Thus, we predicted that when tested in pairs, ducklings incubated at different temperatures would have similar success rates, and once one duckling exited the nest, the other duckling would attempt to follow. Alternatively, if there was no social enhancement, we expected that our results would be similar to those in the Individual Experiment, and that ducklings incubated at the higher temperature would be more successful at exiting the nest than those incubated at the lower temperature.

MATERIALS AND METHODS

Study species

The wood duck is a common species of waterfowl that nests in tree cavities and nest boxes across the United States (Hepp and Bellrose 2013). Their average clutch size is 12 (Bellrose and Holm 1994), but clutches can reach >40 eggs in some populations due to conspecific brood parasitism (Morse and Wight 1969; Eadie et al. 1998). Recent work has shown that average incubation temperatures vary both among and within nests (Hope, DuRant, et al. 2018), and that consistent differences in temperatures among eggs within nests increase with clutch size, from a difference of 0.5 °C among average egg temperatures in small nests (12 eggs) to a difference of 3.1 °C in large nests (24 eggs; Hope et al., unpublished data). Thus, wood duck broods are normally composed of ducklings that have hatched from eggs that have been incubated at different average temperatures.

Hatching within small clutches is synchronous and usually occurs 6–18 h after the first egg pips (Gottlieb 1963), although eggs in large clutches experience more than 3 d of developmental asynchrony (Kennamer et al. 1990) likely due to a combination of differences in the date eggs were laid and to within-clutch differences in incubation temperatures (Hope, DuRant, et al. 2018). Eggs take, on average, 32 h to hatch after pipping (Bellrose and Holm 1994), but this also varies with incubation temperature (DuRant et al. 2011). Once the first egg pips, the hen begins to vocalize while in the nest and continues to do so for 20–36 h (Gottlieb 1963). Ducklings are precocial and are active within about 7 h after hatching. After the ducklings hatch and when the environment is suitable (e.g., no visible predators), the hen leaves the nest and vocalizes at a fast rate from below (Gottlieb 1963). Ducklings must respond to their mother's call, climb up and out of the nest cavity, and jump down to meet their mother and siblings. Ducklings usually perform this nest exodus within 24 h of hatching (Hepp and Bellrose 2013), but will still perform this behavior until 4 d after hatching (Siegfried 1974). The hen will vocalize beneath the nest until most of her brood has joined her, which usually takes ~5 min (Gottlieb 1963; Siegfried 1974; Bellrose and Holm 1994), but can occasionally take longer (Bellrose and Holm 1994). This is a crucial event because ducklings that cannot exit die in the nest (usually only 1–2 ducklings; S. Hope, R. Kennamer, W. Hopkins, personal observation). Further, because there are many predators that eat ducklings, it is common for a female to flee from a predator with only the ducklings that have already exited (Bellrose and Holm 1994). Thus, those that are too slow at exiting are left behind and have a lower chance of survival without their brood mates and maternal care (Bellrose and Holm 1994). On the other hand, ducklings that exit too quickly before their nest mates may be vulnerable to lurking predators, so exiting simultaneously with nest mates may be the optimal strategy.

Egg collection and incubation

We collected eggs from a population of wood ducks breeding in nest boxes on the Department of Energy's Savannah River Site (SRS) in South Carolina, United States (33.1 °N, 81.3 °W) from 6 March 2015 to 29 March 2015 for the Individual Experiment and 29 February 2016 to 16 March 2016 for the Pairs Experiment. We checked nest boxes daily on a series of 12 ephemeral wetlands, which have nest boxes that have been maintained for >30 years. We marked eggs for lay date, collected up to 10 eggs from each nest, and replaced eggs with wooden eggs to prevent hens from abandoning (Hepp et al. 1987). Eggs were transported at ambient temperature to Virginia Tech, rotated twice daily, and incubated within 10 d (Walls et al. 2011) in Grumbach incubators (model BSS 420, Asslar, Germany). For the Individual Experiment, eggs were incubated at 3 different overall mean temperatures: 35.0, 35.8, and 37.0 °C. We chose these temperatures because they are within the natural range for wood ducks and they have been shown to produce ducklings with different phenotypes in previous experiments (DuRant, Hopkins, Hepp, et al. 2013). For the Pairs Experiment, eggs were incubated at 2 different overall mean temperatures: 35.0 and 36.0 °C. We chose these temperatures because a 1 °C difference in mean temperature is enough to produce different phenotypes, and is also a realistic temperature difference among eggs within natural nests (Hope, DuRant, et al. 2018). Eggs from the same nest and the same lay date were distributed among treatments. Incubators were programmed to reach maximum temperatures that were higher than the mean temperatures (listed above), and had two 75-min cooldown periods (~3 °C decrease in temperature) at 08:15 AM and 06:30 PM to simulate hens leaving the nest for foraging (Manlove and Hepp 2000). This allowed incubators to maintain the overall mean temperatures. The temperatures reported here for each experiment are the average temperatures recorded using *i*Buttons® in the incubators. Due to a minor discrepancy in incubator performance in the second year of the study, the actual temperatures that were recorded (36.0 °C) were slightly higher than what we programmed (35.8 °C). This 0.2 °C discrepancy in mean incubation temperature between the 2 experiments and the fact that they were conducted in 2 different years prevented direct statistical comparisons between experiments, but neither of these factors detracts from our overall conclusions. The average humidity for all incubators was kept between 60% and 65%. Once pipped, eggs were placed in a hatcher with a constant temperature of 36 °C and humidity kept between 72% and 82%. We placed a speaker inside the hatcher that played wood duck hen vocalizations, to mimic auditory cues that ducklings would experience in a nest once pipped, and to stimulate auditory imprinting (Gottlieb 1963).

General husbandry

Once hatched, we recorded the hatch time, and then weighed and color-banded the ducklings. During the Individual Experiment, we checked for hatching at least every 3 h between 08:00 AM and 05:00 PM and during the Pairs Experiment we checked at least every 2 h and videotaped the hatcher while we were not present to record precise time of hatch. We placed newly hatched ducklings together (no more than 12 per cage) under a 50W infrared heat lamp in a covered cage to simulate dark, communal nest conditions. Ducklings stayed in this environment until they were at least 7 h old, but not older than 27 h, and we then performed the nest exodus trial (overall average age ± standard deviation [SD] during trial = 14.8 ± 4.6 h). Although ducklings did not hatch in the nest boxes in which we conducted behavioral trials, we think it is likely that keeping ducklings in these conditions before the trial was sufficient to mimic natural nest conditions. After the trial, we measured tarsus length and ducklings were housed in cages in groups of 2 or 3 to undergo a series of trials for other studies. Differences in hatch success, incubation period, hatch mass, and tarsus length are reported in Table 1. After all studies were complete, ducklings were humanely euthanized and sex was determined by inspecting both external genitalia and internal gonads. All procedures were approved by the Virginia Tech Institutional Animal Care and Use Committee.

Individual experiment

During the Individual Experiment, ducklings were tested individually on their ability to exit the nest box, the speed at which they did so, and their associated behaviors (i.e., latency of first movement, jump, call, and climbing attempt, and the number of jumps and climbs). The trial was conducted in a wooden nest box (20 × 20 × 50 cm) identical to nest boxes in the field, but with one Plexiglas wall which allowed for behavior to be videotaped. Wooden planks surrounded the Plexiglas wall and left only a small opening for a video camera, so that the wall looked dark to the duckling. A light was attached outside and above the nest box exit hole and pointed down into the box to simulate natural daylight and facilitate better video recording. Thus, the only light sources were coming from directly

Table 1

Means (±SD) of hatching success, incubation period, hatch mass, and tarsus length for ducklings incubated at different temperatures in 2 different experiments

	Individual Experiment			Pairs Experiment	
	Incubation temperature treatment (°C)				
Variable	35.0	35.8	37.0	35.0	36.0
Hatch success (%)	48	80	83	62	74
Incubation period (days)	39.5 ± 1.1	36.0 ± 1.0	32.6 ± 0.8	38.5 ± 0.9	35.7 ± 1.0
Hatch mass (g)	28.0 ± 2.7	27.8 ± 2.4	28.9 ± 2.5	27.8 ± 3.2	27.9 ± 3.4
Tarsus length (mm)	19.4 ± 0.7	18.9 ± 0.7	18.6 ± 0.7	19.6 ± 0.9	19.4 ± 0.9

above and outside the exit hole, which mimics natural conditions. Wire mesh was attached below the hole (11.5 × 34.5 cm) to aid the ducklings in climbing, which is common for nest boxes in the field. The nest box was on the ground, and a trough of water was placed below the hole for ducklings to land in once they jumped out.

Each duckling (N = 144 ducklings from 36 different nests) was placed in the box and, outside of the box, we played a recording of a wood duck hen call mixed with duckling calls to simulate natural conditions and motivate the duckling to exit. Both hen call (https://www.youtube.com/watch?v=0nFIIPtm844; accessed 19 December 2018) and duckling call (https://www.youtube.com/watch?v=XhTEk31kzuI; accessed 19 December 2018) MP3s were downloaded from YouTube. The hen call was recorded from a wood duck nest in Smithfield, NC. Portions of each MP3 were mixed together using the program Audacity® version 2.1.2 (Audacity Team 2015). The hen call played in a pattern of 2 min on/2 min off and the duckling call played in a pattern of 30 s on/30 s off for the duration of the trial. The recording was played, at the same volume setting for each trial, from an iPod© (Apple Inc.) on an iHome© (Apple Inc.) speaker placed ~0.5 m away from the nest box. The trial ended when the duckling jumped out of the nest box, or after 30 min. Although Gottlieb (1963) found that all ducklings in 8 natural nests exited within 4 min from when the hen began to vocalize from beneath the nest, and a previous lab-study only gave ducklings 5 min to exit the nest (Siegfried 1974), we chose 30 min as a conservative time limit. In this study, 39% of ducklings did not exit within the 30 min time frame. From the videos, one person (S.F.H.) later recorded the time of the duckling's first movement, jump, call, and climbing attempt, the number of jumps and climbs, and the latency to leave the box.

Pairs experiment

During the Pairs Experiment, ducklings were tested in pairs (N = 54 pairs; 108 ducklings from 31 different nests), with one duckling from each treatment (35 °C and 36 °C). Ducklings that were similar in age (h) were paired (average ± SD difference in age = 3.39 ± 3.44 h, range = 0–15.7 h). We tried to avoid pairs of ducklings that originated from eggs from the same nest, but 1 out of the 54 pairs consisted of ducklings from the same nest because we prioritized similarity in age. Ducklings were individually marked with numbers on their heads using non-toxic white correcting fluid, so they were identifiable in the video recording. The trial was conducted with the same nest box configuration and audio recording as in the Individual Experiment.

The trial ended when both ducklings exited the nest box, or after 30 min. In this study, 46% of ducklings did not exit within the 30 min time frame. From the videos (Supplementary Movie 1), one person (S.G.V.M.) recorded the same behaviors as in the Individual Experiment, along with noting which duckling exited the nest first, and quantifying the number of jumps and climbs that the duckling left behind in the box made before and after the first duckling exited.

Statistical analyses

All analyses were conducted in R version 3.3.1 (R Core Team 2016) and we used the package *lmerTest* (Kuznetsova et al. 2016). For all models, incubation temperature was the categorical independent variable. The age of the duckling at the time of the trial (h), sex, lay date, and body condition (the residuals of body mass vs. tarsus length linear regression) were originally included in all analyses as covariates, but we used backward elimination for insignificant terms and only report significant or marginally significant covariates. We consider $P < 0.05$ as significant, but also report $0.05 < P < 0.10$ as trends. Because ducklings from the same clutch were used, clutch was included as a random effect in each model. Also, for analyses of the Pairs Experiment, the pair (ducklings tested together) was included as a random effect to account for any effect of pairing. We visually inspected graphs of the residuals of our models to ensure they met the assumptions of normality and homoscedasticity. When models did not meet assumptions, we first attempted to transform the data to meet assumptions, and if transformations did not work, we used general linear models with non-normal error distributions.

To determine if incubation temperature affected the proportion of ducklings that were able to exit the nest box in each experiment, we used generalized linear mixed models (*glmer*) with a binomial error distribution. Whether or not the duckling exited the box (binary: yes or no) was the response variable in both models.

Next, to determine if incubation temperature affected the latency for ducklings to exit the nest box, we used linear mixed effects models (*lmer*). All ducklings that exited the nest box on their own were included in these analyses (Individual Experiment: N = 88 ducklings from 33 nests; Pairs Experiment: N = 58 ducklings from 29 nests). The latency to exit (s) was used as the response variable. Latency to exit was log-transformed for the Individual Experiment model to meet the assumptions of normally-distributed and homoscedastic residuals. The data from the Pairs Experiment met model assumptions and did not require transformation.

To further investigate nest exodus performance in the Pairs Experiment, we tested whether incubation temperature influenced which duckling first exited the nest by using a *glmer* with a binomial error distribution. Whether or not the duckling was the first of its pair to exit (binary: yes or no) was the dependent variable. Only pairs in which at least one duckling exited were used in this analysis (N = 37 pairs with ducklings from 29 nests).

To examine whether incubation temperature influenced duckling behavior during the trial, we used principal components analyses (PCA; *princomp*) with correlation matrices for each experiment. For both PCAs, the latency time to first move, jump, call, and climb, the number of jumps per minute and the number of climbs per minute were included. If a duckling did not perform any of these behaviors, they were given a score of 30 min for the latency of that behavior. For both PCAs, scree plots indicated that PC1 explained most of the variation (59% in both experiments), so we used PC1 for each experiment as the dependent variable in the model. The PC1 scores for the Individual Experiment were highly left-skewed, so we transformed them to be right-skewed (multiplied by −1 and added 3) and used a *glmer* with a Gamma distribution. We used a *lmer* for the Pairs Experiment because the data met all assumptions.

Lastly, to investigate whether the second duckling's behavior changed after the first duckling exited, we used 2 models to compare the number of jumps and number of climbs that each duckling took before and after the first duckling exited. Our sample size for these analyses was 37 ducklings from 22 different nests because we did not have before/after behavior data for pairs where neither duckling exited. For both models, the time (categorical: before or after), incubation temperature, and their interaction were the independent variables and duckling ID was a random effect. The first model used the number of jumps as the dependent variable and we used a *lmer* with a log+1 transformation to meet model assumptions. The second model used the number of climbs as the dependent variable and we used a *glmer* with a Gamma distribution because the data were highly right-skewed.

RESULTS

Nest exodus

When ducklings were tested individually (Individual Experiment), a larger proportion of ducklings incubated at the higher temperatures were successful at exiting the nest than those incubated at the lower temperature ($F_{2,\,140} = 12.1$; $P < 0.0001$; Figure 1a). Post hoc analysis (*lsmeans with Tukey adjustment*) revealed that the proportion of successful ducklings incubated at the 2 higher temperatures did not differ significantly ($P = 0.08$), but both had greater success (35.8 °C: 39 out of 60 successful; 37.0 °C: 39 out of 45 successful) than those incubated at the lower temperature (35.0 °C: 10 out of 37 successful; intermediate–low temperature: $P = 0.003$; high–low temperature: $P < 0.0001$). When ducklings were tested in pairs (Pairs Experiment), incubation temperature was not related to exit success ($F_{1,\,103} = 2.0$; $P = 0.17$; Figure 1b). However, the relationship between lay date and exit success was marginally significant ($F_{1,\,103} = 4.4$; $P = 0.053$), where ducklings hatched from eggs laid at a later date tended to be less likely to successfully exit than those laid earlier in the season (effect size = −13.25; *effsize*; Torchiano 2017).

For ducklings that successfully exited, latency to exit the nest box tended to be negatively related to incubation temperature when ducklings were tested individually (Individual Experiment; $F_{2,\,85} = 3.1$; $P = 0.052$; Figure 2a). In pairs, latency to exit was not related to incubation temperature (Pairs Experiment; $F_{1,\,27} = 1.0$; $P = 0.32$; Figure 2b), but it was negatively related to duckling age in hours ($F_{1,\,53} = 5.9$, $P = 0.02$; effect size = −2.13).

Contrary to our predictions, incubation temperature did not affect whether a duckling was the first to exit the nest box in the Pairs Experiment ($F_{1,\,70} = 0.94$; $P = 0.35$; Figure 3).

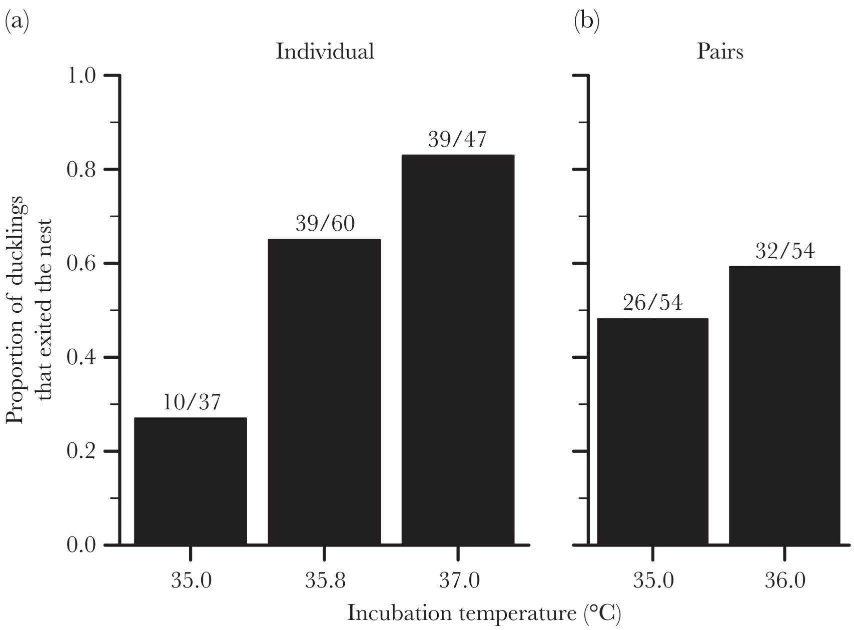

Figure 1
Incubation temperature and social context influence nest exodus success. When tested individually, fewer ducklings that hatched from eggs incubated at the lowest temperature (35.0 °C: $N = 37$ ducklings from 24 nests) successfully exited the nest than those that hatched from eggs incubated at the 2 higher temperatures (35.8 °C: $N = 60$ ducklings from 34 nests; 37.0 °C: $N = 47$ ducklings from 30 nests) (a). When tested in pairs (b; one low [35.0 °C] and one high [36.0 °C] incubated duckling in each pair), incubation temperature did not affect nest exodus success (35.0 °C: $N = 54$ ducklings from 25 nests; 36.0 °C: $N = 54$ ducklings from 27 nests). Numbers indicate the proportion of ducklings that successfully exited the nest box within 30 min, out of the number tested from each incubation temperature.

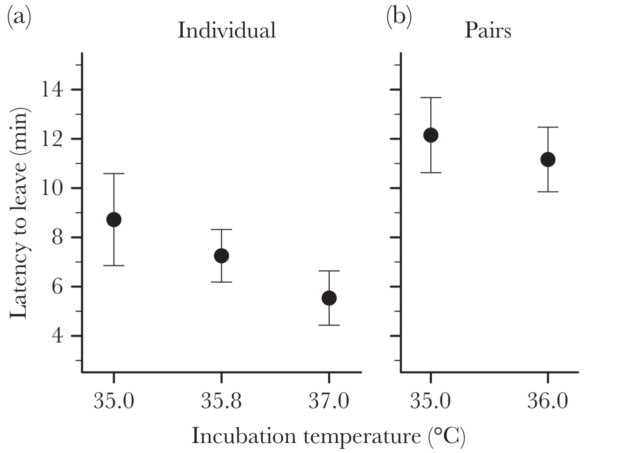

Figure 2
Effect of incubation temperature on the latency to leave the nest box. Latency to exit the nest (min; means ± SE) tended to decrease with incubation temperature when ducklings were tested individually (a; 35.0 °C: N = 10 ducklings from 10 nests; 35.8 °C: N = 39 ducklings from 26 nests; 37.0 °C: N = 39 ducklings from 26 nests), but there was no difference in latency to leave the nest when tested in pairs (b; 35.0 °C: N = 26 ducklings from 20 nests; 36.0 °C: N = 32 ducklings from 19 nests). Only ducklings that successfully exited on their own were included in the analysis.

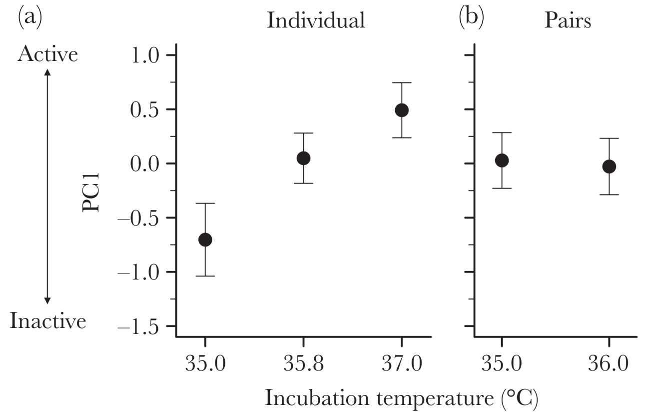

Figure 4
Incubation temperature and social context influence duckling behaviors during exodus from the nest. Ducklings that hatched from eggs incubated at higher temperatures (35.8 °C: N = 60; 37.0 °C: N = 47) were more active in the nest box than those incubated at the lowest temperature (35.0 °C: N = 37) when tested individually (a). Incubation temperature did not affect activity when ducklings were tested in pairs (b; 35.0 °C: N = 54; 36.0 °C: N = 54). Separate PCAs were conducted for the Individual Experiment (a) and the Pairs Experiment (b), and in both cases, a higher PC1 score (means ± SE) indicates that the duckling had a shorter latency to move, jump, call, and climb, and jumped and climbed more often.

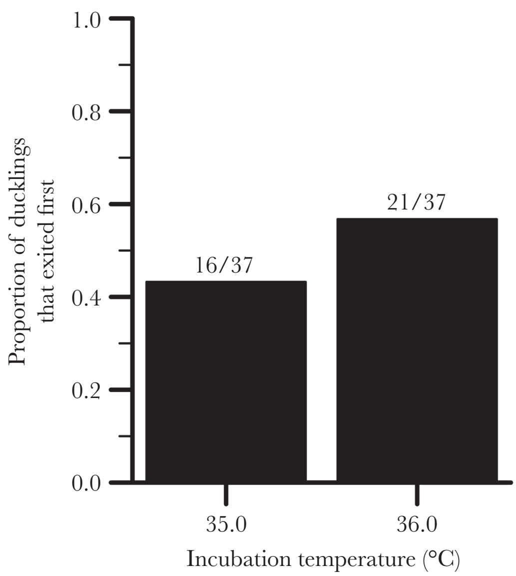

Figure 3
Incubation temperature does not influence which duckling exited first when ducklings were tested in pairs. Pairs consisted of one low (35.0 °C) and one high (36.0 °C) incubated duckling (N = 37 pairs consisting of ducklings from 29 nests). Numbers indicate the proportion of ducklings incubated at each temperature that exited the nest first during the trial.

Duckling behaviors

In the Individual Experiment, PC1 loaded negatively with latencies to move (−0.448), call (−0.458), jump (−0.500), climb (−0.437), and positively with the number of jumps per minute (0.274) and the number of climbs per minute (0.271). Thus, a higher PC1 score indicated that the duckling was quicker to move, call, jump, and climb, and jumped and climbed more. Duckling activity levels increased as incubation temperature increased ($F_{2,\ 138}$ = 4.6; P < 0.001; Figure 4a). A post hoc test (*lsmeans with Tukey adjustment*) revealed that ducklings incubated at the lowest temperature were significantly less active than those incubated at both of the higher temperatures (high–low temperature: P = 0.0008; intermediate–low temperature: P = 0.03). However, ducklings incubated at the intermediate and high temperatures did not differ in activity levels (P = 0.3). There was also a trend towards females being more active than males ($F_{1,\ 138}$ = 2.6, P = 0.057; effect size = −0.27).

In the Pairs Experiment, PC1 loaded negatively with latencies to move (−0.419), call (−0.453), jump (−0.490), climb (−0.434), and positively with the number of jumps per minute (0.277) and the number of climbs per minute (0.338). As observed in the Individual Experiment, a higher PC1 score indicated that the duckling was quicker to move, call, jump, and climb, and jumped and climbed more. In contrast to the Individual Experiment, however, incubation temperature was not related to behavior ($F_{1,\ 52}$ = 0.055; P = 0.81; Figure 4b). However, there was a marginal relationship between behavior and lay date ($F_{1,\ 64}$ = 3.2, P = 0.08; effect size = 4.95), where ducklings hatched from eggs laid at a later lay date tended to be less active than those laid earlier in the season.

In the Pairs Experiment, once the first duckling exited the nest box, the second duckling jumped ($F_{1,35}$ = 13.5; P < 0.001; Figure 5a) and climbed ($F_{1,35}$ = 27.7; P < 0.001; Figure 5b) >4 times more than they did before the first duckling exited, regardless of their incubation temperature (in all cases, $F \leq 0.22$ and $P \geq 0.77$ for incubation temperature main effect and interaction with time [before or after]).

DISCUSSION

We demonstrated that a change in incubation temperature of <1 °C and the early social environment interacted to affect the

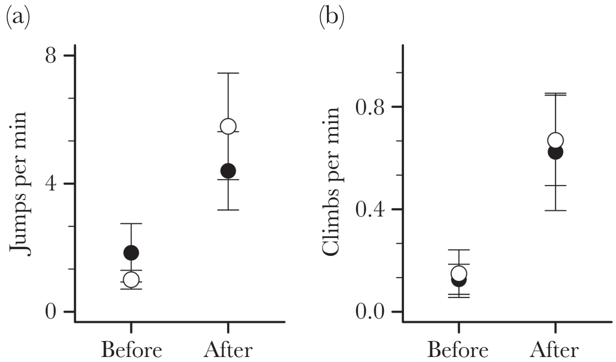

Figure 5
When ducklings were tested in pairs, the duckling that was left in the nest box jumped (a; 35.0 °C: N = 21 ducklings from 14 nests; 36.0 °C: N = 16 ducklings from 15 nests) and climbed (b; 35.0 °C: N = 21; 36.0 °C: N = 16) more per min (means ± SE) after the first duckling exited the box than before it exited. Jumps and climbs before and after were similar among incubation temperature treatments. Filled points = 35.0 °C; open points = 36.0 °C.

ability of precocial ducklings to exit the nest, a critical early-life event. When tested individually, ducklings incubated at the lowest temperature were less successful at exiting the nest than those incubated at slightly higher temperatures. However, social interactions mitigated these effects and, when tested in pairs, ducklings incubated at different temperatures had similar exodus success rates. It appears that success rates converged because ducklings incubated at the low temperature experienced social enhancement and increased motivation to exit when in the presence of a duckling incubated at the higher temperature. In contrast, those incubated at a higher temperature displayed consistent behavior, or even slightly poorer performance, in the presence of social interactions with a duckling from the cooler incubation temperature. Regardless of incubation temperature, all ducklings appeared to have increased motivation to exit once they were alone because after one duckling in the pair exited the nest, the duckling that remained behind jumped and climbed more often. These results advance our understanding of how parental effects may differentially influence offspring behavior and performance depending on their early social context.

We found that when tested individually, ducklings incubated at 35 °C were less active, slower, and less successful at exiting the nest than those incubated at higher temperatures. We did not find a significant difference in exodus success between ducklings incubated at the higher 2 temperatures, suggesting that there may be a thermal threshold for promoting exodus performance. Lower performance in low temperature-incubated ducklings is consistent with previous studies that showed that a small decrease in average incubation temperature can produce a diverse array of phenotypic differences in birds. In wood ducks, ducklings incubated at a lower temperature grow slower (DuRant et al. 2010), have reduced locomotor performance (Hopkins et al. 2011), inefficient thermoregulatory abilities (DuRant, Hopkins, Wilson, et al. 2012; DuRant, Hopkins, Carter, et al. 2013), reduced immunocompetence (DuRant, Hopkins, Hawley, et al. 2012), altered glucocorticoid and thyroid hormone levels (DuRant et al. 2010; DuRant et al. 2014), and reduced survival (Hepp and Kennamer 2012), compared with those incubated at a higher temperature. Further, altricial blue tits incubated at lower temperatures have slower growth rates and higher metabolic rates than those incubated at higher temperatures (Nord and Nilsson 2011). Unlike some alternative phenotypes that may be advantageous depending on the environmental context (e.g., a small body size may reduce the total energy costs of self-maintenance), the effect of a low incubation temperature on the ability to exit the nest is almost certainly disadvantageous, because failure to complete a timely exodus dramatically decreases the chances of survival (Bellrose and Holm 1994).

Our behavioral (i.e., jumps and climbs) and performance metrics (i.e., latency to exit) reveal possible correlates that may help explain the variance in nest exodus success. For example, ducklings incubated at a low temperature may have been less successful when tested individually due to lower persistence or less motivation compared with those incubated at higher temperatures. Indeed, in the Individual Experiment, ducklings incubated at the lowest temperature made fewer jumps and climbs, and had longer latencies to begin activity than those incubated at higher temperatures (Figure 4a). This agrees with Siegfried (1974), who found that wood duck ducklings that successfully exited an artificial cavity jumped more per minute than those that did not exit successfully. Further, ducklings incubated at the lower temperature may have been less motivated to exit the nest than those incubated at the higher temperatures when there was no social stimulus. Our results from the Pairs Experiment support this possibility. Once there was a source of social motivation, ducklings incubated at the lower temperature were just as successful at exiting the nest as those incubated at the higher temperature (Figure 1b). Additionally, ducklings that were left behind in the box jumped and climbed more once the first duckling left, likely due to increased motivation to exit (Figure 5a,b).

It is also possible that differences in exodus success were due to energetic or morphological constraints. For example, it may be more energetically demanding for a duckling incubated at a lower temperature to jump or climb than it is for a duckling incubated at a higher temperature. DuRant, Hopkins, Wilson, et al. (2012) found that wood ducks incubated at a lower temperature expend more energy during a thermoregulatory challenge than those incubated at higher temperatures, and thus, it is possible that similar inefficiencies exist when jumping and climbing. It is also possible that ducklings incubated at a lower temperature had expended more energy during incubation (DuRant et al. 2011) or depleted more of their yolk reserves before hatching (Olson et al. 2006). However, if this were the case, we would have expected ducklings incubated at the lower temperature to have a lower body mass at hatching than those incubated at the higher temperature, which was not the case (Table 1). Another possibility is that structural size contributed to the differences in exit success. However, we think that this is unlikely because neither body mass nor tarsus length was related to exit success in either experiment (all $F \leq 2.3$, $P \geq 0.13$).

Interestingly, social interactions mitigated the effects of incubation temperature on nest exodus success that were present when ducklings were tested individually. When tested in mixed-incubation temperature pairs, there was no effect of incubation temperature on nest exodus success, nor on the probability of which duckling exited the nest first. This convergence was primarily due to an increase in success by the ducklings incubated at the low temperature, whereas those incubated at the higher temperature (35.8–36.0 °C) displayed similar, or even slightly lower, success in the presence of social interactions. For low temperature-incubated ducklings (35.0 °C), success increased from 27% in the Individual Experiment to 48% in the Pairs Experiment (Figure 1). In contrast, exodus success for high temperature-incubated ducklings (35.8 and

36.0 °C) varied from 65% in the Individual Experiment to 59% in the Pairs Experiment (Figure 1). Thus, our results collectively suggest that ducklings from different incubation temperatures responded differently to social stimuli.

The enhanced success of ducklings incubated at the low temperature while in pairs may be due to social enhancement (Carere et al. 2005), where the behavior of one duckling causes another duckling to increase the frequency of the same behavior. This has been documented in altricial species, where nestlings alter their begging rates in response to the begging rates of their nest mates (Leonard and Horn 1998; Kitaysky et al. 2001; Rodríguez-Gironés et al. 2002; Carere et al. 2005) and fledge synchronously despite asynchronous hatching and differing body sizes (Nilsson and Svensson 1993; Bowers et al. 2013; Radersma et al. 2015). It makes sense that social enhancement would play a role in wood duck nest exodus because, even if a duckling is not in the best condition to leave the nest, it is still usually more advantageous to leave with their siblings to avoid being left behind (Bellrose and Holm 1994).

In contrast to outcomes produced from low incubation temperatures, ducklings incubated at higher temperatures appear to have relatively similar exit success both while in pairs and individually. This may be because ducklings incubated at the higher temperature are less influenced by social interactions, and their probability of exit success depends primarily on physiological traits. Interestingly, however, a few lines of evidence suggest that ducklings incubated at the higher temperature may in fact display lower exodus performance when paired with a duckling incubated at a lower temperature. First, a slightly lower proportion of ducklings incubated at the higher temperature exited while in pairs than when tested individually (Figure 1). Second, of those that successfully exited, ducklings incubated at higher temperatures displayed longer latencies to exit while in pairs than when tested individually (Figure 2). Third, we investigated this further by determining the frequency of pairs in which both ducklings exited, both failed to exit, or only one duckling exited (Figure 6). This comparison revealed that ducklings performed the same way (either both succeeded or both failed) 70% of the time. Importantly, ducklings incubated at the higher temperature almost never failed

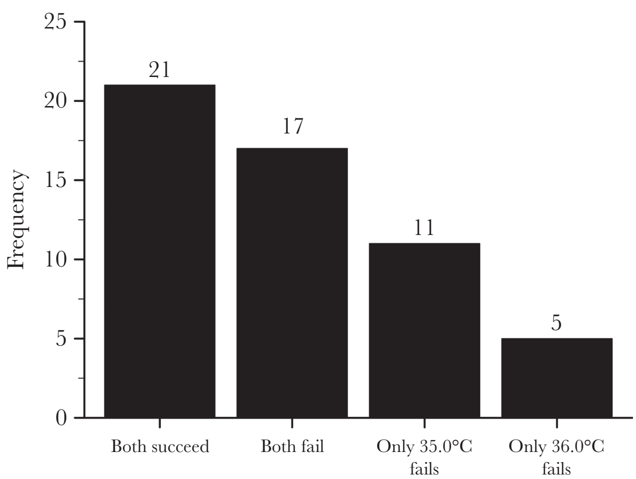

Figure 6
The frequency of times that, within a duckling pair in the Pairs Experiment, either both ducklings succeeded in exiting the nest, both failed to exit, only the duckling incubated at the low temperature failed, or only the duckling incubated at the high temperature failed. Note that ducklings behave similarly (either both succeed or both fail) 70% of the time.

if their low-temperature incubated partner succeeded (only 9% of the time), suggesting that the performance of ducklings incubated at the higher temperature is indeed influenced to some degree by social interactions. The high temperature-incubated ducklings may be displaying social conformity because, although they are physiologically capable of exiting when alone, many fail to exit when in pairs, and this happens almost exclusively when the other duckling also fails. However, it is still unknown why both ducklings failed so often (31%) while in pairs. It is possible that ducklings are physically interfering with each other (e.g., pushing) or engaging in beneficial social interactions instead of attempting to exit (e.g., preening).

Our finding that social interactions mitigated the effects of incubation temperature raises interesting questions regarding how our observations translate to nest exodus performance under natural circumstances. For instance, if social interactions lead to ducklings incubated at both high and low temperatures exiting the nest at the same time, there may be post-exodus fitness consequences for individuals experiencing lower temperatures during development. Because average egg temperatures vary within a clutch (Hope, DuRant, et al. 2018) and there are numerous developmental asymmetries among ducklings incubated at different temperatures (DuRant, Hopkins, Hepp, et al. 2013), ducklings that may have exited the nest too early in order to follow their nest mates may be at a disadvantage once out of the nest. For example, lower incubation temperatures produce ducklings that are poor thermoregulators during the first day of life compared with those produced from higher incubation temperatures (DuRant, Hopkins, Wilson, et al. 2012), and the environment outside of the nest box most certainly poses greater thermal challenges than within the box. Thus, following nest mates may have its own fitness consequences if an individual has deficits due to suboptimal developmental conditions.

Additionally, ducklings may not always experience social interactions under natural circumstances, and incubation temperature may be especially important for shaping nest exodus behavior when there is hatching asynchrony. Eggs incubated at the lowest temperatures take the longest to hatch (Hepp et al. 2006) and developmental asynchrony increases with clutch size (Kennamer et al. 1990) likely due to within-clutch variance in incubation temperature (Hope, DuRant, et al. 2018). This problem is exacerbated in wood ducks because of high rates of conspecific brood parasitism (Eadie et al. 1998). Thus, it may be common for ducklings incubated at the lowest temperatures within enlarged clutches to hatch last, and thus exit last, and in some cases singly. Then, once alone, these ducklings will likely be unsuccessful. This may result in ducklings being abandoned and dying in the nest, which we commonly observe each nesting season at our field sites (S. Hope, R. Kennamer, and W. Hopkins, personal observation).

Because we focused on mixed-temperature pairs in this study, we were not able to fully disentangle the influence of simply the presence of a partner from the influence of the temperature at which that partner was incubated. However, we have some evidence that the temperature at which each partner was incubated influences the outcome of their social interactions. During the Pairs Experiment, we opportunistically tested some same-temperature pairs. We tested 9 low–low temperature pairs and found that, in 7 of those pairs, both ducklings failed to exit. We also tested 2 high-high temperature pairs and found that in one pair both ducklings exited and in the other pair one duckling exited. Although these sample sizes are small, it provides further anecdotal evidence that social facilitation alone does not determine exit success, and that the temperature at which the partner was incubated matters. These observations suggest that additional experimentation may be needed to fully disentangle the relative importance of social interactions and incubation temperature for exodus success.

In addition to the observed effects of incubation temperature and social context, we also found a noteworthy trend suggesting that lay date was related to both nest exodus success and activity levels. Ducklings hatching from eggs laid later in the season were less likely to exit the nest and were less active in their attempts to exit. This is consistent with other studies that found lower hatching success and poorer quality offspring as the reproductive season progressed (Hochachka 1990; Verhulst et al. 1995; Brinkhof and Cave 1997; Harriman et al. 2017). These differences in quality may be due to either individual differences among hens, where different hens invest differentially in egg quality, or to differences in environmental conditions as the season progresses.

In conclusion, our study sheds light on how parental effects and the early social environment can interact to influence a critical early-life event. Incubation temperature influenced exodus performance differently depending on whether ducklings were tested individually or in pairs. This shows how parental effects can be context-dependent and highlights the importance of taking the early social environment into account when studying parental effects on offspring behaviors. In wood ducks, incubation temperatures vary both among and within nests (Hope, DuRant, et al. 2018), and our study shows how variation in incubation temperature within nests may influence offspring behavior both directly, and indirectly by shaping the composition of the post-hatch social environment. Further, because within-clutch temperature variation (Hope, DuRant, et al. 2018) and developmental asynchrony (Kennamer et al. 1990) increase as clutch sizes increase, our study has implications for understanding constraints on the evolution of clutch size and the costs of brood parasitism.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Hope, Kennamer, van Montfrans, et al. (2018).

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