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Age related productivity and consistency of nest initiation timing of wild mallards in eastern North Dakota

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AGE RELATED PRODUCTIVITY AND CONSISTENCY OF NEST INITIATION TIMING OF WILD MALLARDS IN EASTERN NORTH DAKOTA

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ABSTRACT

Mallards *Anas platyrhnchos* are arguably the most researched waterfowl species in North America. They exhibit great flexibility in certain breeding metrics such as timing of nest initiation and clutch size. A study on captive female Mallards (Batt and Prince 1979) fed *ad libitum*, held in identical breeding compartments, and paired with the same mate in each year of the study exhibited substantial variation in the timing of nest initiation within a given year, yet some individual females demonstrated consistency in initiation date among years. My objective was to examine breeding metrics such as timing of nest initiation and clutch size and to evaluate age-related productivity in conjunction with those metrics. More specifically, I wanted to know if individual females were consistent in first initiated nests among years. Secondly, I wanted to know if age affected both the timing of nest initiation and clutch size. From 2006-2009 nest searching crews found 2274 Mallard nests and captured 944 females using various trapping techniques. I found strong evidence for variation among birds within year. I failed to find a significant influence of individual variation among birds between years. Age was not significant in impacting when an individual nests. The effects of nest year were also tested but were not significant. For my clutch size analysis, all 944 females captured were used and categorized to an age group based on wing feather characteristics. Age, year, and julian date all had significant impacts on clutch size. After second year (ASY) females had 0.32 more eggs than second year (SY) females. Clutch size varied by year and declined seasonally, such that for every day of delay clutch size was reduced by 0.05 eggs. Mallards exhibit great flexibility in the timing of nest initiation for which they breed. However, approximately 36% of the females show consistency in their individual

nesting dates which were prior to the mean annual initiation date. Some individuals consistently nested later than the mean annual initiation date. Nevertheless, there appears to be strong directional selection for early nesting.

INTRODUCTION

Mallards (*Anas playyrhynchos)* are one of the most extensively studied waterfowl in the world (Krapu 1981). Interestingly, they are one of the first ones to reach the breeding grounds and are regularly reported as an early nesting species, yet they exhibit great variability in the timing of nest initiation as well as clutch size (Batt and Prince 1979). Much of the variation in nesting date and clutch size has been attributed to Mallards high propensity to renest (Swanson et al. 1986, Coulter and Miller 1968), environmental factors such as habitat and weather conditions (Krapu and Doty 1979), body condition (Devries et al. 2008), or the age of an individual female (Ryder 1980).

A study of captive Mallards showed that females demonstrated a wide range of nest initiation dates within a given year, but individual females also exhibited consistency in nesting dates among years (Batt and Prince 1979). Not only did they witness consistency in early nesters but late nesters as well. Consistency in late nesting is an interesting result because females that nest early in the breeding season have several reproductive advantages, such as larger clutch sizes, higher survival of ducklings to the fledging stage, higher post fledging survival and recruitment, and a greater opportunity to renest if their first nest fails. Individual consistency of nest initiation timing has also been documented in wild populations of Steller's Eiders (Spurr and Milne 1976), Adélie Penguins (Spurr 1975), Manx Shearwaters (Harris 1966), Short-tailed Shearwaters (Serventy 1963), Yellow-eyed penguins (Richdale 1957), White Winged Scoters (Koskimies 1957), and Great Tits (Kluijver 1951). However, no studies of wild Mallards have been able to corroborate the findings of Batt and Prince (1979). A high nest failure rate for most populations of wild Mallards (Emery et al. 2005, Sovada et al. 2001) makes it difficult to test the date consistency hypothesis because nest failure makes it unclear if any nest is a first nest or a replacement clutch. Documenting consistency in nest initiation requires identifying individuals in successive years and having high certainty that nests found are the first nests of the season. An ongoing program established before this study by the Delta Waterfowl Foundation uses professional trappers to reduce meso-mammalian nest predators on township-sized blocks to increase waterfowl nest success. Research evaluating nest success at multiple scales indicates that predator reduction substantially improves nest success (Pieron and Rohwer 2010, Chodachek and Chamberlain 2006, Garrettson and Rohwer 2001). Therefore, high nest success coupled with a well established sample of banded female mallards (M. Pieron, unpublished data) made it possible for me to recapture individual females in multiple years. This allowed me to test the hypothesis that wild female Mallards would show consistency in their individual nest initiation dates among years.

I also had an interest in examining age-related productivity. Forslund and Pärt (1995) found that reproductive parameters typically improve with age as a result of increased breeding experience, greater foraging ability, and elevated reproductive effort. Older females typically exhibit higher nesting propensity, nest earlier within a season, nest more persistently, and lay larger clutches than younger females (Losito et al. 1995, Rohwer 1992). Mallards that nest early recruit more young into the next generation than late nesters (Dzus and Clark 1998), therefore the timing of nest initiation would be expected to influence lifetime reproductive success (Drent and Daan 1980). Female age has a strong influence on timing of nest initiation and clutch size in waterfowl (Rockwell et al. 1983, Baillie and Milne 1982). Because age can influence both nesting date and clutch size I wanted to asses the impact of age on these traits and see if the relationship between clutch size and nesting date remained apparent for age classes. The second hypothesis I tested was that female age (Second year (SY) vs. After second year (ASY)) and timing of nest initiation affected a female's clutch size. I predicted that clutch size could be potentially affected by an individual female and when she initiated her nest.

METHODS

Study Site

This project was conducted in the drift prairies of Eastern North Dakota, USA, during 2008-2009 in Benson, Nelson, Towner, and Wells County. Most of the region was dominated by small grain, oilseed, and row crop agriculture. Natural habitats are also present yet they are highly fragmented. My research focused on land enrolled in the Conservation Reserve Program or in Federal Waterfowl Production Areas. Avian predators such as red-tailed hawks (*Buteo jamaicensis*), Swainson's hawks (*Buteo swainsoni*), and northern harriers (*Circus cyaneus*) were observed regularly (C. Martin, University of Guelph, unpublished data). Common mammalian predators consisted of Coyotes (*Canis latrans*), Striped skunks (*Mephitis mephitis*), Raccoons (*Procyon lotor*), American Badgers (*Taxidea taxus*), American Mink (*Mustela vison)*, and Franklin's ground squirrels (*Spermophilus franklinii*). Due to sarcoptic mange in the area over the last decade, red fox (*Vulpes vulpes*) densities have been very low across the region.

Field Methods

In 2008 I conducted research on 6 township-sized (93.2-km^2) study sites that were part of the operational predator management program. In 2009 my research continued on only four of those study sites, which were no longer under active predator management. Nest searching plots consisted of 80 to 160 acres of planted perennial cover within each of the study plots (Cando, Minnewauken, Harlow, Mcville, Whitman and Bowdon) that were not randomly selected, but were selected based on the number of female mallards that were banded in that particular area by previous graduate students during 2006-2007 field seasons. Based on the banding information from the previous graduate students I had approximately 3-4 plots per study site. I selected sites where I had the greatest opportunity of finding high numbers of Mallard nests and the greatest opportunity of recapturing marked birds.

Plots were searched using slightly modified nest searching techniques (Klett et al. 1986, Higgins et al. 1969,) and completed three times at 2-3 week intervals beginning in early May (Arnold et al. 2007). To ensure consistency between crews and sites, I always used a 50m chain pulled by all-terrain vehicles driven in 1st gear, which was an effective way of regulating speed. Crews consisted of two technicians. To maximize the detection of nests and to avoid times when hens may be on incubation breaks, nest searching began at 0800 and ceased by 1400 hours (Loos and Rohwer 2004, Gloutney et al. 1993, Klett et al. 1986). In the latter part of the breeding season I continued searching until 1600 hours to find as many mallard nests as possible. A nest was defined as any scrape or bowl containing $\geq$1 egg (Stephens et al. 2005). Once a nest was located I recorded the Universal Transverse Mercator coordinates and marked the nest using a numbered wooden lathe placed 10 m from the nest. I also placed an orange metal rod (3mm diameter, 0.95 m length) directly at the nest bowl. Each orange metal rod was marked with a small piece of neon pink flagging for easier detection when I was ready to trap the nest.

For every nest I recorded the clutch size and candled eggs to determine stage of development at time of discovery, and every 6 to 10 days thereafter, until the nest either hatched or was destroyed by predators (Weller 1956). A nest was considered successful if $\geq$1 egg hatched and abandoned if the female was absent and there was no advancement in incubation. Nest initiation dates were determined by backdating with the assumption that females lay one egg per day.

In my 2006-2008 field seasons, I trapped female mallards on or after 18 days of incubation to decrease trap-induced abandonment (Rotella and Ratti 1990). In my 2009 field season, female mallards were trapped at various stages of incubation. I changed protocol to increase capture rates because some early nests were destroyed by predators or females abandoned due to inclement weather conditions (i.e. snow) before I had time to capture them.

To trap nesting female I used mist nets (Bacon and Evrard 1990), long handled nets (Loos and Rohwer 2002), walk in traps (Dietz et al. 1994), and sliding door traps (Weller 1957) from 2006-2009. After considerable experimentation with each method, mist nets were almost exclusively used in the 2009 field season because they were most effective at capturing multiple ducks throughout the day. Mist nets were tied between two pieces of PVC pipe carried by 2-3 technicians. Trapping was conducted during daylight hours. All captured hens were fitted with standard United States Fish and Wildlife Service bands, and bill length, head length, nare width, wing chord, tarsus length, and weight were all recorded. I also collected the second secondary covert of each female for age categorization. I attempted to catch every Mallard female at least once. At some nests I used several different techniques in an attempt to capture the female.

Female age was based on wing feather characteristics (Krapu et al. 1979; J. H. Devries and R. G. Clark unpublished data). I dried each secondary covert for 24 hours at 50 degrees Celsius in a forced air oven (Greenberg et al. 1972), weighed them on a

Mettler balance to the nearest 0.01 mm, and then dot counted the black and white surface area on 1mm x 1mm transparent grid paper. Each feather was dot counted twice by two different observers and if any discrepancies arose in a feather it was counted a third time. Aging techniques only allowed for separation into two age classes, SY or ASY. Discriminate function is as follows: y = -8.78 + 0.236 * second secondary covert weight (mm^2) + 0.012 * second secondary covert area of black and white markings; if y<0 then age = SY; if y>0 then age = ASY (Krapu et al. 1979 technique as modified by J. H. Devries and R. G. Clark unpublished data).

Statistical Methods

Consistency

For analyses of nesting date consistency, I truncated the data set to only include individual females that had a clutch size of 9 or greater in both years of capture. This was intended to reduce the number of renests that were included in these analyses. I also controlled for a year effect by calculating the mean initiation date for all clutches ≥9 eggs. I used each individual female's deviation from the mean nesting date in their year of capture for analyses of consistency. I conducted a regression analysis to test for potential effects of age, year, nest year, and individual female nested in year on julian initiation date (Proc Mixed; SAS Institute, Cary, NC). Nest year was a categorical variable that I used to see if females that nested early in the first year exhibited early nesting in the subsequent year and vise versa for late nesting females. Individual female was a random variable. The global model included interactions of age and year and followed a backward selection procedure with variable reduction by assessment of *P*-values ($\alpha = 0.05$). Residuals were assessed to ensure that assumptions of regression analysis were met. After variable reduction, I evaluated the residual *P*-value to assess within-bird variation and the random bird (year) *P*-value to assess among-bird variation in initiation date.

Clutch Size

Regression models were also used to evaluate potential factors influencing clutch size. All individuals captured were used in this analysis. I included the variables clutch size as a dependent variable with year (2006, 2007, 2008, 2009), age (ASY or SY), and julian date as explanatory variables. Initially, the global model included all interactions. Backward variable selection followed the same procedure as our consistency analyses. Residuals were assessed to ensure that assumptions of regression analysis were met.

RESULTS

Consistency

I found 2274 mallard nests from 2006-2009. I captured 944 females out of that group in the same time period. Only 8 of 157 females (5%) abandoned their nest due to investigator activity when trapping at early incubation stages (0-5 days) in 2009. Fifty-three individuals met the criteria of ≥9 eggs in both years of capture and were used for analyses of consistency in nest dates. I calculated a mean julian initiation date for each year (Table 1). I found strong evidence for variation among birds within year (Z=3.59, *P*≤0.001: Fig. 1) of nest initiation date. Interestingly, there was a lack of evidence for significant variation within birds between years (Z=1.47, *P*=0.0703). Age (F=1.99, *P*=0.1648) and nest year (1^{st} capture year to 2^{nd} capture year) did not influence nest initiation date (F=2.93, *P*=0.1176).

Clutch Size

All 944 females captured were used for my clutch size analyses and categorized to an age group. Age (F=5.20, *P*=0.0014), year (F=8.64, *P*=0.0034), and julian date (F=191.88, *P*<0.0001) all had significant impacts on clutch size (Table 2). The interaction of age by julian date was not significant (F=0.55, *P*=0.4578). As expected, adult females had a larger mean clutch size than juveniles, but the effect size was small (ASY females had 0.32 more eggs than SY females). Clutch size varied by year and was lowest in the year with the latest mean nest initiation date (Table 3). Finally, clutch size declined with nesting date (Fig. 2) for both SY and ASY females, such that for every 20 days of delay in nest initiation clutch size was reduced by 1 egg.

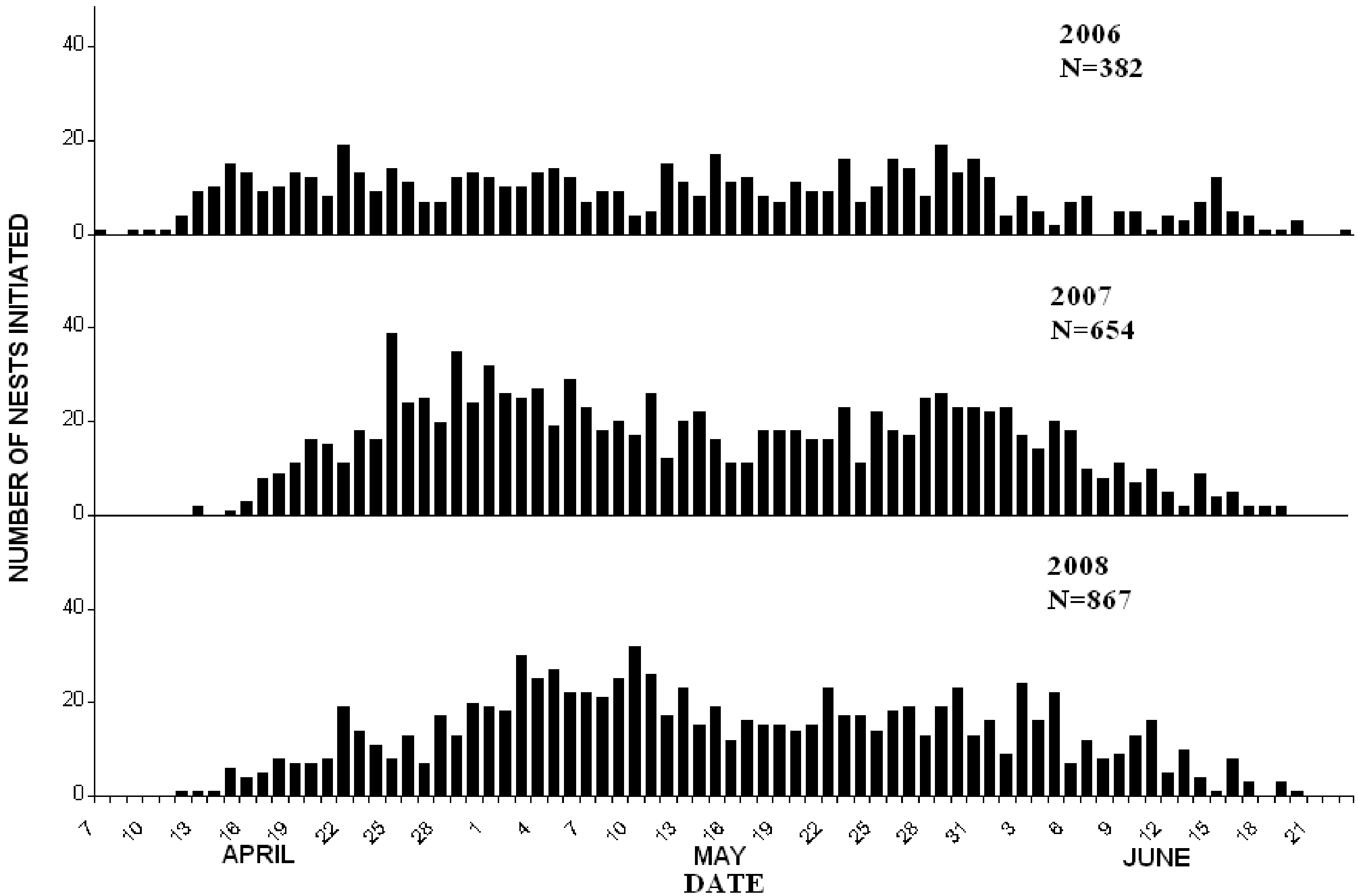

Figure 1. Frequency of Mallard nest initiation dates in eastern North Dakota, USA, during 2006-2008. This includes all Mallard nests that were found and monitored

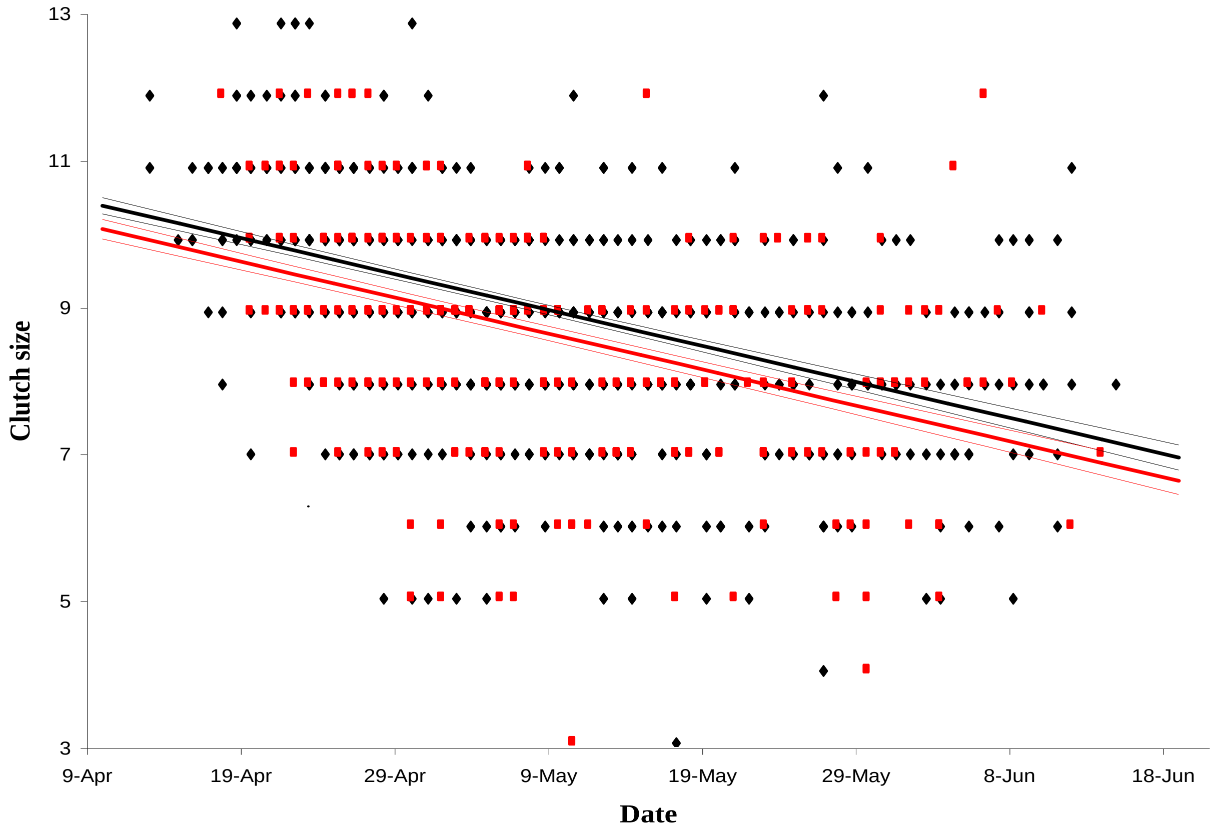

Figure 2. Model based mean clutch sizes (± SE) for ASY (black line) and SY (red line) females in relation to initiation date in eastern North Dakota, USA, 2006-2009.

Table 1. Average nest initiation date of captured female Mallards (± SE) with clutch sizes of ≥9 for each year of the study in eastern North Dakota, USA.

Year	Sample Size	Mean Date	SE
2006	8	29 April	4.52
2007	24	29 April	2.61
2008	42	12 May	2.02
2009	33	27 April	2.29

Table 2. Factors affecting clutch size of Mallard nests in eastern North Dakota, 2006-2009. Parameter estimates, confidence intervals, and test statistics are from a reduced regression model.

			95% CI			
Variable	**df**	**β**	**Lower**	**Upper**	**T**	**P**
Intercept	944	15.38	14.51	16.25	34.54	<0.01
Year06	944	-0.63	-1.03	-0.24	-3.17	0.02
Year07	944	-0.55	-0.85	-0.25	-3.61	<0.01
Year08	944	-0.46	-0.76	-0.16	-2.97	0.03
Adult(ASY)	944	0.32	0.11	0.53	2.94	0.03
Julian	944	-0.05	-0.06	-0.04	-13.85	<0.01

[a] I arbitrarily set the effect size for yr = 2009 and age = juvenile (SY) to zero.

[b] Day 1 is 1 January.

Table 3. Average clutch size for all captured female Mallards (± SE) for each year in eastern North Dakota, USA.

Year	Sample Size	Mean	SE
2006	89	8.98	0.18
2007	313	8.73	0.09
2008	391	8.59	0.08
2009	157	9.87	0.13

DISCUSSION

Consistency

I arbitrarily defined consistency to be within 7 days of a female's first initiated nest in a previous year. Approximately 17% of recaptured females initiated nesting within 3 days of the nest initiation date recorded in the first year they were captured and approximately 36% were within 7 days (Fig. 3). Females that showed consistency in nesting dates (N=14) tended to nest prior to the mean nesting date in both years of nesting (Fig. 4). All 4 individuals that had the same relative nesting date in both years were early nesting females (Fig. 4). Eleven of the 14 females showing consistency nested early, whereas only 3 of 14 females that showed consistency nested later than the mean in both years. Therefore, my hypothesis that wild female Mallards would show consistency in their individual nesting dates among years was supported with my sample of banded birds.

In a captive study of wild stock Mallards, females exhibited consistency in first nest initiation dates whether they were early or late nesting females (Batt and Prince 1979). Those females had relatively low variability for individual nesting dates in subsequent years even though there was a high degree of variation in the entire sample of nesting dates. In that study, birds were fed *ad libitum*, kept in the same breeding compartments, and paired with the same mate every year, which may explain why they exhibited remarkable consistency during the duration of the study. My results for wild Mallards showed that early nesting females exhibited greater consistency than those females that nested after the mean annual initiation date. However, my sample of Mallards and their consistency in nesting dates in comparison to the captive study conducted by Batt and Prince (1979) were likely decreased because of the variation in natural environments and because I likely included some renests in the sample. Truncating the data set to only include birds with ≥9 eggs is also likely to exclude some consistent late nesters.

Consistency in nesting dates across years, especially for late nesters, was a surprising result in the Batt and Prince (1979) study, and remains so in my study of wild Mallards. There appears to be strong directional selection for early breeding, therefore I expected that the timing of nest initiation has consequences for lifetime reproductive success (Drent and Daan 1980, Blums and Clark 2004). Early nesting Mallards lay larger clutches than later nesters. Early nests have higher survival of ducklings to the fledging stage (Guyn and Clark 1999, Dzus and Clark 1998, Rotella and Ratti 1992). Post fledging survival of ducklings and recruitment into the breeding population is higher for early hatched young (Blums and Clark 2004, Rohwer 1992). Early nesting females also have greater opportunities to renest in the event of nest failure. These findings suggest strong benefits to early nesting and help explain the consistency of early nesting by female Mallards. However, the consistency in late nesting by captive Mallards (Batt and Prince 1979) and by some wild females in my study is difficult to explain. Perhaps there is some survival advantage to later nesting that balances the apparent production benefits of early nesting, as suggested by Toft et al. (1984). There could also be an advantage to later nesting as shown by Garrettson and Rohwer (2001) and Pieron and Rohwer (2010) where nest success increases as the breeding season progresses.

Clutch Size

Females exhibited smaller clutch sizes as the breeding season progressed and juveniles had smaller clutch sizes than adults. Age was significant in the model but the difference between adult and juvenile clutch sizes when corrected for nesting date was only 0.32 eggs. Seasonal declines in clutch size in my study are similar to findings from a range of studies of wild waterfowl nesting in temperate regions (Devries et al. 2008, Krapu et al. 2004, Rohwer 1992, Cowardin et al. 1985, Dzubin and Gallop 1972). However, why clutch sizes decrease throughout the breeding season still remains unclear. There is much speculation that clutch size declines are caused by a timing issue (Rohwer 1992). As the season progresses hens are running short on time for their ducklings to fledge and fly south before it gets to cold therefore enabling them to lay smaller clutches. The faster a female can hatch out a nest the higher her chances are for recruiting her young into the population.

The many studies that have been conducted on Mallards with regards to age influences on clutch size have yielded conflicting results while examining differences in intercepts (Table 4). Despite a large sample size (N=2,410), Devries et al. (2008) found no relationship between age and clutch size. A study conducted by Cowardin et al. (1985) with a smaller sample size (N=338) also found that age did not influence clutch size, but young females nested later than older females. However, they believed that despite their small sample size there may be an age effect on clutch size beyond that of date because the difference approached significance. Cowardin et al. (1985) suggests that older females may have had larger clutch sizes than Mallards in their first breeding year but the difference was undetectable because of the sample size. Even in a captive population there was no difference between clutch sizes for yearling and older birds (Batt and Prince 1978). Interestingly, in another study a significant interaction was detected between age and year (Lokemoen et al. 1990). This interaction clouded the relationship between age and clutch size but was still significant. My results are more closely supported by Swanson et al. (1986) and Krapu and Doty (1979), who both found that age influences clutch size.

Unless you are certain that every nest found is indeed the first initiated nest of the season it is difficult to attribute age as an influence on clutch size. In all of the studies of Mallards mentioned, including this one, the age influence can be confounded by renesting events. With Mallards' high propensity to renest (Krapu and Doty 1979) it is unlikely that many late nesting females are nesting for the first time especially ASY females.

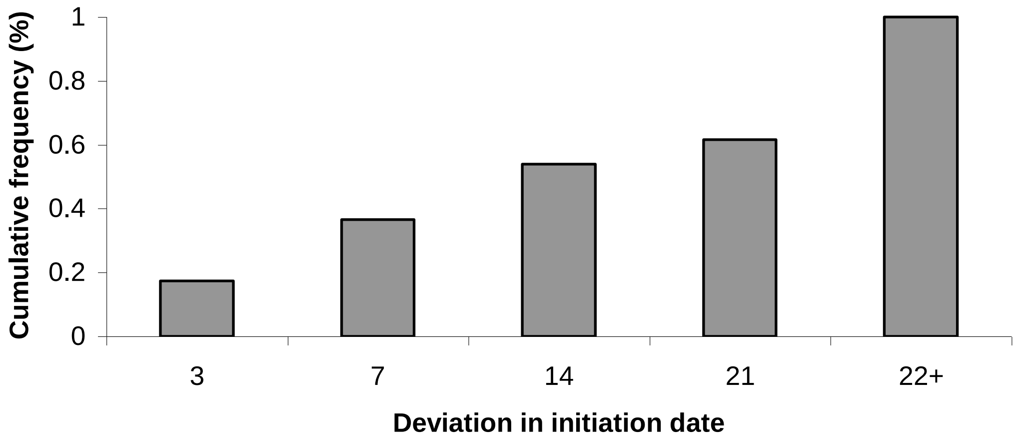

Figure 3. Deviation in dates of first nest initiation for 53 individual Mallard females that nested in 2 subsequent years in eastern North Dakota, and had clutch sizes of ≥9. Frequencies are cumulative.

Table 4. The effects of female age on clutch size from other studies of Mallards

Location	Sample Size	P-Value	Effect Size[a]	Source
North Dakota, USA	944	0.0014	0.32	Kimmel et al. 2010
Prairie Parklands, Canada	2,410	-	-	Devries et al. 2008
North Dakota, USA	461	0.008	0.47	Lokemoen et al. 1990
North Dakota, USA	8	<0.01	-	Swanson et al. 1986
North Dakota, USA	338	0.07	0.90	Cowardin et al. 1985
North Dakota, USA	53	<0.05	1.00	Krapu and Doty 1979
Manitoba, Canada[b]	60	-	-	Batt and Prince 1978

[a] Difference in clutch sizes of ASY and SY females, ASY females were larger
[b] Birds held in captivity with *ad libitum* food

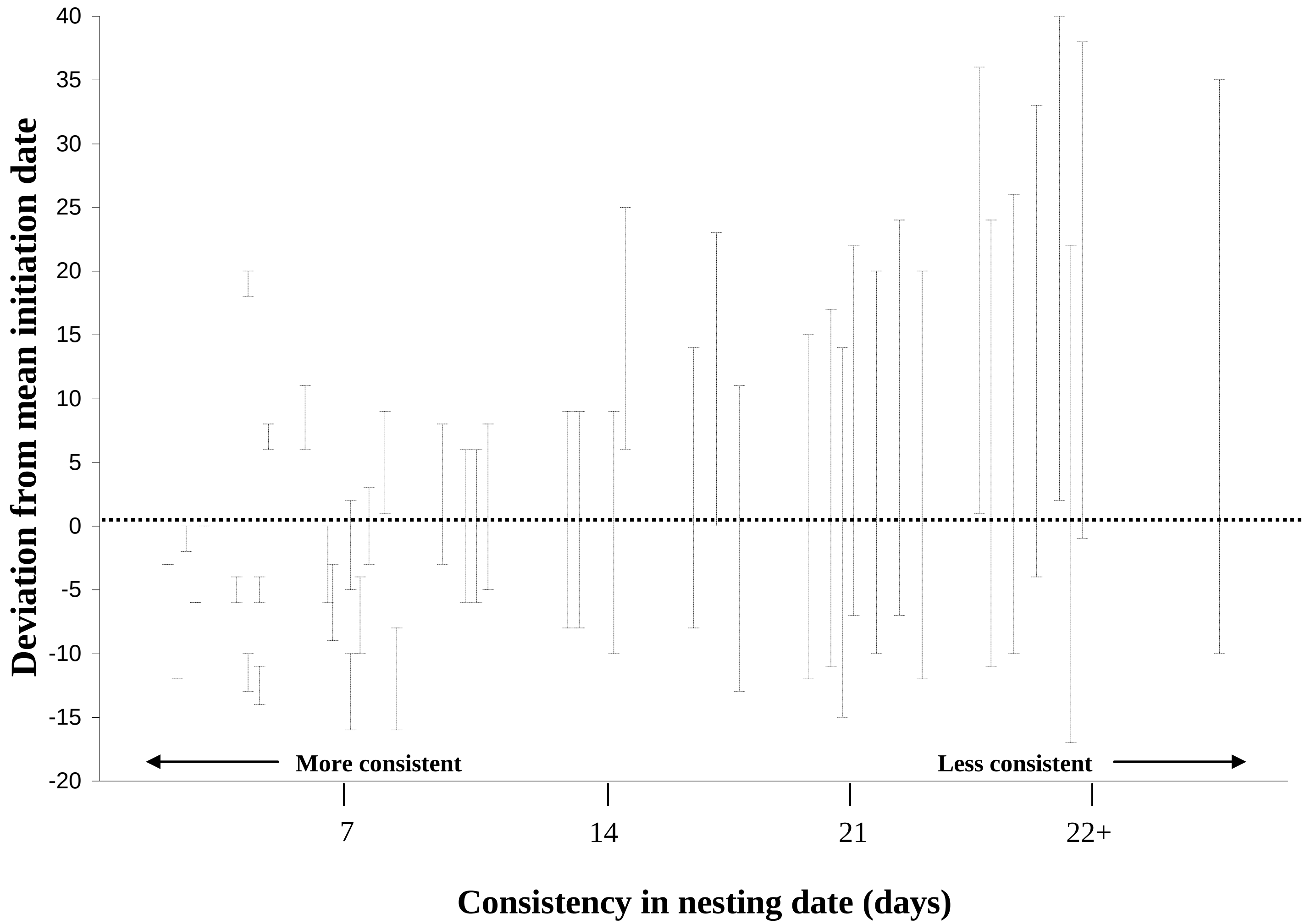

Figure 4. Individual deviation of presumed first-nest initiation dates for 53 individual Mallards that nested in 2 subsequent years on study sites in eastern North Dakota. Horizontal marks denote nest initiation dates relative to mean dates for all Mallard nests with ≥9 eggs during that year. Zero on the y-axis represents the mean initiation date for all nests with ≥9 eggs among years (2006-2009).

SUMMARY

Throughout a single breeding season hen Mallards exhibit substantial variation in nest initiation dates ranging from April until mid June. This has also been shown in captive populations of Mallards. Interestingly, roughly one third of the population in this study of wild Mallards (~36%) nested within 7 days of their previous year's first initiated nest. Also, each of those individuals were early nesters nesting prior to the mean annual initiation date. This suggests that there is some level of consistency within individual females among years. With the advantages that early nesting females have, it is not surprising to see consistency in early breeding. Early nesters have larger clutch sizes, higher survival of ducklings and higher recruitment rates. It is difficult to explain why I found consistency in females nesting later than the mean annual initiation date. It could be correlated to an apparent nest success advantage that some studies have shown increases as the breeding season progresses. Nevertheless, further research needs to be conducted examining the consistency hypothesis when the technology allows us to differentiate between first initiated nests and renesting events. Such technologies would include advanced telemetry units that would not affect the behavior of the bird. Until then it will be difficult to accurately examine the hypothesis of nest initiation consistency within an individual without including renesting events.

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VITA

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