

INTRACLUTCH EGG-SIZE VARIATION IN MAGELLANIC PENGUINS

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Abstract. We investigated patterns and consequences of intraclutch egg-size variation in Magellanic Penguins (*Spheniscus magellanicus*). First-laid eggs were significantly larger than second-laid eggs, although the mean difference represented only 2% of an average egg's volume. The degree of intraclutch egg-size variation was similar among years and females of different ages. Intraclutch egg-size variation did not affect intraclutch differences in chick hatching weights or fledging success. We found no selective advantage for laying eggs of different sizes. Because both eggs have an equal probability of being lost, chance favors equal provisioning of eggs. Egg volume explained 35% of the variation in hatching weight but did not determine fledging success. Laying order, year, and female age were better predictors of fledging success than egg size. Factors such as laying and hatching order, parental quality, oceanographic conditions, fights, and predation are more important in determining chick survival than are differences in egg size.

Key words: egg-size variation, fledging success, Magellanic Penguins, resource allocation, *Spheniscus magellanicus*.

Variación Intra-Nidada del Tamaño del Huevo en *Spheniscus magellanicus*

Resumen. Investigamos los patrones y las consecuencias de la variación intra-nidada del tamaño del huevo en *Spheniscus magellanicus*. Los huevos de la primera puesta fueron significativamente mayores que los huevos de la segunda puesta, aunque la diferencia media sólo representó el 2% del volumen total de un huevo promedio. El grado de variación intra-nidada del tamaño del huevo fue similar entre años y hembras de edades diferentes. La variación intra-nidada del tamaño del huevo no afectó las diferencias intra-nidada del peso de eclosión de los pichones o el éxito de emplumamiento. La puesta de huevos de diferentes tamaños no representó una ventaja selectiva. Debido a que ambos huevos tienen la misma probabilidad de desaparecer, el azar favorece el aprovisionamiento

igualitario de los huevos. También determinamos la importancia del año, la edad de la hembra, el volumen del huevo y el orden de la puesta en relación al peso de eclosión y la probabilidad de emplumamiento. El volumen del huevo explicó el 35% de la variación en el peso de la eclosión pero no determinó el éxito de emplumamiento. El orden de la puesta, junto con el año y la edad de la hembra, predijeron mejor el éxito de emplumamiento que el tamaño del huevo. En términos generales, los factores como el orden de puesta o eclosión, la calidad de los padres, las condiciones oceanográficas, las peleas y la depredación son más importantes en determinar la supervivencia de los pichones que las diferencias en el tamaño del huevo.

In many bird species, females differentially allocate resources to eggs within a clutch, and often the pattern is tied to laying order (reviewed by Slagsvold et al. 1984). The hypothesis that intraclutch egg-size variation in birds is an adaptive trait that increases the reproductive success of females is supported by evidence that larger eggs produce heavier chicks that have a higher probability of survival (reviewed by Williams 1994). In many cases, laying or hatching order is more important than egg size in determining which chicks hatch or survive (Lamey 1992, Robertson and Cooke 1993, Williams et al. 1993). Thus, differential egg investment could serve to further advantage particular eggs in the laying sequence (brood reduction; Ricklefs 1965, Slagsvold et al. 1984, St. Clair 1992, Viñuela 1997). Alternatively, increased investment in eggs disadvantaged by hatching order could improve the probability that those eggs will result in surviving offspring (brood survival; Slagsvold et al. 1984, St. Clair 1992, Viñuela 1997).

Egg-size variation within a clutch may be adaptive, or due to physiological or nutritional constraints, or both. Viñuela (1997) concluded that intraclutch egg-mass variation in Black Kites (*Milvus migrans*) was likely caused by nutritional constraints on breeding females or was due to the greater survival of chicks from larger eggs, which usually hatch first. Kilpi et al. (1996) suggested that egg-size variation in Herring Gulls (*Larus argentatus*) reflected food availability and was nonadaptive. Nilsson and Svensson (1993) also argued that energetic constraints on breeding females were responsible for intraclutch egg-mass variation, and reported that supplemental food reduced the amount of intraclutch egg-mass variation in Blue Tits (*Parus caeruleus*). In contrast, food supplementation did not reduce intraclutch egg-size variation in Amer-

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ican Kestrels (*Falco sparverius*, Wiebe and Bortolotti 1996). In a review of egg-size variation in birds, Christians (2002) reported that repeatability and heritability estimates for egg size were high, with 18 of 28 studies finding a significant effect of food supplementation on egg size, and concluded that physiological traits of females were most likely to determine egg size.

Patterns of intraclutch egg-size variation differ among penguin species. Little Penguins (*Eudyptula minor*) lay two eggs of different linear dimensions but equal volumes, and hatching success of the eggs is similar (Kemp and Dann 2001). In Chinstrap Penguins (*Pygoscelis antarctica*), intraclutch variation in egg volume is low and does not determine differences in hatching size or growth (Moreno et al. 1994, Belliure et al. 1999). In crested penguins (e.g., Macaroni Penguins [*Eudyptes chrysolophus*], Rockhopper Penguins [*E. chrysocome*], and Fiordland Crested Penguins [*E. pachyrhynchus*]), the second egg can be 70% larger than the first (Warham 1975), and although both may hatch, usually only the second chick survives (Williams 1990, Lamey 1990, 1993). Neither Lamey (1993) nor St. Clair (1992) found support for the hypothesis that crested penguins invest minimally in the first-laid egg because it is usually lost during fights. Williams (1990) suggested that the rate of yolk deposition, which might be slower when the first egg is developing, is responsible for the differences in egg size in Macaroni Penguins.

Both Galapagos Penguins (*Spheniscus mendiculus*) and Magellanic Penguins (*S. magellanicus*) usually lay longer first eggs and wider second eggs (Boersma 1976, Boersma et al. 1990). Although they differ in linear dimensions, Magellanic Penguin eggs are typically similar in volume (Boersma et al. 1990). First and second eggs are equally likely to be lost, suggesting that laying order has little effect on egg mortality (Boersma et al. 2004). First eggs usually hatch two days before second eggs, and first chicks are almost twice as likely as second chicks to survive (Boersma 1992). Our goals were to examine intraclutch variation in egg size in Magellanic Penguins to determine possible causes of this size variation, and whether it affects chick hatching weight or fledging probability.

METHODS

STUDY AREA AND FIELD METHODS

We have studied Magellanic Penguins at Punta Tombo, Argentina (44°02'S, 65°11'W) since 1983 (Boersma et al. 1990). In September, October, or occasionally as late as November, females typically lay two eggs of similar size over a four-day interval (Boersma and Stokes 1995, Boersma et al. 2004). We checked nests for eggs every one to six days to determine egg-laying dates and labeled eggs with a sharpie marker by laying order and nest number. We measured the length and width of eggs to the nearest tenth of a millimeter with Vernier dial calipers. From 1983–1986, eggs were also weighed to the nearest gram within five days of laying.

We weighed newly hatched chicks to the nearest gram using Pesola 50 g and 100 g spring scales and larger chicks with 3 kg or 6 kg spring scales with 25 g or 50 g increments. Chicks were labeled by nest number and hatching order with temporary fiber-tape

bands around their flippers. Every ten days until chicks died or fledged we weighed and measured them and replaced the fiber band. Chicks were assumed to have fledged if they were healthy when last seen and weighed at least 1800 g after 10 January.

STATISTICAL ANALYSES

We calculated egg volume ($\text{length} \times \text{width}^2$; Reid and Boersma 1990) and added the volumes of first and second eggs to obtain clutch volume. In all analyses, we treated the degree of intraclutch egg-size variation (i.e., difference in volume) between the two eggs of a clutch as a continuous variable, calculated by subtracting the volume of the second egg from that of the first. Thus, degree of intraclutch egg-size variation is a directional, signed variable (positive values indicate that the first egg was larger, negative values indicate that the second egg was larger).

We used a paired *t*-test to compare the volumes of first and second eggs for all clutches that were included in our analyses of fledging success. Since we did not always weigh eggs in the same years that we measured chick hatching weight and fledging success, we determined the relationship between egg volume and egg weight using a correlation analysis.

To investigate possible causes of intraclutch egg-size variation, we used a linear mixed-effects model (LMEM), with female age and year as fixed effects, and female band number (i.e., female identity) as a random effect to account for the lack of independence between multiple clutches laid by the same female. Although year and age are perfectly correlated within a female, interannual variation in environmental conditions may have effects independent of any female's age. Known-age females (banded as a chick or juvenile) ranged from 4–18 years old. The number of clutches (one clutch per year) per female ranged from one to nine.

For analyses of chick hatching weights, we used only two-egg nests of known-age females in which both eggs were measured, survived to hatching, did not hatch in reverse order, and in which the chicks were weighed within one day of hatching. Chicks may or may not have been fed before their first weighing, but either is equally likely for all chicks in our sample. Chicks were weighed within one day of hatching from 1996 to 2002, but data from 2000 were incomplete, so we used only data from 1996–1999 and 2001–2002. We calculated mean hatching weights of first and second chicks for each year.

We used LMEMs to look at predictors of chick hatching weight and differences in chick hatching weights within a clutch. For individual chicks, we analyzed the effect of female age, year, egg volume, and egg laying order (first or second) on hatching weight. Female band number and clutch number were included as random effects due to the lack of independence between clutches laid by the same female and between two eggs of the same clutch. Clutches were numbered so that both eggs of a clutch shared the same number, but each clutch received a unique number. We determined if the difference in hatching weight between the two chicks of a clutch was explained by degree of intraclutch egg-size variation, female age, or year with a LMEM that included female band number as a ran-

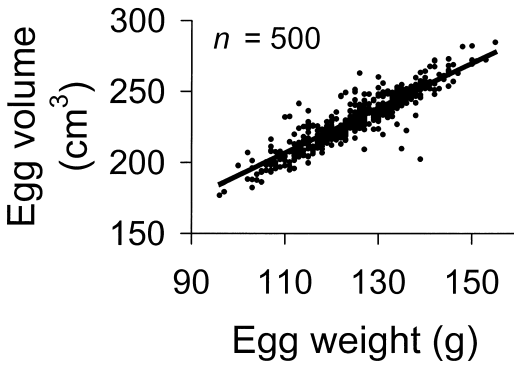


FIGURE 1. Simple linear correlation between egg weight and egg volume in Magellanic Penguins (*Spheniscus magellanicus*) after eliminating outliers >3 SD from the mean weight. For clarity only 500 random points of the 5565 values are shown. Note: axes do not start at zero.

dom effect. Difference in hatching weight was calculated by subtracting the hatching weight of the second chick from that of the first.

Finally, we used generalized linear mixed models (GLMM) to examine possible predictors of fledging success. We placed the same restrictions on fledging success data as on hatching weight data, except that chicks did not have to be weighed within one day of hatching. Thus, the data on fledging success includes 1993–2002. Fledging success for an individual chick was coded as a logistic variable (0 = chick did not fledge, 1 = chick fledged). We included year, female age, egg volume, and laying order as fixed effects, and female band number and clutch number as random effects. With another GLMM, we analyzed the effect of year, female age, and degree of intraclutch egg-size variation on the fledging success of the clutch, which was also coded as a logistic variable (0 = neither chick fledged, 1 = one or both chick(s) fledged). Female band number was included as a random effect for this model.

Values are reported as means \pm SE. All statistical tests were performed in R (R Development Core Team 2004), and all t -tests were two-tailed. Statistical significance was accepted at $\alpha = 0.05$.

RESULTS

Egg weight and volume were positively correlated ($r = 0.91$, $t_{5585} = 167.1$, $P < 0.001$). We eliminated outliers >3 SD from the mean weight (125 g), which included weights as low as 30 g, to better show the relationship within the range of normal variability (Fig. 1). This slightly reduced the sample size and fit ($r = 0.90$, $t_{5563} = 157.4$, $P < 0.001$).

Intraclutch egg-size differences ranged from -65.7 cm^3 (second egg 29% larger than first) to 94.8 cm^3 (first egg 42% larger than second). The mean difference in volume between the first and second egg of a clutch was 4.5 ± 0.6 cm^3 , approximately 2%. First eggs (229.7 ± 1.0 cm^3) were significantly larger than second eggs (225.2 ± 0.9 cm^3 ; t -test: $t_{405} = 7.3$, $P < 0.001$).

MODELS

Intraclutch egg-size variation. The degree of size variation between the two eggs of a clutch was not significantly affected by female age (LMEM: $t_{401} = -0.8$, $P = 0.44$) or year (LMEM: $t_{401} = 1.3$, $P = 0.21$; Table 1).

Hatching weight. The mean hatching weight of first chicks was greatest in 1998 (97 ± 3 g, $n = 25$), whereas the mean hatching weight of second chicks was highest in 2001 (92 ± 3 g, $n = 11$). Mean hatching weights of first and second chicks were lowest in 2002 (83 ± 2 g, $n = 11$ and 84 ± 3 g, $n = 11$, respectively).

Egg volume had a significant effect on hatching weight (LMEM: $t_{108} = 10.0$, $P < 0.001$), explaining 35% of the variation when regressed alone against hatching weight (SLR: $R^2 = 0.35$, $F_{1,218} = 119.3$, $P < 0.001$; Fig. 2). Female age (LMEM: $t_{43} = 1.0$, $P = 0.35$), year (LMEM: $t_{43} = -1.6$, $P = 0.12$), and laying order (LMEM: $t_{108} = -0.4$, $P = 0.70$) did not have significant effects on hatching weight. Thus, only egg volume remained in the final model after stepwise selection (Table 1).

The difference in hatching weight between the first and second chick of a nest was not predicted by the degree of intraclutch egg-size variation (LMEM: $t_{42} = 1.7$, $P = 0.10$), female age (LMEM: $t_{42} = 0.2$, $P = 0.87$), or year (LMEM: $t_{42} = -0.9$, $P = 0.37$; Table 1).

Fledging success. Laying order was the most powerful predictor of fledging success for an individual chick (GLMM: $t_{404} = -5.0$, $P < 0.001$), followed by year (GLMM: $t_{249} = -2.9$, $P < 0.01$) and female age

TABLE 1. Regression analyses of intraclutch egg-size differences, chick hatching mass, and fledging probabilities in Magellanic Penguins. Each row represents a regression analysis, testing up to four variables (columns). + indicates the variable has a significant effect; - indicates no relationship detected; * indicates a significant relationship based on P -value, but the variable was not selected in the stepwise regression procedure; blank indicates the variable was not included in the model.

	Year	Female age	Egg volume	Laying order	Intraclutch egg size difference
Intraclutch egg-size difference	-	-			
Chick hatching mass	-	-	+	-	
Intraclutch chick mass difference	-	-			-
Fledging probability	*	*	-	+	
Probability of 1 or 2 chicks fledging from clutch	+	+			-

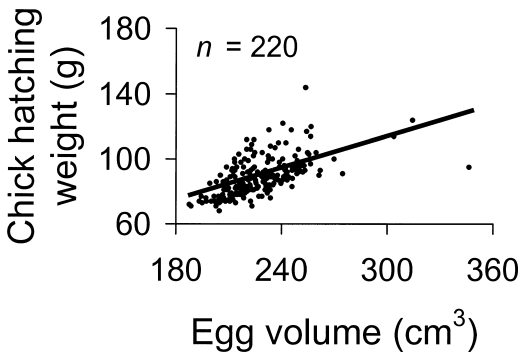


FIGURE 2. Simple linear regression of Magellanic Penguin (*Spheniscus magellanicus*) chick weight within one day of hatching and egg volume from all known-age female two-egg nests in which both eggs were measured, survived to hatching, and did not hatch in reverse order from 1996–1999 and 2001–2002. Egg volume explained 35% of the variation in chick hatching weight. Chick hatching weight = $10.60 + 0.34 \times (\text{egg volume})$. Note: axes do not start at zero.

(GLMM: $t_{249} = 2.2$, $P = 0.03$). Egg volume did not have a significant effect on whether a chick fledged (GLMM: $t_{404} = 0.9$, $P = 0.38$). After stepwise selection, the final model included only laying order (Table 1).

The fledging success of a clutch (i.e., whether neither chick or at least one chick fledged) was significantly affected by year (GLMM: $t_{248} = -3.2$, $P = 0.002$) and female age (GLMM: $t_{248} = 2.8$, $P = 0.005$), but not by degree of intraclutch egg-size variation (GLMM: $t_{248} = -1.2$, $P = 0.24$). Both year and female age remained in the final model after stepwise selection (Table 1).

DISCUSSION

Egg volume was positively related to chick hatching weight, and first eggs were significantly larger than second eggs, although the mean difference in volume was only 2% and is likely biologically unimportant. In Magellanic Penguins, increased investment in first eggs makes evolutionary sense, since first chicks are more likely to survive than second chicks (Boersma 1992). This pattern is opposite to that seen in crested penguins, for which the differences in survival are more extreme (Lamey 1990). Egg-size variation in Magellanic Penguins, however, does not seem to influence fledging success. Since differences in egg investment do not translate into differences in reproductive success, no selective pressures to favor one egg over the other would be expected. Laying order had the largest effect on fledging probability.

First eggs usually hatch two days before second eggs, suggesting that differential investment in first-hatched chicks leads to their increased survival and fledging success. Greater investment in first chicks is likely a consequence of timing: if a mate returns to the nest soon after the first chick has hatched but before the second chick hatches, the first chick will likely be fed and will thus be larger than the second. As rearing progresses, parents commonly continue to preferen-

tially feed the larger first chick (Boersma 1992, Boersma and Stokes 1995).

Differences in egg size are therefore relatively unimportant for chick survival, which is largely determined by hatching order and the timing of first feeding (Boersma 1992, Boersma and Stokes 1995). The latter may in turn be related to parental quality, which Reid and Boersma (1990) found to be more important than egg size for chick survival.

The degree of intraclutch egg-size variation was low and did not differ significantly among years, indicating that females are fairly consistent in how they divide resources between eggs, in spite of interannual variability in environmental conditions. Likewise, female age did not influence the degree of intraclutch egg-size variation, demonstrating that females apportion resources in a similar way regardless of their age. Because our sample included multiple years of data on the same females, we can also conclude that intraclutch egg-size variation does not vary with female breeding experience. Black Kites (Viñuela 1997) and Snow Geese (*Anser caerulescens*, Robertson et al. 1994) similarly lack change in intraclutch egg-size variation with breeding experience.

Although we did not detect evidence of significant annual variation in the hatching weights of chicks, mean hatching weights varied by several grams among years. The year of lowest mean hatching weight for both first and second chicks was 2002. Adults were in poor body condition, and many females failed to return in time to lay eggs that year (PDB, unpubl. data).

Year significantly affected fledging probability at the level of individual eggs and whole clutches, suggestive of interannual variation in food availability. For example, for both first and second chicks, 1996 was the year of highest fledging success and 2000 was the lowest. In 1996, the colony experienced the greatest reproductive success in the years 1983–2002. Similarly, 2000 was the year of second lowest reproductive success (PDB, unpubl. data). Female age was also an important predictor of fledging success, suggesting that female breeding experience may play a role in determining reproductive success.

Our results are consistent with Williams' (1994) conclusion that egg size has little impact on chick survival. In his review of the effects of intraspecific variation in egg size on offspring fitness in birds, Williams (1994) found only three studies (out of the 40 considered) that both controlled for potentially correlated factors and detected a significant effect of egg size on chick survival to fledging. Williams (1994) found greater support for a positive effect of egg size on chick survival soon after hatching, and suggested that this might be the most important consequence of egg-size variation.

A complex suite of factors, including predation and intraspecific aggression, influences the survival and fledging success of Magellanic Penguin chicks (Yorio and Boersma 1994a, 1994b, Stokes and Boersma 2000, Renison et al. 2002). Egg and chick mortality rates at Punta Tombo are high, with fewer than one in four eggs producing fledglings (Boersma et al. 1990, Boersma and Stokes 1995). Females have an equal probability of losing either egg (Boersma et al. 2004), se-

lecting against differential provisioning of eggs. Consequently, females generally invest fairly equally in both eggs, and intraclutch egg-size variation is relatively inconsequential.

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INCUBATION LENGTH OF DABBLING DUCKS

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Abstract. We collected unincubated eggs from wild Mallard (*Anas platyrhynchos*), Gadwall (*A. strepera*), Blue-winged Teal (*A. discors*), and Northern Shoveler (*A. clypeata*) nests and artificially incubated them at 37.5°C. Average incubation lengths of Mallard, Gadwall, and Northern Shoveler eggs did not differ from their wild-nesting counterparts, but artificially incubated Blue-winged Teal eggs required an additional 1.7 days to hatch, suggesting that wild-nesting teal incubated more effectively. A small sample of Mallard, Gadwall, and Northern Shoveler eggs artificially incubated at 38.3°C hatched 1 day sooner, indicating that incubation temperature affected incubation length. Mean incubation length of Blue-winged Teal declined by 1 day for each 11-day delay in nesting, but we found no such seasonal decline among Mallards, Gadwalls, or Northern Shovelers. There is no obvious explanation for the seasonal reduction in incubation length for Blue-winged Teal eggs incubated in a constant environment, and the phenomenon deserves further study.

Key words: Blue-winged Teal, dabbling ducks, Gadwall, incubation length, Mallard, Northern Shoveler, seasonal decline.

Duración del Período de Incubación en Patos del Género *Anas*

Resumen. Recolectamos huevos no incubados de nidos de patos silvestres de las especies *Anas platyrhynchos*, *A. strepera*, *A. discors* y *A. clypeata* y

los incubamos artificialmente a 37.5°C. La duración del período de incubación de los huevos de *A. platyrhynchos*, *A. strepera* y *A. clypeata* no difirió de la observada en aves nidificantes silvestres, pero los huevos de *A. discors* incubados artificialmente tardaron 1.7 días adicionales en eclosionar, lo que sugiere que los individuos silvestres incubaron los huevos con mayor efectividad. Una muestra pequeña de huevos de *A. platyrhynchos*, *A. strepera* y *A. clypeata* incubados artificialmente a 38.3°C eclosionaron un día más temprano, lo que indica que la temperatura afecta la duración del período de incubación. La duración promedio de la incubación de *A. discors* disminuyó en un día por cada 11 días de tardanza en la nidificación, pero no encontramos disminuciones estacionales de este tipo en *A. platyrhynchos*, *A. strepera* y *A. clypeata*. No existe una explicación obvia para la reducción estacional en la duración de la incubación de huevos de *A. discors* incubados en un ambiente constante, un fenómeno que requiere ser estudiado en mayor profundidad.

Feldheim (1997) documented widespread variation in incubation length within five species of prairie-nesting dabbling ducks (*Anas* spp.), including a significant negative correlation between incubation length and nest initiation date in all five species. Similar negative correlations between incubation length and nest initiation date have been observed in other wild-nesting birds (Nolan 1978, Colwell and Oring 1988, Moreno and Carlson 1989). The causes of these seasonal declines in incubation length are unknown, but some proposed explanations include higher ambient temperatures that promote higher incubation temperatures or reduced egg cooling during recesses (Hepp et al. 1990), seasonal increases in incubation constancy (Aldrich and Raveling 1983), correlated responses to seasonally declining clutch size (Feldheim 1997) or egg

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size (Flint and Sedinger 1992), progressive development of the incubation patch (Nolan 1978), or seasonal changes in the development rates of embryos (MacCluskie et al. 1997).

In a field environment where incubation duration is the product of variation in ambient temperatures, parental attendance patterns, and attributes of the embryo (among other things), determining which of these factors influence seasonal patterns in incubation duration is difficult, if not impossible. To document inherent physiological variation in incubation length that was not confounded by natural variation in ambient temperature, nest environment, or parental behavior, we collected unincubated dabbling duck eggs from wild nests and incubated them in a constant communal environment. The objectives of our study were threefold: 1) to test for interspecific variation in incubation length among Mallards (*Anas platyrhynchos*), Gadwalls (*A. strepera*), Blue-winged Teal (*A. discors*), and Northern Shovelers (*A. clypeata*) by incubating their eggs in a common environment and comparing our results to wild-nesting data, 2) to see if variation in incubation temperature (37.5°C versus 38.3°C) affects incubation length, and 3) to test for inherent seasonal declines in incubation length by collecting eggs throughout the nesting season and incubating them in a controlled artificial environment.

METHODS

We collected eggs from free-living dabbling ducks nesting near Minnedosa, Manitoba, Canada (50°10'N, 99°47'W). Nests were located and monitored using standard techniques for prairie-nesting ducks (Klett et al. 1988); most nests were found by dragging fields of potential nesting cover using a 25-m chain pulled between two all-terrain vehicles. We started nest searching during the first week of May and continued until mid-July in both 1999 and 2000.

If a clutch appeared to be incomplete and unincubated when found, eggs already present in the nest were marked with an indelible marker. We revisited the nest the following evening and collected any new unmarked eggs, and we continued with these daily visits until no new eggs were found (Arnold 1993). After eggs were collected they were marked for individual identification, packed into plastic egg trays, stored in a refrigerator at 7.2°C for up to 3 days, and rotated twice a day throughout storage.

Stored eggs were transported every third day to artificial incubators at the Delta Waterfowl Research Station near Portage la Prairie, Manitoba, and incubated at 37.5°C and 70% relative humidity until they became pipped. In 1999, we included a second incubator set at 38.3°C and 70% relative humidity, but this treatment was discontinued in 2000 due to poor hatchability (24 of 80 eggs, 30%). After they became pipped, eggs were transferred to a third incubator set at 37.5°C and 85% relative humidity. Regular checks of this incubator were made every 8 hours to determine hatching time, defined as the moment the duckling emerged from the shell. Ducklings that hatched between visits were assigned a hatching time midway between the last two incubator checks. We deleted one Mallard egg and one Gadwall egg that required >31 days to hatch

because their hatching times were unusually slow (they took >5 days longer than their next closest conspecific). Hatched ducklings were raised to fledging age and released back into the wild.

We used a nested analysis of covariance (PROC MIXED; SAS Institute 2000) to explore sources of variation in incubation length in relation to species, year, incubation temperature (37.5°C vs. 38.3°C), and laying date (day 1 = 11 May). Because replicate eggs from the same clutch were not necessarily independent (i.e., there may have been a maternal or heritable effect on incubation duration), individual clutches were treated as random effects by nesting them within the year-by-species interaction effect. We began our analysis with a full model that included all four main effects plus all estimable two-way interactions, and we sequentially deleted the weakest not significant ($P > 0.05$) predictors based on F -tests calculated from Type 3 sums of squares. We provide model-based least squares means or effect sizes (\pm SE) for all significant effects.

For comparison with wild data, we compared mean incubation periods from our sample of eggs artificially incubated at 37.5°C with Feldheim's (1997) data from wild-nesting birds in nearby North Dakota using 2-sample t -tests with unequal variances.

RESULTS

We measured incubation periods of 208 eggs from 117 different clutches, including 36 Mallards (from 23 clutches), 46 Gadwalls (30 clutches), 81 Blue-winged Teal (45 clutches), and 45 Northern Shovelers (19 clutches). Replicate eggs from the same clutch were not independent; clutch effects accounted for 30% of the covariance in the nested analysis of covariance, so it was important to use a nested analysis to control for this effect. Incubation length was significantly related to species ($F_{3,111} = 6.7, P \leq 0.001$), incubation temperature ($F_{1,86} = 17.5, P \leq 0.001$), laying date ($F_{1,86} = 7.7, P = 0.007$), and the laying date by species interaction ($F_{3,86} = 6.6, P < 0.001$). Year and all other interaction effects were not significant ($P > 0.19$). After controlling for date and temperature effects, Northern Shoveler eggs hatched the fastest (22.9 ± 0.2 days), Blue-winged Teal (23.4 ± 0.3 days) and Gadwall (23.8 ± 0.3 days) eggs were intermediate, and Mallard eggs took the longest to hatch (24.5 ± 0.2 days). Controlling for species and date effects, eggs incubated at 38.3°C hatched about 1 day sooner (23.1 ± 0.2 days, $n = 24$) than did eggs incubated at 37.5°C (24.2 ± 0.1 days, $n = 184$). Finally, after controlling for temperature effects, Blue-winged Teal eggs that were laid one day later in the nesting season hatched an average of 0.09 ± 0.03 days sooner ($P = 0.004$), but the daily declines for Gadwalls (0.00 ± 0.03), Mallards (0.01 ± 0.03), and Northern Shovelers (0.01 ± 0.02) were not significantly different from 0 ($P > 0.75$). Over the 61 days that we collected teal eggs, predicted incubation periods declined by 5.5 days (Fig. 1). By contrast, predicted incubation periods declined by 0.3 days over the 37-day period we collected Mallard eggs, declined by 0.2 days over the 30 days we collected shoveler eggs, and increased by 0.05 days over the 38 days we collected Gadwall eggs.

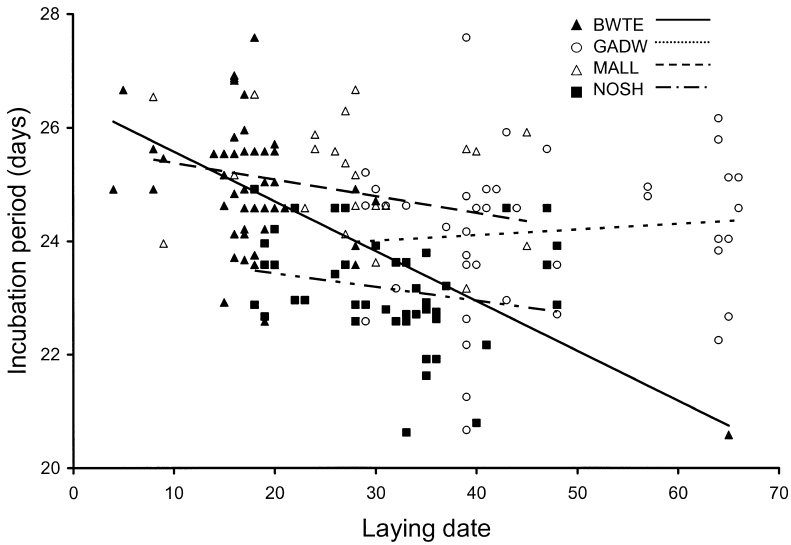


FIGURE 1. Incubation length (days) of Blue-winged Teal (BWTE), Gadwall (GADW), Mallard (MALL), and Northern Shoveler (NOSH) eggs in relation to laying date (day 1 = 11 May). Regression lines for each species are from a nested analysis of covariance, but only the teal regression was significant.

Mean incubation periods of Mallards, Gadwalls, and Northern Shovelers did not differ from Feldheim's (1997) data for wild-nesting ducks in North Dakota (Table 1; $t \leq 1.7$, $P \geq 0.10$), but our artificially incubated Blue-winged Teal eggs required an additional 1.7 days to hatch ($t_{253} = 7.5$, $P \leq 0.001$).

DISCUSSION

We documented significant interspecific variation in incubation lengths of dabbling duck eggs incubated in a common environment, and this variation increased slightly after controlling for laying date. Northern Shoveler eggs hatched most quickly and Mallards hatched most slowly, regardless of the variation in laying date. Arnold (1993) also found that artificially incubated Northern Shoveler eggs hatched more quickly than Blue-winged Teal and Mallard eggs, even after controlling for egg size. But Feldheim (1997) documented incubation lengths in the wild for these same four species and found that Northern Shovelers did not hatch more quickly than the other species. Although Feldheim's (1997) estimate of incubation length for Blue-winged Teal was 1.7 days shorter than our results based on artificial incubation, none of his other spe-

cies' incubation lengths differed from our data by more than 0.5 days. There is nothing strikingly different about the incubation temperatures or rhythms of wild-nesting Blue-winged Teal in comparison to the other species we examined (Afton and Paulus 1992), and we are unable to explain these contrasting results between artificial and natural incubation. Blue-winged Teal begin effective incubation during egg laying, so it's possible that the shorter incubation periods of Feldheim's wild-nesting Blue-winged Teal were an artifact of measuring incubation starting with the last laid egg, but this bias should have affected the other species as well (Loos and Rohwer 2004).

Although our experiment on incubation temperatures was hampered by poor hatchability in the 38.3°C incubator, we found that eggs incubated at warmer temperatures hatched on average 1 day sooner. Prince et al. (1969) experimentally varied incubation temperatures of captive Mallard eggs and found that incubation periods decreased monotonically across a broad range of increasing incubation temperatures (35.6°C to 39.4°C), including about a 2-day decline between 37.5°C and 38.3°C.

TABLE 1. Mean incubation periods (days) of Blue-winged Teal, Gadwall, Mallard, and Northern Shoveler eggs artificially incubated at 37.5°C and 38.3°C, with comparable data from wild-nesting birds (Feldheim 1997). Data are presented as means \pm SE (n).

Species	37.5°C	38.3°C	Wild nesting
Blue-winged Teal	24.9 \pm 1.1 (81)	—	23.2 \pm 2.0 (106)
Gadwall	24.4 \pm 1.0 (36)	23.2 \pm 1.9 (10)	24.1 \pm 1.2 (31)
Mallard	25.0 \pm 0.9 (32)	24.0 \pm 1.1 (4)	24.5 \pm 2.1 (66)
Northern Shoveler	23.4 \pm 0.9 (35)	22.4 \pm 0.9 (10)	23.8 \pm 1.6 (12)

We observed a significant decline in incubation length for Blue-winged Teal eggs laid later in the nesting season. This decline averaged 1 day for every 11-day delay in laying over the approximate 2-month period in which we collected teal eggs. A single late season egg collected on 4 July (day 65) had a much shorter incubation length than other teal eggs. Although this data point has substantial leverage (Fig. 1), we obtained virtually identical results with this single egg deleted from the analysis (i.e., the seasonal decline for Blue-winged Teal was 0.09 ± 0.03 , $P = 0.005$). Working with artificially incubated Blue-winged Teal, Northern Shovelers, and Mallards, Arnold (1993) found similar evidence of a seasonal decline in incubation length, but it was confounded by egg volume. Using species-specific egg volumes, Arnold found estimates of daily declines in incubation periods of 0.05, 0.03, and 0.00 days for Blue-winged Teal, Northern Shovelers, and Mallards, respectively (Arnold 1993). Under natural incubation, Feldheim (1997) documented ubiquitous seasonal declines in incubation length for all four species included in our study, plus Northern Pintails (*Anas acuta*). Daily declines in incubation length in Feldheim's study ranged from 0.08 to 0.15 days (Feldheim 1997), consistently higher than the values we (and Arnold [1993]) observed under artificial incubation.

Various factors might account for seasonal declines in incubation length under natural conditions, including differences in availability or use of nutrient reserves during incubation by early versus late-nesting females (Esler and Grand 1994), changes in ambient temperature that affect either incubation temperature or egg cooling rates during incubation recesses (Prince et al. 1969, Haftorn and Reinertsen 1985), seasonal declines in egg size (Flint and Sedinger 1992) or clutch size (Feldheim 1997) that affect incubation efficacy, changes in incubation constancy (Afton and Paulus 1992), or inherent differences in rates of embryonic development (MacCluskie et al. 1997). Eggs in our study were incubated in a near-constant artificial environment, thereby controlling for most of the exogenous factors above. We therefore hypothesize that eggs laid later in the nesting season had faster inherent rates of development (Arnold 1993). Alternatively, late-season eggs might hatch at a less advanced stage of development (Hepp 2004). Nevertheless, the much stronger relationships between incubation length and laying date observed under field conditions by Feldheim (1997) suggest that exogenous factors have a greater collective influence on seasonal declines in incubation length than do intrinsic factors.

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