2005

Environmental factors influencing incubation constancy and recess frequency in Gadwall (Anas strepera) in the prairie pothole region of North Dakota

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ENVIRONMENTAL FACTORS INFLUENCING INCUBATION CONSTANCY AND RECESS FREQUENCY IN GADWALL (*ANAS STREPERA*) IN THE PRAIRIE POTHOLE REGION OF NORTH DAKOTA

A Thesis

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Master of Science

in

The School of Renewable Natural Resources

by
Nicole F. Lorenz
B.S., Loyola University of New Orleans, 1997
May 2005

ACKNOWLEDGMENTS

I would like to thank my major professor, Dr. Frank Rohwer. Prior to the start of my first semester as a graduate student, Frank extended an invitation for me to stay with him and his family until I was able to find an apartment. That kind gesture has stayed with me and is a testament to his dedication and support of his graduate students. I want to thank him for his guidance and constant editorial comments that have turned this thesis into something that I can be proud of. I would also like to that my committee members, Dr. Mike Chamberlain for hanging in there with me through this long process, and Dr. Allen Rutherford for joining my committee on such short notice.

I would like to give a special thank you to Dr. Mark Mitchell. He was originally on my committee until fieldwork in the Galapagos prevented him from attending my defense. Over the years he was a great source of inspiration to me, always there with encouraging words and a positive attitude.

I would like to thank Liz Loos for all of the time she spent helping me make sense of SAS code, and for her statistical advice. She was always available to answer any questions I might have, and never hesitated to offer her time and expertise to help me when I needed it.

I am forever grateful to all of my family, friends, and co-workers that have supported me during this endeavor. Their continued encouragement, and the countless hours of babysitting my daughter Phoebe, provided me with precious time to work on this thesis. To Meg Streiff and Michelle Fischer, I looked forward to our weekly gatherings. These meetings helped to keep me motivated and productive. I would especially like to thank my parents, Fallon and May Lorenz, who have always encouraged me to follow my

dreams. They demonstrated to me through their own lives that hard work and determination would make those dreams come true.

Finally, I would like to tell my husband, best friend, and confidant, Scott Hemmerling, that I am forever in his debt. He was my cheering section, and constantly reminded me that my goals were attainable, even when there seemed to be no light at the end of the tunnel. Above all, he believed in me and allowed me to believe in myself. For his unconditional love, support, advice, ideas, and time, I say thank you.

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ABSTRACT

I examined nest attendance patterns for 132 Gadwall (*Anas strepera*) females breeding in the prairie pothole region located in Towner County, North Dakota from May to July 2000 - 2001. Overall, Gadwall had a daily incubation constancy of 76.5 ± 10.8%, and daily recess frequency of 2.2 ± 1.1 with each recess lasting 179.8 ± 133.8 minutes. Unlike other waterfowl species, Gadwall increased incubation constancy and decreased recess frequency as daily high temperature increased and showed no change in constancy with precipitation. Gadwall incubation constancy did not fit the body-size hypothesis, as Gadwall have a lower incubation constancy compared to species smaller in size. This may be because Gadwall have the latest peak clutch initiation of all dabbling ducks, providing the advantage of dense nesting cover and warmer ambient temperature compared to earlier nesting species. Of the 132 females, 19 (14%) delayed nocturnal incubation resulting in a significant difference in incubation constancy (P= 0.001) and recess frequency (P = 0.001) from those that did not delay nocturnal incubation. However, components of the incubation rhythms, after the onset of nocturnal incubation were similar for both groups.

INTRODUCTION

Nest attendance and daily incubation patterns for prairie nesting waterfowl during the breeding season are a critical aspect of reproductive success. The incubation strategy for Gadwall (*Anas strepera*) females and other waterfowl species includes a trade-off between maintaining a favorable environment for embryo development, meeting metabolic requirements of the incubating parent, and minimizing the risk of predation (Afton 1980, Flint and Grand 1999). The ability of a female to balance embryo requirements with her own energetic needs is a daily struggle often influenced by environmental conditions including temperature and precipitation. In addition, nest initiation date and the stage of embryo development could be important factors influencing incubation rhythms. An inability by the female to maintain a suitable balance between investment in her clutch and her energetic needs may result in nest abandonment (Korschgen 1977), or affect her survival (Manlove and Hepp 2000). Therefore, an appropriate incubation strategy by a bird during the breeding season is a crucial component to a successful nest.

In general, birds have the capability of storing and utilizing energy reserves in the form of fat (Hohman 1986), protein, and calcium (Ankney and MacInnes 1978). Large-bodied waterfowl, such as geese (Anserini), have a greater capacity for storing these nutrients than small-bodied waterfowl (Mallory and Weatherhead 1993). Unlike larger species, Gadwall and other relatively small-bodied waterfowl (Anatini, Aythyini) are unable to rely heavily on stored nutrient reserves for egg laying and incubation. These species must rely more on exogenous resources to meet energetic requirements (Yerkes 1998; Manlove and Hepp 2000), feeding extensively during much longer, and

more frequent incubation breaks than geese (Thompson and Raveling 1987). Reliance on exogenous resources means females spend time away from the nest, resulting in lower incubation constancy.

Body condition, indexed by mass, is a good indicator of the amount of stored fat females have access to during incubation. Therefore, body mass and its influence on incubation rhythms is one element that has been the focus of recent research. Female Canada Geese (*Branta canadensis*; Aldrich and Raveling 1983) and Mallard (*Anas platyrhynchos*; Gatti 1983) with a higher body mass at the start of incubation, were more attentive to their nests than lighter females. On the other hand, Redhead (*Aythya americana*; Yerkes 1998) and Blue-winged Teal (*Anas discors*; Loos 1999) with lower body mass at the end of incubation had higher incubation constancy.

Variation in body size and body condition are not the only factors that influence nest attendance patterns. The time females spend on the nest is impacted by changes in weather conditions, laying date, and stage of embryo development. Studies on Northern Shoveler (*Anas clypeata*; Afton 1980), Common Goldeneye (*Bucephala clangula*; Mallory and Weatherhead 1993), Redhead (Yerkes 1998), Spectacled Eider (*Somateria fischeri*; Flint and Grand 1999), Blue-winged Teal (Loos 1999), Wood Duck (*Aix sponsa*; Manlove and Hepp 2000), Greater Snow Geese (*Chen caerulescens atlantica*; Poussart et al. 2000), Mallard and Pintail (*Anas acuta*; Hoover 2002) have related incubation rhythms to environmental factors, such as temperature and precipitation, embryo development, and laying date.

Most temperate nesting waterfowl seem to follow similar incubation patterns. Females often decrease nest constancy with an increase in ambient temperature (Caldwell

and Cornwell 1975, Afton 1980, Ringelman et al. 1982, Mallory and Weatherhead 1993, Eichholz and Sedinger 1999). Increased amounts of precipitation generally result in increased nest constancy (Caldwell and Cornwell 1975, Afton 1980, Eichholz and Sedinger 1999). In addition, females often decrease nest attendance during later stages of embryo development (Afton 1980, Mallory and Weatherhead 1993, Eichholz and Sedinger 1999, MacCluskie and Sedinger 1999).

Other researchers have looked at the relationship between nest attendance, laying date and length of the incubation period. Feldheim (1997) found a negative relationship between laying date and the length of the incubation period for five species of dabbling duck, including Blue-winged Teal, Mallard, Gadwall, Northern Pintail, and Northern Shoveler. In addition, Goldeneye, Blue-winged Teal, Mallard and Northern Pintail show an inverse relationship between nest constancy and the length of the incubation period (Zicus et al. 1995, Loos 1999, Hoover 2002). However, some waterfowl show no connection between nest constancy and incubation duration (Flint and Grand 1999, Manlove and Hepp 2000, Hoover 2002).

Gadwall incubation patterns and variables that influence these patterns have not been adequately assessed. In general, Gadwall reach the northern Great Plains about April 1st and continue arriving on the breeding grounds, in large numbers, for the entire month. In addition to their late arrival, compared to most other dabbling ducks, Gadwall delay nest initiation 23-28 days once in North Dakota (Bellrose 1980, Beauchamp et al. 1996). This delay gives Gadwall the latest peak clutch initiation (June) of all dabbling ducks (Beauchamp et al. 1996).

For Gadwall, the influence of weather, laying date, and stage of the embryo on nest attendance and recess frequency could differ from waterfowl species with earlier nest initiation dates. The above variables may influence late nesting Gadwall differently than early nesting Northern Pintail and Mallard (beginning in early April) or intermediate nesting Northern Shoveler (Beauchamp et al. 1996).

The objectives of this study were to examine the relationships of: 1) ambient temperature, and precipitation on nest constancy and recess frequency; 2) embryo development on nest constancy and recess frequency; 3) laying date on nest constancy and recess frequency; 4) recess duration on recess frequency; 5) nest constancy and laying date on incubation duration; and, 6) recess frequency and recess duration on incubation duration.

METHODS

Study Area

Fieldwork was conducted in Towner County, North Dakota (48.4º N, 99.2º W) in 2000 and 2001 from April through July. Study sites were located on privately owned lands enrolled in the Conservation Reserve Program and federally owned Waterfowl Production Areas between Egland, ND and Cando, ND.

Topography

North Dakota is divided into 4 main topographical regions: the Great Plains, the Missouri Coteau, the Glaciated Plains, and the Red River Valley (Enz 2003). The study was done in the Glaciated Plains, which extend from the east to the central part of the state (Enz 2003). This region is characterized by a flat to gently rolling landscape dotted with temporary, seasonal, semi-permanent and permanent wetlands (Kantrud 1985). These wetlands, known as the prairie potholes, extend from central Alberta to central Iowa (Kantrud et al. 1989). When conditions are favorable, the prairie pothole region can produce close to 50% of the annual fall flight of ducks (Baldassarre and Bolen 1994).

Climate

Duck production varied greatly from year to year in the prairie pothole region largely due to erratic precipitation patterns that alter the number of pond basins available for breeding (Klett et al. 1988). Optimal environmental conditions exist during years with heavier precipitation, resulting in a large number and acreage of seasonal wetlands that contain surface water. Dabbling ducks often respond with higher population densities in this breeding area (Stewart and Kantrud 1973).

Average annual precipitation in North Dakota ranges from less than 33 centimeters in the northwest to more than 51 centimeters in the southeast. During the summer, rainfall hits its peak in June when amounts range from just over seven and one half centimeters in the extreme northeast and northwest to more than ten centimeters in several areas in the southern half of the state (Jensen no date). Annual temperatures in North Dakota range from 3°C in the northeast to 6°C along the southern border. Daily high temperatures reach a peak in July ranging from 19°C in the northeast to 23°C in parts of the south (Jensen no date).

Elevations in northeastern North Dakota are generally among the lowest in the state, however, Towner County (along with neighboring Cavalier, Walsh, and Ramsey counties) has elevations exceeding 533 meters. In general, higher elevations usually show a 2° to 4° decrease in temperature for every 305 meters. The average annual temperature in Towner County area is less than 3°C. During the summer months there is often a trough of cooler temperature located in Towner County, making it one of the coolest areas in the state (Jensen no date).

Field Procedures

Nest searching. -- For this study, nest searches were conducted between 0600 to 1400 hours. Nests were located by dragging a 50-70 meter chain between two all-terrain vehicles or tractors through nesting cover. The noise from the vehicles and disturbance of the vegetation by the chain would flush the female, allowing the researcher to locate the nest (Higgins et al. 1969, Hohman 1986, Klett et al. 1986). Once nests were located, they were marked by placing a 1 m wooden lathe (Grand and Flint 1997, Loos 1999) approximately 3 m north of the nest (Loos 1999). In addition, a bright orange metal rod

approximately 1 m in length and 3 mm in diameter was placed next to the nest (Loos 1999). The nest markers, which have no influence on nest success (Greenwood and Sargeant 1995, Grand and Flint 1997), were used to help the researcher locate the nest upon subsequent visits.

Data recorded for each nest included species, the date and time the nest was found, the number of eggs in the nest, and the stage of incubation (Loos 1999, Hoover 2002). For nests found during the laying stage, differences in the appearance and temperature of eggs in the nest were used to determine if an egg had been laid that morning. An egg slightly warmer and lighter in color than other eggs in a nest was usually an indication that the female had laid an egg for that day (Loos 2004). For nests found during the incubation stage, field-candling techniques (Weller 1956) were used to estimate stage of development (Caldwell and Cornwell 1975). This information, along with the assumption that one egg is laid each day (Alisauskas and Ankney 1992), allowed me to backdate to determine nest initiation date.

Measurement of Incubation Behavior.-- Once a nest was located, a temperature sensing "hobo egg" was placed in the center of the Gadwall nest. The hobo egg contained a thermistor connected to a microcomputer data logger (Hobo Temp XT, Onset Computer Corporation, Pocasset, Massachusetts, USA). The microcomputer was enclosed in a plastic container, which protected it from the elements, and was hidden in vegetation near the nest.

The hobo egg, as described by Loos (1999), was made from a hollowed out chicken egg. A 5-15 mm hole was placed at the midpoint of the long axis of the egg, and the contents of the egg were drained. Eggshells were rinsed with water and soaked in

chlorine bleach for 2-5 minutes to remove the shell membrane. After drying, the shell was reinforced with 1-2 mm of epoxy glue on the interior surface. A thermistor was placed at the top of the egg through the drainage hole and attached with a small piece of electrical tape. The final step in the construction of the hobo egg was the placement of a curved metal plate (15 mm X 15 mm X 0.5 mm) welded to a 10 cm metal stake that was glued over the drainage hole. The stake and hobo egg was inserted into the ground near the center of the nest bowl, ensuring contact between the female and the thermistor. The data logger recorded temperatures every 5 minutes for 6 days. On the 6^{th} day nest checks were conducted. At this time I recorded the condition of the nest, the status of the female, the number of eggs that remained in the nest, and the progression of embryo development. Data loggers were then downloaded onto a laptop computer.

Temperature data from the hobo egg for each female were examined as graphical data and on spreadsheets. Because females generally incubate eggs at a consistent temperature, both forms of visual examination allowed me to determine female arrival and departure times based on temperature fluctuations. A 1.5°C increase from the lowest recorded temperature during the recess indicated the arrival of the female on the nest (Loos 1999). A 1.5°C decrease in temperature, maintained for three time intervals (15 minutes) indicated the departure of the female from the nest. When temperature decreases occurred, but were not maintained for three time intervals (less than 15 minutes), the female was considered to be on the nest and involved in comfort movements or resettlements (Caldwell and Cornwell 1975, MacCluskie and Sedinger 1999). Using hobo temperature data to monitor incubation constancy in prairie dabbling

ducks provides an accurate measure of daily nest attendance patterns (Hoover et al. 2004).

I calculated incubation constancy as the percentage of time spent on the nest during a 24-hour period beginning at midnight. Minutes on the nest was the total number of minutes a female spent on the nest during a 24-hour period beginning at midnight. Recess frequency was the total number of times a female left the nest per day. Recess duration was the mean recess length per day for each female (Loos 1999, Hoover 2002). I calculated the overall incubation constancy by averaging the daily incubation constancies for each female. Likewise, overall recess frequency was the average of daily recess frequencies, and overall recess duration was the average of mean daily recess durations. The incubation period was defined as beginning the day after the last egg was laid (Loos 1999) and ending 24 hours prior to hatch. Nests that did not have four complete days of data were removed from the data set. In addition, any day with less that 24 hours of nest attendance was excluded from analyses.

Weather Parameters.-- Ambient temperature and precipitation data were obtained from the National Weather Service in North Dakota. Ambient temperature was recorded at the weather station in Rugby, Pierce County, North Dakota (48.4°N, 100.0°W) and precipitation data were recorded at the weather station in Cando, Towner County, North Dakota (48.5°N, 99.2°W).

Statistical Analysis

I typically flushed females at 6-day intervals to download data. To determine if days of nest checks should be excluded from the analysis, I conducted a paired t-test

(PROC TTEST; SAS Institute Inc. 1999) to compare time on the nest on the day I flushed the female to the mean time the day before I flushed the female.

Descriptive Statistics.-- I calculated daily and mean incubation constancy, total amount of time (minutes) females remained on the nest each day, the average number of recesses females took each day, recess duration (minutes), and length of the incubation period for each female in the study (PROC UNIVARIATE; SAS Institute Inc. 1999).

Incubation Constancy.-- The influence of ambient temperature (daily high temperature and daily low temperature), precipitation, incubation stage, nest initiation date, and the interaction of Julian date and the above variables on female daily nest attendance were examined using a mixed linear model with repeated measures (female; PROC MIXED, SAS Institute Inc. 1999). I used backward selection to remove non-significant interactions and main effects ($\alpha < 0.05$) to arrive at my final model. There were 19 females in my study group that delayed nocturnal incubation from 1-6 days. I examined the influence of nocturnal incubation on incubation constancy using an Analysis of Covariance (ANCOVA; PROC MIXED), with repeated measures (female). The ANCOVA had two groups of nests: females that began nocturnal incubation the day the last egg was laid ("normal") and females that delayed nocturnal incubation for 1 or more days. Julian date, incubation stage, daily high and low temperature and precipitation were used as covariates in the model.

Incubation Recesses.--The influence of ambient temperature, precipitation, stage, laying date, daily mean recess duration, and daily time off the nest and the interaction of Julian date and the above variables on female daily recess frequency were examined using a mixed linear model with repeated measures (PROC MIXED, SAS Institute Inc.

1999). I used backward selection to remove non-significant interactions and main effects ($\alpha < 0.05$) to arrive at my final model. I examined the influence of ambient temperature (daily high temperature and daily low temperature), precipitation, stage of the egg, and nest initiation date on female recess frequency using a mixed linear model with repeated measures. I examined the influence of nocturnal incubation on recess frequency using an Analysis of Covariance (ANCOVA; PROC MIXED), with repeated measures (female) that controlled for Julian date, incubation stage, daily high and low temperature, and precipitation effects. Females were once again split into normal nests and delayed nests.

A pattern of recess frequency over a 24-hour period was established by dividing a single day into 24, 1-hour time intervals. The pattern of recess initiation times was examined by regressing the number of recesses on the hour of day using polynomial analyses (PROC GLM).

Incubation Period.-- The influence of mean incubation constancy, nest initiation date, the number of recesses per day, and recess duration on the length of the incubation period was examined using a mixed linear model (PROC MIXED; SAS Institute Inc. 1999). This analysis included only successful nests discovered during the laying stage. Successful nests were defined as nests that hatched at least one egg.

RESULTS

Nest attendance data were collected from 132 female Gadwall. Nest initiation dates ranged from May 14 to July 1 with the average initiation date of June 1, and clutch sizes ranged from 7 to 12 eggs per nest, averaging 9.53 eggs (± 1.17). I had a minimum of 4 days and a maximum of 24 days of incubation constancy for each female totaling 1720 incubation days. Weather data were collected for each day of the period of study, a total of 136 days (Table 1). During this time, ambient temperatures ranged from a low of –2.1°C in May to a high of 31.8°C in July.

There was a significant difference in incubation constancy between the day a female was flushed and the day before the flush. Females decreased time on the nest by approximately 86.5 (± 21.1) minutes on days when they were flushed. Thus, I excluded from analyses constancy data for any day a female was flushed by an observer, which reduced the number of incubation days available for analyses to 1632.

Overall Descriptive Statistics

Females spent 76.5% (± 10.77) of their day on the nest totaling approximately 1101.7 (± 155.12) minutes on the nest every day (Table 2). Females took an average of 2.2 (± 1.11) recesses each day with an average recess duration of 179.8 (± 133.80) minutes. For 80 females in my study, I was able to calculate the length of the incubation period (day after the last egg was laid and ending 24 hours prior to hatch), which lasted an average of 25.1 days.

Of 132 females, 19 (14%) delayed nocturnal incubation beyond the day after they laid their last egg. Three of these females were early nesters (initiating nests ≤ May 27th), 11 were mid-season nesters (initiating nest between May 28th-June 5th), and five were

Table 1. Daily environmental patterns in Towner County, North Dakota for the time period of May to July 2000-2001.

Component	Mean	SD	Medium	Range	N (days)
High temperature (ºC)	22.9	5	23.1	8.5-31.8	136
Low temperature (ºC)	10.5	4.6	10.6	-2.1-18.9	136
Precipitation	3.57	12.23	0	0-122.7	136

Table 2. Daily nest attendance patterns for incubating Gadwall in Towner County, North Dakota for the time period of May to July 2000-2001.

Component	Mean	SD	Median	Range	N
Incubation constancy (% of day)	76.50	10.77	77.78	10.76-100	1632
Minutes on nest per day	1101.72	155.12	1120.00	155-1440	1632
Number of recesses per day	2.21	1.11	2.00	0-8	1632
Recess duration per recess (minutes)	179.81	133.80	142.50	30-1185	1632
Incubation period (days)	25.13	2.30	25.00	21-31	80

late season nesters (initiating nests ≥June 6th). For the Gadwall in this study, 48.7% of females began nocturnal incubation the first day after the last egg was laid. By the second day, 68.9% of females had begun incubation, 75.5% had begun by day three, 88.7% began by day four, and 95.1% by day five. Analysis of covariance that controlled for the effects of Julian date, incubation stage, daily high and low temperature and Julian*incubation stage interaction revealed a significant difference in incubation constancy ($F_{1,130}$ = 83.13, P = 0.001, slope = -235.47) and recess frequency ($F_{1,130}$ = 39.17, P = 0.001, slope = -0.850) between females that did and did not delay nocturnal incubation. Thus, subsequent analyses were conducted separately on females that delayed nocturnal incubation and those that did not.

Incubation Constancy

Incubation constancy of Gadwall that did not delay nocturnal incubation was significantly influenced by Julian date, incubation stage, daily high and low temperature, and the interaction of Julian date*stage (Table 3). Gadwall decreased the time they spent on the nest as Julian date, incubation stage, and daily low temperature increased. In addition, females spent more time on the nest as daily high temperature increased. The significant interaction between Julian date*incubation stage for daily incubation constancy reflects differing patterns of incubation constancy for nests initiated early in the season than those initiated later.

Incubation constancy of Gadwall that delayed nocturnal incubation was significantly influenced by incubation stage, daily high and low temperature, and the interaction of Julian date*incubation stage (Table 4). Gadwall decreased the time they spent on the nest as daily low temperatures increased. In addition, females spent more

Table 3. Mixed model multiple regression with repeated measures of various influences on daily incubation constancy in Gadwall that did not delay nocturnal incubation.

Variable	*F*-value	df[a]	*P*-value	Parameter estimate
Julian date	13.66	1156	0.0002	-4.9046
Incubation Stage	6.56	1156	0.0106	-31.7072
High temperature	33.69	1156	0.0001	5.1918
Low temperature	41.23	1156	0.0001	-7.1866
Precipitation	1.22	1155	0.2692	0.4020
Julian date x stage	6.65	1156	0.0101	0.1818

[a] Degrees of freedom for numerator = 1

Table 4. Mixed model multiple regression with repeated measures of various influences on daily incubation constancy in Gadwall that delayed nocturnal incubation.

Variable	*F*-value	df[a]	*P*-value	Parameter estimate
Julian date	0.28	327	0.6003	2.0066
Incubation Stage	39.61	329	0.0001	151.98
High temperature	20.01	329	0.0001	8.9530
Low temperature	4.13	329	0.0430	-5.5129
Precipitation	1.98	328	0.1601	-1.3824
Julian date x stage	34.73	329	0.0001	-0.7482

[a] Degrees of freedom for numerator = 1

time on the nest as incubation stage and daily high temperature increased. The significant interaction between Julian date*incubation stage in their effect on daily constancy once again reflects different patterns of incubation constancy for nests initiated earlier in the season than those initiated later in the season.

Incubation Recess

Recess frequency of Gadwall that did not delay nocturnal incubation was significantly influenced by Julian date, incubation stage, daily high temperature, precipitation, total minutes off the nest, recess duration and the interactions of Julian date*incubation stage and Julian date*recess duration (Table 5). Gadwall decreased the number of recesses as daily high temperature, and precipitation increased. In addition, females increased the number of recesses as Julian date, incubation stage, total minutes off the nest, and recess duration increased. The significant interactions between Julian date*incubation stage and Julian date*recess duration in their effect on recess frequency reflects a different number of recesses taken for nests initiated earlier in the season than those initiated later in the season.

Recess frequency of Gadwall that delayed nocturnal incubation was significantly influenced by Julian date, incubation stage, daily high and low temperature, total minutes off the nest, recess duration and the interactions of Julian date*incubation stage and Julian date*recess duration (Table 6). Gadwall decreased the number of recesses as daily high temperature increased. In addition, females increased the number of recesses as Julian date, incubation stage, daily low temperature, total minutes off the nest and recess date*recess duration in their effect on recess frequency reflects a different number of

Table 5. Mixed model multiple regression with repeated measures of various influences on daily recess frequency in Gadwall that did not delay nocturnal incubation.

Variable	*F*-value	df[a]	*P*-value	Parameter estimate
Julian date	30.60	1153	0.0001	0.03669
Incubation Stage	13.56	1153	0.0002	0. 1992
High temperature	9.41	1153	0.0022	-0.01357
Low temperature	2.05	1152	0.1524	0.008238
Precipitation	7.23	1153	0.0073	-0.00525
Total minutes off nest	1125.62	1153	0.0001	0.005638
Recess duration	28.55	1153	0.0001	0.01588
Julian date x stage	11.49	1153	0.0007	-0.00104
Julian date x recess duration	65.18	1153	0.0001	-0.00014

[a] Degrees of freedom for numerator = 1

Table 6. Mixed model multiple regression with repeated measures of various influences on daily recess frequency in Gadwall that delayed nocturnal incubation.

Variable	*F*-value	df[a]	*P*-value	Parameter estimate
Julian date	36.52	325	0.0001	0.1240
Incubation Stage	32.56	325	0.0001	0.8832
High temperature	6.20	325	0.0133	-0.02961
Low temperature	6.58	325	0.0108	0.04024
Precipitation	0.13	324	0.7186	-0.00225
Total minutes off nest	12.93	325	0.0004	0.001140
Recess duration	53.37	325	0.0001	0.05382
Julian date x stage	29.23	325	0.0001	-0.00471
Julian date x recess duration	56.72	325	0.0001	-0.00033

[a] Degrees of freedom for numerator = 1

recesses taken for nests initiated early in the season than those initiated later in the season.

Polynomial regression revealed a significant quadratic term ($P = 0.003$) in the relationship between the hour of recess initiation and recess frequency (Type I SS). The hourly timing of recess initiation showed a gradual increase of recess frequencies beginning near dawn, peaking at 1600, and then sharply decreasing as evening approached. Few recesses were initiated between 2200 to 0300 (Figure 1).

Incubation Period

In mixed model multiple regression time spent on the nest and recess frequency significantly influenced the length of incubation period (Table 7). Females that spent more time on the nest had a shorter incubation period than those that spent less time on the nest (Figure 2). In addition, females that took a greater number of recesses had a shorter incubation period.

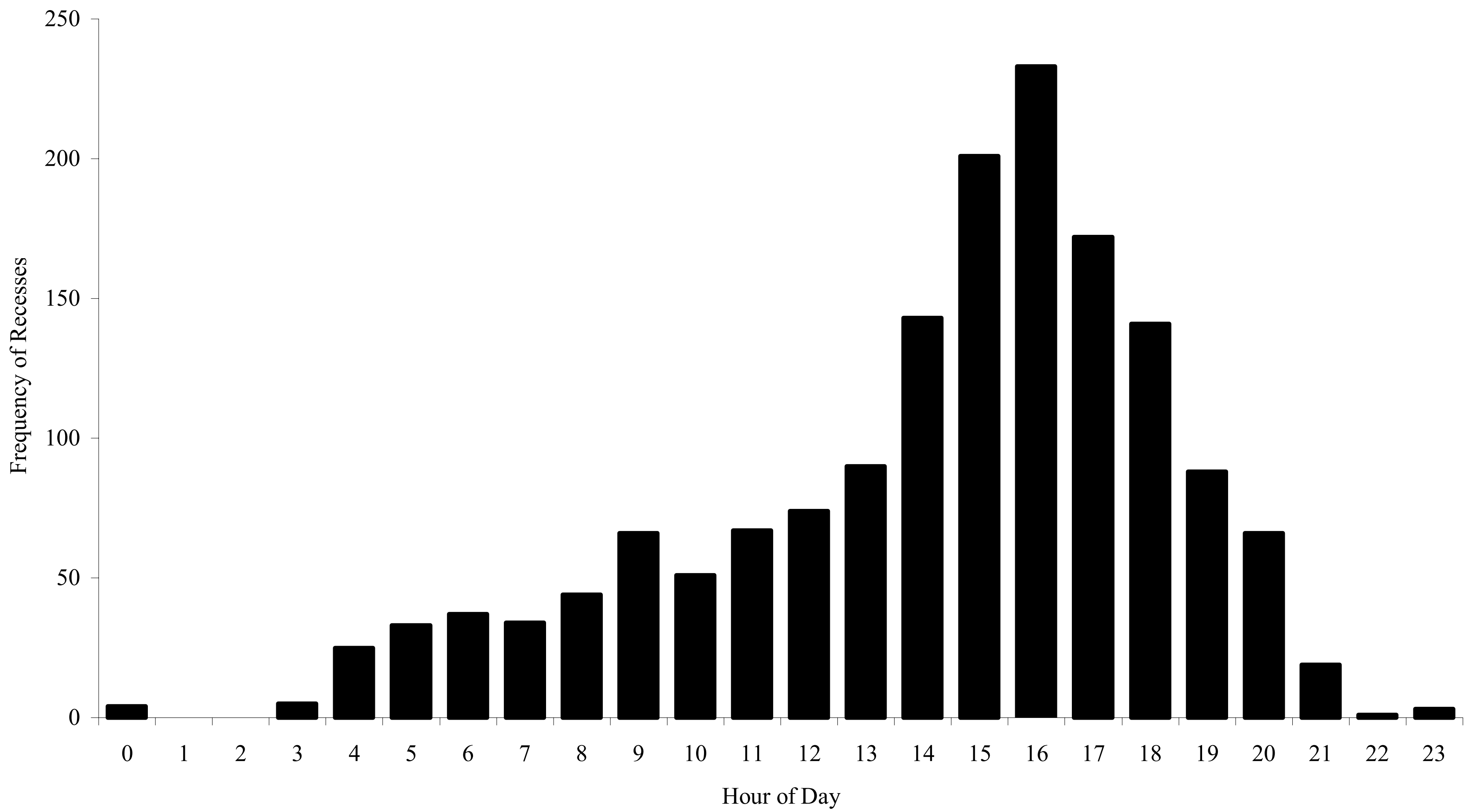

Figure 1. Initiation of incubation recesses by hour of day in Gadwall (significant quadratic relationship *P* = 0.003).

Table 7. Mixed model multiple regression with repeated measures of various influences on incubation period in Gadwall.

Variable	*F*-value	df[a]	*P*-value	Parameter estimate
Incubation constancy (minutes per day)	30.90	66	0.0001	-0.02015
Nest initiation date	0.01	64	0.9185	-0.00351
Number of recesses per day	6.44	66	0.0135	-0.9239
Recess duration (minutes)	0.14	65	0.7053	0.004313

[a] Degrees of freedom for numerator = 1

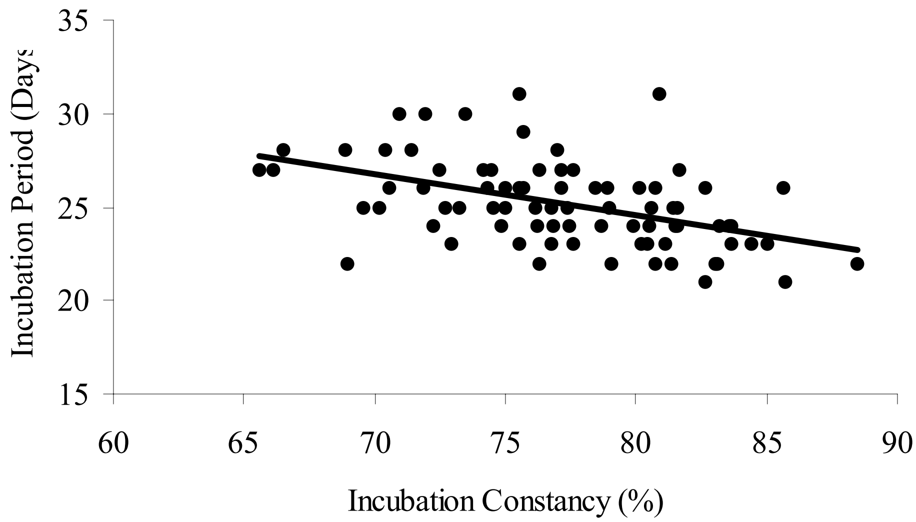

Figure 2. The relationship between incubation constancy and the length of the incubation period (P=0.017) in Gadwall nesting in northeastern North Dakota.

DISCUSSION

Female Gadwall display a different incubation strategy than other temperate nesting waterfowl of similar size and metabolism. Gadwall in this study exhibited much lower incubation constancies and higher recess frequencies than expected based on body size alone. These results are consistent with others reported for Gadwall (Afton and Paulus 1992), although estimates of incubation constancy from my study are lower than published reports. However, these differences may be due to the small sample size of the previous study.

With an average weight of 697 grams prior to incubation, Gadwall are among the heaviest of the five common species of prairie breeding dabbling ducks (Afton and Paulus 1992; Table 8). The body size hypothesis proposed by Afton (1980) and Afton and Paulus (1992) suggests that incubation constancy is positively related to body weight for birds, especially ducks, while recess frequency is generally inversely related to body weight. I would have expected, based on this hypothesis, that intermediate-sized Gadwall would require fewer recesses to feed because of a relatively more efficient use of endogenous reserves.

Contrary to expectations, incubation constancy for the 132 Gadwall females monitored in this project was only 76.5%. Prior work on temperate and prairie nesting ducks revealed average constancies above 80% for species smaller and larger than Gadwall, including American Black Duck (86.7%; Ringelman et al. 1982), Ringed-Necked Duck (85%; Hohman 1986), Northern Shoveler (84.6%; Afton 1980), Mallard (83.2% Hoover 2002), Redhead (82%; Yerkes 1998), Pintail (81.6%; Hoover 2002),

Table 8. Environmental variables and incubation patterns of common species of prairie nesting waterfowl.

Component	Gadwalls	Mallards[2]	Pintails[3]	Northern Shovelers[4]	Blue-winged Teal[5]
Weight (g)	697.0[1]	1047.0	612.0	569.0	356.0
Incubation constancy (%)	84.9[1] 77.6	94.6 89.2 83.2	86.3 81.6	84.6 89.7	83.2 81.1 80.0
Recess frequency per day	1.9[1] 2.3	1.8 2.7	1.7 2.0	2.3 3.0	3.3 2.7
Effects of Environmental Variables on Incubation Constancy					
High temperature	Increased	Decreased	?	Decreased	No effect
Low temperature	Increased	?	?	Increased	Increased
Stage	Decreased	No effect	Increased	Decreased	Increased
Precipitation	No effect	Increased	Increased	Increased	Decreased

[1]Afton and Paulus 1992
[2]Caldwell and Cornwell 1975; Afton and Paulus 1992; Hoover 2002
[3]Afton and Paulus 1992; Hoover 2002
[4]Afton 1980; Afton and Paulus 1992
[5]Afton and Paulus 1992; Loos 1999

Blue-winged Teal (81.1%; Loos 1999), and Common Goldeneye (81%; Mallory and Weatherhead 1993).

My results suggest that body size is not the only factor influencing Gadwall nest attendance. I propose that the nest attendance patterns of Gadwall are heavily influenced by the fact that Gadwall are late season nesters. Researchers have generally acknowledged that one main advantage to nesting later in the season is a higher nest success rate. As upland nesting cover becomes denser with vegetation growth later in the season, nests are better concealed and more dispersed, reducing the foraging efficiency of predators (Greenwood et al. 1995). However, this advantage must be balanced against several disadvantages including declines in clutch size, reduced re-nesting potential, and decreased brood survival rates (Rohwer 1992). I would suggest that late season nesters have lower incubation constancy due to increasing ambient temperatures as incubation progresses.

In addition to nesting later in the season, a large percentage of Gadwall in this study delayed nocturnal incubation anywhere from 1 to 6 days. This range of values exceeds those of other ground-nesting ducks such as Mallard (Caldwell and Cornwell 1975), Northern Shoveler (Afton 1980), Blue-winged Teal and Lesser Scaup (Afton and Paulus 1992). Previous studies have suggested that delaying nocturnal incubation would result in a greater risk of egg predation and/or embryo damage from chilling (Afton and Paulus 1992). Being late season nesters, I would suggest that Gadwall are able to delay nocturnal incubation longer than other species because of warmer ambient temperatures. In addition, greater ground cover later in the season greatly reduces the risk of predation (Greenwood et al. 1995), ultimately reducing the need to immediately initiate nocturnal

incubation. Components of the incubation rhythms, after the onset of nocturnal incubation were similar for both groups.

My results show that incubation constancy decreased over the incubation period, a pattern often attributed to increasing ambient temperature with increasing incubation period (Mallory and Weatherhead 1993, Yerkes 1998). Previous research on Mallard (Caldwell and Cornwell 1975), Northern Shoveler (Afton 1980), Black Duck (Ringelman et al. 1982), Common Goldeneye (Mallory and Weatherhead 1993) and Black Brant (*Branta bernicla nigricans*; Eichholz and Sedinger 1999) all demonstrated a decrease in nest constancy with an increase in ambient temperature. In the case of late nesting waterfowl such as Gadwall, this pattern is heightened. With peak clutch initiation in June, Gadwall face far fewer cold days than the above species, which have peak nest initiations in April or May.

As the temperature reached its peak intensity for the day, females in my study remained on their nest longer and took fewer recesses. This is consistent with previous studies that found females remain on the nest when temperatures exceed 32°C (Caldwell and Cornwell 1975). Once temperatures reach this point, females can be observed panting and changing resting positions to expose more body surface to allow for greater cooling (Caldwell and Cornwell 1975). Therefore, I suggest incubation breaks at the hottest part of the day may allow eggs to become too hot, potentially reaching lethal temperatures for the embryos (Snart 1970).

Gadwall are herbivorous outside of the breeding season (Ankney and Alisauskas 1991). Herbivorous waterfowl typically spend a large proportion of the day foraging, owing to the relatively low digestible energy density of leafy vegetation (McKnight

1998). Ultimately, their inefficiency at foraging for invertebrates, a needed source of protein during the breeding season, causes females to expend greater amounts of energy in the foraging process (Ankney and Alisauskas 1991) during nesting.

Female foraging activities are altered with increased thermoregulatory costs during periods of lower ambient temperatures. Waterfowl tend to increase intake of food items, but forage less selectively at lower temperatures (McKnight 1998). I propose that thermoregulatory costs will also be important on wet days. Ultimately, there is a trade-off the female must make during these weather conditions. Females must not allow the cost of re-warming the eggs back to optimal incubation temperature to outweigh the amount of energy gained from foraging (Klassing 1998). With ambient temperatures near 20°C when a female Gadwall arrives on the nest in June, the time required to heat eggs to developmental temperatures would be much shorter than for early nesting females arriving in April or May (Loos and Rohwer 2004). Warmer ambient temperatures allow Gadwall to minimize egg cooling and maintain normal incubation rhythms even on wet days.

Precipitation decreased recess frequency, but did not affect Gadwall incubation constancy during the years of this study. Many open-nesting birds increase attentiveness during rain (Afton and Paulus 1992) including Mallards (Caldwell and Cornwell 1975), Northern Shovelers (Afton 1980), and Black Brant (Eichholz and Sedinger 1999). However, these species generally have peak nest initiation in April or May. In response to rainfall occurring at colder temperatures, females increase incubation constancy even though this increased attendance may require added short-term use of exogenous

resources to meet their energy needs for thermoregulation. Gadwall are often nesting at warmer ambient temperatures and face fewer thermoregulatory constraints.

As daily low temperatures decreased, incubation constancy increased, while recess frequency remained unaffected. Thermoregulatory costs of the female may explain the pattern of incubation constancy on days with lower daily ambient temperatures. Avian eggs often cool quicker than they can be re-warmed (Drent 1970), therefore foraging recesses should be influenced by the time and energy a female must utilize returning eggs to an optimal temperature for embryo development (Thompson and Raveling 1987). On days with lower ambient temperatures, the cost of foraging may not balance the cost of re-warming the eggs upon return to the nest. As a result, females remain on the nest for a higher percentage of the day when daily temperature was low.

I also examined the influences of Julian date on nest constancy and recess frequency. Gadwall decreased nest constancy and increased recess frequency as Julian date increased. Peak nest initiation for the Gadwall in my study occurred between May 27th and June 4th. However, 34% of the birds initiated nesting on June 5th or later. Many females initiating nests in early June are re-nesting after one or more previous unsuccessful attempts (Strohmeyer 1967, Carlson 1981). Re-nesting females may have less energy reserves compared to first-nesting females. If re-nesting females have fewer endogenous reserves, then they probably have to forage often to meet the demands of incubation.

The same incubation patterns found for Julian date were also found for stage. As stage increased, nest constancy decreased and recess frequency increased. Embryo thermogenesis may partially explain these results. In many waterfowl species, egg

temperatures gradually rise as the incubation period progresses (Caldwell and Cornwell 1975). Moreover, as the embryo develops, it generates increasing amounts of metabolic heat. The heat generated in later stages of the incubation period can represent a substantial proportion of heat required for egg development (Drent 1970). As a result of higher heat production, there is a reduction in egg cooling during parental absences. Therefore, heat production by the growing embryo would help create a warmer nest environment, allowing the female to leave the nest for longer periods of time without incurring a great penalty in egg development (Afton 1980, Aldrich and Raveling 1983, Poussart et al. 2000). Studies looking at Ring-Necked Pheasants (*Phasiaanus colchicus torquatus*; Kessler 1962), Canada Geese (Aldrich and Raveling 1983), Common Goldeneyes (Mallory and Weatherhead 1993), Northern Shovelers nesting in both the prairies (Afton 1980) and the subarctic (MacCluskie and Sedinger 1999), and Black Brant (Eichholz and Sedinger 1999) all showed a similar pattern of decreased nest constancy during later stages of incubation.

The negative relationship between constancy and stage may be further influenced by the depletion of female nutrient reserves. As incubation progresses, females lose a large amount of their initial body weight. By the later stages of the incubation period, females are relatively depleted of their endogenous reserves, and often increase foraging to maintain or acquire sufficient energy to support body metabolism, resulting in higher recess frequencies and lower nest attendance (Hohman 1986, Mallory and Weatherhead 1993, Poussart et al. 2001).

In conclusion, Gadwall have the lowest nest constancy of the five most common prairie-nesting waterfowl. These results cannot be solely explained by inter-specific

variations in body weight between Gadwall and other dabbling ducks. In fact, given the poor food quality of herbivorous waterfowl, body weight loss of incubating Gadwall is not significantly different than other Anas species (Afton and Paulus 1992). I propose that the body-size hypothesis should be modified to account for environmental variables faced by Gadwall and other late season nesters. Whereas early nesting waterfowl are forced to remain on the nest longer in cold temperatures, relying more heavily on endogenous reserves, late nesters, such as Gadwall, are able to remain off the nest for longer periods of time. This allows incubating females to forage more effectively, therefore balancing their own energetic needs with those related to creating an optimal nest environment for the eggs.

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VITA

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