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Patterns of female nest attendance in northern pintails and mallards

Andrea Kim Hoover
Louisiana State University and Agricultural and Mechanical College, ahoove1@lsu.edu

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PATTERNS OF FEMALE NEST ATTENDANCE IN NORTHERN PINTAILS AND
MALLARDS

A Thesis

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ABSTRACT

I examined the accuracy of using data collected by temperature sensing dummy eggs (hollow and switch) to determine female nest attendance in waterfowl. I monitored 3 northern pintails (*Anas acuta*) and 6 mallards (*A. platyrhynchos*) using closed circuit video recording. Differences in the time spent on the nest for an 8-hour recording period between dummy eggs and camera were similar between type (hollow and switch eggs, $P = 0.93$), species ($P = 0.07$), and date ($P = 0.42$). My results show that temperature data from hollow and switch eggs are an effective and accurate method to monitor female nest attendance for prairie-nesting waterfowl.

I investigated the effects of nest site cover and nest site temperatures on the patterns of female nest attendance in pintails and mallards. I monitored nest attendance of 82 pintails (1094 days) and 94 mallards (761 days) in North Dakota in 2000-2001 using temperature sensing dummy eggs in nest bowls. Time spent on the nest per day (constancy) was lower for pintails ($81.6 \pm 0.31\%$) than mallards ($83.2 \pm 0.46\%$; $P = 0.03$), and pintails took more recesses per day (2.64 ± 1.07) than mallards (1.77 ± 1.07, $P < 0.001$). For early nesting pintails and mallards, constancy decreased with increasing nest site cover (lateral concealment) and increased slightly for late nesting females ($P < 0.01$). However, experimentally adding or removing nest site cover at mallard nests did not affect constancy ($P = 0.13$). For both species, females spent more time on the nest late in incubation when it rained than when it did not rain ($P = 0.02$). Pintails spread their incubation recesses more evenly over the daylight period than mallards, which concentrated their recesses in the evening ($P < 0.001$). Maintaining a higher constancy resulted in a shorter incubation period for pintails ($P < 0.01$) but not for mallards ($P = 0.59$). My results suggest that other factors

such as body size and condition, or trade-offs between female condition and the risk of predation may influence female nest attendance in pintails and mallards to a greater extent than nest site cover.

INTRODUCTION

Numerous studies have described patterns of female nest attendance for incubating waterfowl (see Afton and Paulus 1992) and it is apparent that waterfowl exhibit a variety of incubation rhythms. Recent research on incubation has primarily examined the influence of female body size and condition, however, variation in incubation rhythms also can be attributed to nest site selection (Ringelman et al. 1982, Hohman 1986). Presumably, incubation strategies are under selection pressures to meet thermal requirements for developing embryos, maintain a favorable energy balance for females, and minimize the risk of predation for the female and her eggs (Afton and Paulus 1992). I suggest that the optimal amount of nest site cover may reflect a balance of competing needs for direct solar radiation to minimize heat loss by females and for concealing cover from predators. To clarify the relationship between nest site cover and incubation constancy I experimentally tested the effects of nest site cover on incubation constancy in mallards (*Anas platyrhyncho*s) by both increasing and decreasing nest site cover. I also examined the effects of nest site cover on incubation strategies from both inter- and intraspecific perspectives by monitoring nest attendance in northern pintails (*A. acuta*) and mallards.

To monitor nest attendance in pintails and mallards, I used temperature sensing dummy eggs in the nest bowl. Monitoring changes in nest and egg temperatures with dummy eggs has been used in recent years to study waterfowl attendance patterns in redheads (*Aythya americana*; Yerkes 1998), blue-winged teal (*Anas discors*; Loos 1999), northern shovelers (*A. clypeata*; MacCluskie and Sedinger 1999), spectacled eiders (*Somateria fischeri*; Flint and Grand 1999), wood ducks (*Aix sponsa*; Manlove and Hepp 2000), and greater snow geese (*Chen caerulescens atlantica*; Poussart et al. 2000). However, detecting movements of

incubating females on and off the nest with temperature data appears subjective and may

contain significant observer error, which questions the reliability of temperature data to

monitor nest attendance. Therefore, the third objective of my study was to test the accuracy

of temperature data by monitoring pintail and mallard nests continuously using closed circuit

video recording. I also describe the construction and practical application of an inexpensive

video camera system as an alternative way to study parental behaviors and predation of

nesting waterfowl or other birds, and quite possibly for a wide variety of wildlife monitoring

activities.

Chapters of this thesis were written to stand alone; thus some of the study site and

methods sections may be somewhat repetitive.

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**CHAPTER 1. EVALUATION OF NEST TEMPERATURES TO ASSESS FEMALE
NEST ATTENDANCE AND THE USE OF VIDEO CAMERAS TO MONITOR
INCUBATING WATERFOWL**

Studying avian incubation provides insights into reproductive strategies and potential

constraints on reproduction. Methods to assess timing of attentive periods by parent birds at

the nest include direct observations, mechanical devices, time-lapse photography, radio-

telemetry, weight scales, changes in temperature in nests and eggs, and a multiple sensor

system of weight scales and infrared beams (see Afton and Paulus 1992). Monitoring changes

in nest and egg temperatures has been used in recent years to study waterfowl attendance

patterns in redheads (*Aythya americana*; Yerkes 1998), blue-winged teal (*Anas discors*; Loos

1999), northern shovelers (*A. clypeata*; MacCluskie and Sedinger 1999), spectacled eiders

(*Somateria fischeri*; Flint and Grand 1999), wood ducks (*Aix sponsa*; Manlove and Hepp

2000), and greater snow geese (*Chen caerulescens atlantica*; Poussart et al. 2000).

Temperature sensing probes or thermistors are discreetly hidden inside artificial eggs that are

placed in the nest bowl. Temperature data are recorded at specified time intervals on

microcomputers or data loggers. Data loggers can collect data for extended periods of time,

their small size allows them to be hidden next to nests or hundreds of meters away. Low cost,

ease of setup in the field, minimal investigator disturbance to the incubating female, and an

ability to monitor many nests during one breeding season have likely been key factors

contributing to the increased use of temperature sensors with data loggers to monitor nest

attendance.

However, detecting movements of incubating females on and off the nest with

temperature data appears subjective and may contain significant observer error, which

questions the reliability of temperature data to monitor nest attendance. Concern exists that

temperature fluctuations due to female movements on and off the nest cannot be precisely detected, especially when ambient temperatures approach incubating temperatures (Afton and Paulus 1992). The reliability of temperature data has been largely untested. Limited validation of temperature recordings has involved direct observations of nests (Poussart et al. 2000) or flushing females from their nests (Loos 1999, Manlove and Hepp 2000) and comparing these times to temperature changes recorded by data loggers.

Therefore, the objectives of my study were to test the accuracy of temperature data by monitoring Northern pintail (*A. acuta*, hereafter pintail) and mallard (*A. platyrhynchos*) nests continuously over several hours using closed circuit video recording. I also describe the construction and practical application of an inexpensive video camera system as an alternative way to study parental behaviors and predation of nesting waterfowl.

STUDY SITE

I conducted fieldwork during April-July, 2000-2001 in Towner County North Dakota (48°40' N, 99°10'W). This area was characterized by gently rolling hills interspersed with seasonally flooded to semi permanent and permanent wetlands. My study site was primarily comprised of planted grass cover (approximately 80%) on privately owned lands enrolled in the Conservation Reserve Program or federally owned Waterfowl Production Areas. All monitored nests were on the ground in grassland cover.

METHODS

Field Procedures

Temperature Sensing Equipment. -- I positioned 2 different types of temperature sensing dummy eggs (hollow and switch eggs) in the nest bowl to assess presence of the female. Both types of dummy eggs were connected to a microcomputer data logger, (Hobo

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Temp XT or Hobo H8 series, Onset Computer Corporation, Pocasset, Massachusetts, USA).

Each data logger costs $65.00 to $85.00. Data loggers contain an internal clock and can be programmed to record temperatures at a wide variety of intervals; I chose to record temperatures every 5 minutes.

Hollow eggs, described by Yerkes (1998) and Loos (1999), consisted of cleaned out chicken eggs reinforced with a thin (approximately 1 mm) layer of epoxy glue on the inside surface. A thermistor was positioned at the top of the egg such that the thermistor was in close contact with the female. I assumed that positioning the thermistor in this way allowed rapid detection of temperature changes associated with arrival or departure of the female. This hollow egg was glued to a 10 cm stake and positioned in the outer row of eggs within the nest bowl. Flint and MacCluskie (1995) described the switch egg, which has a thermistor at the surface of an artificial egg made of auto body putty. The egg was bisected along the long axis and the top piece rested on a microswitch that was activated when the female's weight compressed the switch during incubation. When the female was absent, the microswitch and circuitry were not activated, so the data logger recorded a reduced temperature, approximately 24°C below the actual temperature. This drastic change in temperature when a female exited or returned to her nest was designed to make her movements obvious when examining recorded temperature data.

Video Monitoring Equipment. -- To evaluate the accuracy of temperature data for monitoring incubation I simultaneously videotaped incubation at nests monitored with both hollow and switch eggs and data loggers. I videotaped incubation using black and white, indoor/outdoor video surveillance cameras (RadioShack Corporation, Fort Worth, Texas, USA; approximate cost was $150), mounted 1.5 m from the nest and 0.5 m above ground. I

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mounted cameras on a 0.8 m metal fencepost using an adjustable bracket that allowed the

camera lens to be directed at the nest site. Vegetation directly in the line of sight was

removed to reduce visual obstruction. Cameras were equipped with an 18.3 m cable that

connected directly to standard videocassette recorders (VCRs; approximate cost was $50) for

recording. The VCRs I used did not have a date and time stamp feature; therefore I placed an

analog clock in front of the nest so that time was recorded by the camera. In the event the

clocks failed, the VCR counter was used to calculate the time from the known time when

recording commenced. Internal clocks on the data loggers and nest site clocks were

synchronized as closely as possible. I used a 12.7 cm, battery-operated portable television

(approximate cost was $30), with external jacks that plugged into the VCRs to provide a

visual projection of the image being recorded on the videotapes at the time of camera setup

and during a tape change. This television ensured proper positioning of the camera to

effectively record the female on the nest and ensured appropriate recording settings on the

VCR. I used a 12-volt, 34-amp, deep-cycle battery (approximate cost was $60) and an

AC/DC converter (approximate cost was $150) to power the camera and VCR (Figure 1.1).

VCRs and camera accessory equipment were housed in a waterproof plastic storage container

(60 liters), while the battery was housed in a separate container. Containers were covered

with burlap cloth for concealment. I typically collected 2, 8-hour (T-160) videotapes of data

per day on an individual incubating female. I made 2 visits to the nest per day to change the

tapes, during one of which I changed the battery. Disturbance to females during each visit

was minimized by the 18.3 m cable, which generally allowed me to change the tape without

flushing the female. Infrared capabilities of the camera made the female visible even in

darkness, permitting observations during nighttime hours.
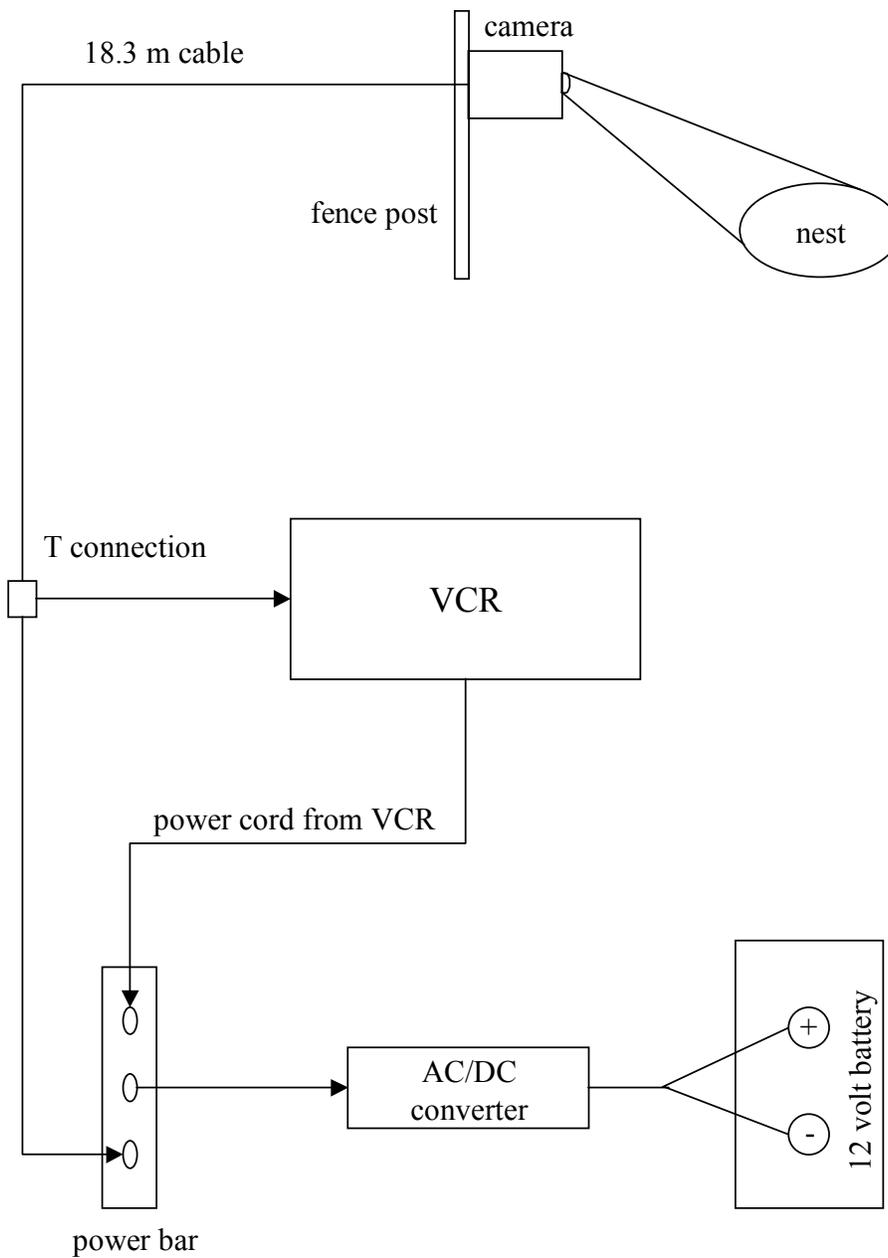
Figure 1.1. Schematic illustrates the camera recording system used to monitor incubating pintails and mallards.

Determinations of Nest Attendance. -- I viewed videotapes and recorded times of female arrivals, exits, and total time sitting on the nest during each 8-hour period (incubating time). I considered data recorded on the videotapes to be the true times of female attendance and thus the baseline for assessing accuracy of hollow and switch eggs. Temperature data from hollow eggs and switch eggs were examined visually as plotted data and on spreadsheets. Times of female arrivals, exits, and incubating time for the same time period as the tapes were determined. For hollow eggs, a set of general rules was designed to interpret female attendance to increase objectivity and maintain consistency in interpretations (Loos 1999). I identified an exit for an incubation recess as a drop in temperature of 1.5°C maintained over 3 time intervals (15 minutes), and I identified an arrival from a recess by a 1.5°C or greater increase from the lowest recorded temperature during that recess. However, temperature data did not always fit perfectly into the patterns described above, and frequent interpretations and adjustments were required by the observer. For instance, decreases in temperatures of 1.5°C were occasionally difficult to detect until much later in the incubation recess. When this occurred, I identified the exit time for that recess by searching backwards until I reached the first substantial drop in temperature, suggesting that the female had covered her eggs and left the nest site. An increase in temperature from the lowest recorded temperature during a recess did not always mean the female had returned to the nest. In this situation, I again identified when the female was likely present at her nest and searched backwards until I could identify when the temperature increased in a consistent manner to indicate that the female had arrived and resumed incubation.

Exits and arrivals for switch eggs were determined in much the same manner as hollow eggs, but when the female exits for a recess the switch opens and the altered circuit

substantially lowers the recorded temperature (typically from 36-37°C to 12-13°C).

However, the switch eggs often had the switch stick in either an open or depressed position.

In these cases, I determined arrivals and exits in the same way as hollow eggs. Determining

female attendance in a manner similar to the hollow eggs when the switch is stuck is not ideal,

as the solid eggs have more thermal inertia than the hollow eggs and temperature changes can

be more difficult to assess.

Statistical Analyses

All analyses were conducted using SAS statistical software (SAS Institute Inc. 1999).

I subtracted incubating times, recess exits, and recess arrivals interpreted from the dummy

eggs from incubating times, recess exits, and recess arrivals derived from the camera system,

thereby pairing observations for each 8-hour tape. I used a repeated measures analysis of

covariance (ANCOVA, PROC MIXED) to determine if the difference in incubating times

differed by type (hollow or switch), species (pintail or mallard), or date. Similarly, I used a

repeated measures ANCOVA to determine if differences in time intervals when a female

exited the nest for a recess or arrived at the nest from a recess differed by type, species, or

date. For all analyses, I included all 2-way interactions and used backward selection

procedure to remove any non-significant interactions ($\alpha < 0.05$). I used Least Squares Means

(LSMEANS) with a Tukey-Kramer adjustment for multiple comparisons to compare means of

significant effects. Means are reported ± 1 standard error.

RESULTS

I monitored 3 pintails (24 tapes) and 6 mallards (93 tapes) during incubation. I

eliminated days during the latter stages of pip and hatch from analyses because nest

temperatures fluctuate widely, which makes it difficult to determine movements on and off

the nest by the female. I also removed 5 tapes from analyses where determinations of female attendance were ambiguous. I recorded 103 (hollow egg) and 102 (switch egg) recess exits, and 116 (hollow egg) and 118 (switch egg) arrivals from recesses.

Incubating times. -- During each 8-hour tape interval, the mean discrepancies in incubating times between dummy eggs and camera were similar between type (hollow eggs 0.54 ± 1.95 minutes, switch eggs 0.77 ± 1.80 minutes; $F_{1,9} = 0.01$, $P = 0.93$), species ($F_{1,8} = 4.06$, $P = 0.07$), and date ($F_{1,212} = 0.66$, $P = 0.42$). All interactions were non-significant and were removed from the model.

Exits and arrivals from recesses. -- Videotapes showed that mean recess duration was 98.6 ± 5.7 minutes. Of all recesses, only 3 were ≤ 21 minutes in duration. I failed to detect 3 recesses with both the hollow and switch eggs. Two of these missed recesses were 3 and 9 minutes in duration. I also missed an additional 2 recesses with only the hollow egg, and an additional 2 recesses with only the switch egg. Both recesses for the hollow egg occurred when the female flushed during a tape change. Furthermore, I detected a 10-minute recess with both the hollow eggs and switch eggs when a female stood vigilant on the edge of the nest bowl but did not depart from the nest site. Because the female did not leave the nest site, I did not consider this to be a recess on the videotape. All missed recesses were excluded from exit and arrival time analyses.

Mean discrepancies in exit times calculated by subtracting dummy egg times from camera times did not differ between type (hollow eggs -3.62 ± 0.91 minutes, switch eggs -4.18 ± 1.64 minutes; $F_{1,9} = 0.09$, $P = 0.77$), or species ($F_{1,8} = 0.03$, $P = 0.87$); but mean discrepancies did differ with date ($F_{1,193} = 6.99$, $P < 0.01$). This discrepancy equated to a 10 minute difference between the earliest and latest date. All interactions were non-significant

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and were removed from the model. Mean discrepancies in arrival times between dummy eggs and camera were similar with species ($F_{1,8}$ = 2.07, P = 0.19), and date ($F_{1,222}$ = 0.00, P = 0.98); but were not similar with type (hollow eggs -4.55 ± 0.31 minutes, switch eggs -6.45 ± 0.58 minutes; $F_{1,9}$ = 8.15, P = 0.02). Discrepancies in arrival times differed for mallards between hollow and switch eggs (difference between LSMEANS = 1.89 ± 0.66 minutes; P = 0.02).

DISCUSSION

Accuracy of Temperature Data to Monitor Nest Attendance. -- Discrepancies from hollow eggs and switch eggs relative to cameras are trivial, suggesting that hollow and switch eggs can both be used to accurately monitor nest attendance of upland nesting waterfowl on the prairies. Although some recesses were missed with the hollow and switch eggs, these missed recesses were very short and inconsequential for accurate evaluation of daily nest attendance. Missed recesses were either rare occurrences of short recesses or anomalies in female attendance, such as when I videotaped a female sneak off the nest only to return 3 minutes later. This female did not cover her eggs, a behavior typical of females before taking a recess; perhaps she was alerted by some potential predator that I could not observe on the tape. Other anomalies in females' nest attendance behaviors may have been an artifact of the frequent number of disturbances to change videotapes and batteries. Videotapes revealed that as I approached, 2 females would not flush, but walked away from the nest. During a tape or battery change I attempted to minimize disturbance to the female as much as possible, and because I did not observe her leave the nest, I would not approach the nest and the eggs would remain uncovered until the female returned. Sneaking off a nest instead of flushing may be particularly prevalent in pintails (Hoover personal observation, K. Richkus personal

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communication). All 3 missed recesses of this type were observed with pintails. Two other short missed recesses may be due to uncovered dummy eggs being exposed to direct sunlight and high ambient temperatures. Females departing from the nest without covering eggs is not typical for waterfowl, so failing to a detect recess when the eggs are uncovered is likely infrequent and an artifact of female disturbance.

The significant interaction of species by type of method might suggest that hollow and switch eggs are not consistent in assessing arrival times from a recess for mallards. However, I believe this interaction is of little concern from a methodological standpoint. The difference in the estimates between the hollow and switch eggs is low, only -2.8 minutes. Temperatures in the nest are only recorded at 5-minute intervals; therefore, the differences may be statistically significant, but are unimportant for accurate monitoring of nest attendance.

MANAGEMENT IMPLICATIONS

Results from my study show that temperature data is accurate in assessing female nest attendance for waterfowl in North Dakota. I cannot however, make conclusions regarding waterfowl nesting in other geographical areas. Waterfowl nesting in southern latitudes may frequently experience ambient temperatures at or near incubating temperatures. Likewise, cavity-nesting waterfowl may experience different temperature regimes than ground nesting waterfowl where dummy eggs may respond differently.

Days from the latter stages of pip and at hatch should be excluded when using temperature data due to the wide fluctuations in temperatures at the nest. Nest exodus can be determined from temperature data; however, the dummy eggs may actually delay nest exodus. I observed a pintail with a complete clutch of 6 dry ducklings, take an hour recess and then brood her ducklings for 24 hours before exodus. She repeatedly attempted to roll and move

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the hollow and switch eggs in her nest bowl, and I suspect she was waiting for the dummy eggs to hatch. The presence of 2 dummy eggs in nests I was monitoring may have exacerbated this delay. Temperature data may not be appropriate for evaluating female attendance patterns during hatch as dummy eggs may alter female behavior.

Days when an observer cannot confidently determine attendance because of fluctuations in recorded temperatures should be removed from analysis. This occurred on 5 of 74 days in my analysis, and I suspect the temperature fluctuations reflect an infrequent malfunction in the data loggers or thermistors.

Uses of Camera System. -- In addition to monitoring nest attendance, video cameras can be used to document nest activities and incubating behaviors of waterfowl. Time-lapse photography was previously used for this purpose, but some activities at a nest were missed because of interval recording (Weller and Derkson 1972). Caldwell and Cornwell (1975) used time-lapse photography to document incubation behaviors of 8 captive mallards and supplemented photography data with direct observations. My system provides a good alternative to direct observations as tapes can be viewed at the researcher's convenience, there is minimal disturbance to the incubating females, and it is possible to gather data on wild birds.

Perhaps more importantly to waterfowl researchers and managers, one could identify predation events at waterfowl nests using these cameras. Predation is the cause of most nest failure for prairie-nesting waterfowl (Sargeant and Raveling 1992, Greenwood et al. 1995), yet attempts to identify predators from the remains at the nest are subjective and inconclusive at best (Sargeant et al. 1998, Lariviere 1999). Pietz and Granfors (2000) and King et al. (2001) successfully used time-lapse recording to identify nest predators of songbird nests in

forested areas and grasslands. Clearly, continuous recording at a nest would provide more

information to further an understanding of nest predation and behavioral ecology of nest

predators (Lariviere 1999). I cannot evaluate if my system would increase predator attraction

based on the camera equipment or increased exposure of the nest, however other studies

report reduced predation at nests with cameras (Thompson et al. 1999, Pietz and Granfors

2000, King et al. 2001).

Numerous features of my camera design support its use. Each unit costs

approximately $500, a significant decrease from currently available systems (Thompson et al.

1999, Pietz and Granfors 2000, King et al. 2001). All components and materials can be

bought locally at hardware and department stores, and further savings are realized because

technical consultation with experts is not required (Pietz and Granfors 2000). One individual

can easily set up the recording system in the field and little maintenance is necessary.

Cameras were durable during inclement weather. Visits to the nest could be reduced with the

use of longer tapes or by using cable extensions so the observer could change tapes at a

distance that would not disturb the female.   I believe my camera system provides a practical

and viable option for recording a wide variety of behavioral data at waterfowl and other avian

nests.

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CHAPTER 2. FACTORS INFLUENCING FEMALE NEST ATTENDANCE FOR NORTHERN PINTAILS AND MALLARDS

Recent research on waterfowl incubation has focused on the influence of female body size and condition on nest attendance. Much of the interspecific variation in incubation rhythms can be attributed to body size (Afton and Paulus 1992). Larger bodied waterfowl can store more endogenous reserves than smaller bodied waterfowl, thereby reducing the need for incubation recesses to feed (Afton 1980, Aldrich and Raveling 1983). Likewise, some of the intraspecific variation in nest attendance can be attributed to body condition; females that exhibited higher incubation constancy experienced greater weight loss for redheads (*Aythya americana;* Yerkes 1998) and blue-winged teal (*Anas discors*; Loos 1999), but not for spectacled eiders (*Somateria fischeri*; Flint and Grand 1999).

Variation in incubation rhythms also can be attributed to nest site selection. American black ducks (*Anas rubripes;* Ringelman et al. 1982) and ring-necked ducks (*Aythya collaris;* Hohman 1986) nesting closer to water take shorter but more frequent incubation recesses than females nesting further upland. The effects of nest site vegetation, concealment, and associated nest site temperatures on both inter- and intraspecific variation in patterns of nest attendance for prairie nesting dabbling ducks is largely unknown. Presumably, incubation strategies are under selection pressures to meet thermal requirements for developing embryos, maintain a favorable energy balance for females, and minimize the risk of predation for the female and her eggs (Afton and Paulus 1992). I suggest that the optimal amount of nest site cover may reflect a balance of competing needs for direct solar radiation to minimize heat loss by females and for concealment cover from predators.

There is little doubt that high predation rates provide strong selection to choose safe nest sites (Sargeant and Raveling 1992, Greenwood et al. 1995, Beauchamp et al. 1996).

Many researchers believe that nests in thicker cover experience greater success (Dwernychuk and Boag 1972, Duebbert and Kantrud 1974, Hines and Mitchell 1983, Cowardin et al. 1985). However, there is much variation within species and between species in nest site cover even at the same location and time. For instance, northern pintails (*Anas acuta* – hereafter pintails) have a propensity to nest in sparse cover more than mallards (*A. platyrhynchos;* Greenwood et al. 1995), which also are early nesting waterfowl. This variation in nesting cover suggests that other factors play a role in nest site selection.

A potential advantage of nesting in sparse cover may be that increased solar radiation allows females to maintain body temperatures with minimal expenditure of energy early in the spring. Accordingly, females selecting sparse cover could reduce demands on endogenous reserves or reduce the number of incubation recesses to forage. This hypothesis suggests that species that use fewer stored reserves to fuel incubation should use sparse cover to help achieve high constancy. This prediction is consistent with the observation that smaller dabbling ducks such as blue-winged teal and northern shovelers (*A. clypeata*) use more sparse cover than mallards or gadwalls (*A. strepera*). Considerable variation within species in female condition at the end of laying also is present (Arnold and Rohwer 1991, Loos 1999). Perhaps some of the interspecific variation in nesting cover is caused by females making a trade-off between nest site concealment and the thermal benefits of more open sites. A simple prediction based on this thermal hypothesis could be that constancy should decrease as nest site cover increases. If a female nests in sparse cover, the increased solar radiation will keep her warmer so fewer stored reserves or feeding periods are required to maintain high incubation constancy. In contrast, a female in greater cover has to actively thermoregulate and may lose more weight or need more incubation breaks to meet energy demands.

My hypothesis of nest site cover as a trade-off between concealment and solar radiation assumes that early nesting females face cold conditions. Accordingly, we would only expect the trade-off to occur early in the nesting season. Thus, I expect selection of sparse cover by some females early in the nesting season, but later in the season, females should select thicker cover for concealment. The ability of individuals to assess their condition and select the appropriate cover density may eliminate the predicted inverse relationship between cover density and incubation constancy early in the season. Females in good condition may select thick cover because they can afford to maintain high constancy by using their stored reserves. In contrast, lean females may initiate nests in sparse cover but achieve similar constancy because of reduced thermoregulatory stress due to direct solar radiation.

To clarify the relationship between nest site cover and incubation constancy I experimentally tested effects of nest site cover on incubation constancy in mallards by both increasing and decreasing nest site cover. If nest site cover influences incubation strategies, I predict that adding vegetation will result in females spending more time off the nest; conversely, removing vegetation should result in females spending more time on the nest. This experiment may have been best conducted on a species that typically nests early in the season and selects sparse cover nest sites, such as pintails. To ease logistic problems I selected mallards as my experimental species because of their abundance and their early nesting.

A second major objective of my study was to examine the effects of nest site cover on incubation strategies from both inter- and intraspecific perspectives by monitoring nest attendance in pintails and mallards. Pintails and mallards are the earliest nesting waterfowl on

the prairies (Duncan 1987, Klett et al. 1988, Greenwood et al. 1995), yet despite this similarity, pintails and mallards differ in other aspects of breeding biology. Pintails have a propensity to nest in sparse cover more than other dabbling ducks (Greenwood et al. 1995), and have a lower propensity to renest relative to mallards (Richkus 2002). In addition, pintails have a smaller clutch size and shorter incubation lengths than mallards (Feldheim 1997). Therefore, the selection of pintails and mallards provides a good comparison of interspecific variation in incubation strategies.

STUDY SITE

I conducted fieldwork during April-July, 2000-2001 in Towner County North Dakota (48°40' N, 99°10'W). This area is characterized by gently rolling hills interspersed with seasonally flooded to semi permanent and permanent wetlands. My study site was primarily comprised of planted grass cover (approximately 80%) on privately owned lands enrolled in the Conservation Reserve Program and federally owned Waterfowl Production Areas.

METHODS

Field Procedures

Nest searching. -- Nests were located in upland vegetation by dragging a 50-70 m chain between 2 all-terrain vehicles or 2 tractors to flush females (Higgins 1977, Klett et al. 1986). Nest searches were conducted between the hours of 0600 to 1400 hours to find females on their nest during both laying and incubation stages (Gloutney et al. 1983, F. Rohwer personal communication). Data recorded for each nest included, species, number of eggs, and stage of incubation based on field candling techniques (Weller 1956).

Determinations of Nest Attendance. -- I positioned one of two types of temperature sensing "dummy eggs" in the nest bowl of pintails and mallards to monitor female nest attendance (see Chapter 1 for results on the reliability of using this technique for monitoring nest attendance in waterfowl). Both types of dummy eggs held a thermistor that connected to a microcomputer data logger, Hobo Temp XT or Hobo H8 series (Onset Computer Corporation, Pocasset, Massachusetts, USA). Data loggers contain an internal clock and can be programmed to record temperatures at a wide variety of time intervals; I chose to record temperatures every 5 minutes. I visited nests every 6 days to download data.

Hollow eggs, described by Loos (1999), consisted of hollowed out chicken eggs reinforced with a thin (approximately 1 mm) layer of epoxy glue on the inside surface. A thermistor was positioned at the top of the egg such that the thermistor was in close contact with the female. Positioning the thermistor in this way ensured rapid detection of the temperature changes associated with arrival or departure of the female. This hollow egg was glued to a 10 cm stake and positioned in the outer row of eggs within the nest bowl. Flint and MacCluskie (1995) described the switch egg, which has a thermistor at the surface of an artificial egg made of auto body putty. The egg was bisected along the long axis and the top piece rests on a microswitch that was activated when the female's weight compressed the switch during incubation. When the female was absent the microswitch and circuitry were not activated, so the data logger recorded a reduced temperature, approximately 24°C below the actual temperature. This drastic change in temperature when a female exits or returns to her nest makes her movements obvious when examining recorded temperature data.

Temperature data from both the hollow eggs and the switch eggs were examined both visually in plotted data and on spreadsheets and times of female arrival and female departure

from the nest were determined. For the hollow eggs, a drop in temperature of 1.5°C maintained over 3 time intervals (15 minutes) was scored as a departure for recess. Arrival from a recess was identified by at least a 1.5°C increase from the lowest recorded temperature during that recess (Loos 1999).

Exits and arrivals for switch eggs were determined in much the same manner as hollow eggs, but when the female exited for a recess the switch opens and the altered circuit substantially lowered the recorded temperature (typically from 36-37°C to 12-13°C). However, the switch eggs often had the switch stick in either an open or depressed position. In these cases, I determined arrivals and exits in the same way as hollow eggs. Determining female attendance when the switch is stuck is not ideal, as the solid eggs have more thermal inertia than the hollow eggs and temperature changes can be more difficult to assess.

For each female, I calculated the proportion of time per day spent on the nest (daily constancy), the number of times the female left the nest per day (daily recess frequency), and the average recess length per day (mean recess duration). For each successful female found during the laying stage, I also calculated the average of daily constancies (overall constancy), the average of daily recess frequencies (overall recess frequency), and the average of mean daily recess durations (overall recess duration) for the incubation period. I defined incubation period as beginning on the day after the last egg was laid and ending at hatch, estimated to be one day before nest exodus (Manlove and Hepp 2000). Days with less than 24 hours of nest attendance data, during laying or during hatch, were removed from analysis (see Chapter 1 for justification).

Nest Site Cover and Temperature. -- I estimated nest site cover from both lateral and overhead perspectives at the time of dummy egg placement into the nest bowl. Lateral concealment was estimated using an average of modified robel pole measurements taken from four cardinal directions 5 m from the nest (Robel et al. 1970). Overhead concealment was estimated using a forest densiometer placed on top of the eggs in the middle of the nest bowl. Nest site temperature was recorded on data loggers at similar 5-minute intervals to nest attendance data. I attached thermistors to the vegetation 10 cm east of the nest bowl so that nest site temperature was be recorded without being influenced by the incubating hen. I used daily precipitation amounts recorded at a National Weather Service station in Cando, Towner County, North Dakota (48.5°N, 99.2°W), which was 4.8 km from my study area.

Vegetation Manipulations. -- I conducted experimental manipulations of nest site cover on mallard nests during incubation. I monitored nest attendance without cover manipulations for a 6-day control period, then randomly assigned nests to either removal or addition treatments for another 6-day period. Removal treatments consisted of cutting individual plants at the ground until the overhead concealment at the nest site approximated 0%. Addition treatments consisted of increasing the stem density of nest site vegetation until the overhead concealment approximated 100%. Added stems were consistent with existing stems at the nest site and were fabricated from local grasses or forbs secured with string around a steel rod and placed in the ground to simulate natural nest cover.

Statistical Analyses

All analyses were conducted using SAS statistical software (SAS Institute Inc. 1999). I blocked on year in all analyses. The experimental unit in all analyses is the individual female and each day is the repeated measures unit. Means are reported ± 1 standard error.

I conducted a paired t-test (PROC TTEST) to compare constancy on the day before flush to the day of flush to determine if days females were flushed by an observer should be removed from further analyses.

Incubation Constancy. -- I used a mixed model repeated measures logistic regression (PROC MIXED, GLIMMIX Macro, SAS Institute Inc. 1999) to determine if daily constancy differed with species (pintail, mallard), nest site cover, nest site temperature, precipitation, date, or stage of incubation. Date was separated into 2 categories; early females initiated nests prior to May 3, late females initiated nests after May 3, corresponding to median nest initiation dates for the pintails and mallards in my study. Stage of incubation also was separated into 2 categories; early incubation occurs from 1 to 13 days, late incubation occurs after 13 days. I included *a priori* 2-way interactions between species, nest site cover, nest site temperature, and precipitation. I used backward selection to remove non-significant interactions and main effects ($\alpha < 0.05$) to arrive at my final model. I used first order auto-regressive covariance structure to describe dependence among repeated measurements over time on each nest. This structure is appropriate when data taken at proximal time periods are more similar than more distal time periods (Jennrich and Schluchter 1986, Zicus et al.1995). I used Least Squares Means (LSMEANS) with a Tukey-Kramer adjustment for multiple comparisons to compare means of significant effects.

Incubation Recesses. -- I used a mixed model repeated measures logistic regression (PROC MIXED, GLIMMIX Macro, SAS Institute Inc. 1999) to determine if mean recess duration differed with species and daily recess frequency, while controlling for the influences of date, stage of incubation, and daily constancy. Similar to the constancy analysis, I separated date into early and late nesting females, and stage of incubation into early and late stages. I included an *a priori* 2-way interaction between species and daily recess frequency. Recesses that extended into the next day were included as recesses for the previous day. I again selected first order autoregressive covariance structure to adjust for dependence among repeated measures over time.

To establish a pattern of recess initiation times for pintails and mallards, I divided days into 4, 6-hour time periods; early morning (0400-1000), midday (1000-1600), evening (1600-2200), and nighttime (2200-0400) and counted number of recesses initiated within each 6 hour time period. I used a Chi Square Test of Independence (PROC FREQ) to determine if number of recesses initiated by each species occurred with different frequencies during different time periods.

Incubation Period. -- I conducted an analysis of covariance (ANCOVA, PROC MIXED) to test effects of overall constancy and nest initiation dates on incubation period. Only successful nests located during the laying stage with known nest initiation dates and incubation periods were used for this analysis. I did not include species in this model because incubation periods of pintails are shorter than mallards (Feldheim 1997), thus models for pintails and mallards were fitted separately. In both models, I included an *a priori* 2-way interaction between overall constancy and initiation date and used backward selection to remove non-significant interactions and main effects ($\alpha < 0.05$) to arrive at my final model.

Experimental Vegetation Manipulations. -- I selected a 5-day control period and a 5-day treatment period because data loggers were downloaded every 6 days; therefore I could remove the first day I began to monitor nest attendance and the day of treatment from analysis to minimize the influence of observer disturbance on the females. I calculated the mean of daily constancy, mean daily nest site temperatures, and nest site cover (lateral obstruction) for the 5-day treatment period and 5-day control period. I subtracted the 5 day treatment means from the 5 day control means; thereby pairing observations and controlling for variation in nest attendance patterns due to individual females. I used a difference in lateral obstruction to estimate a treatment size for the change in nest site cover instead of categorizing 2 treatment levels (add or remove) to account for initial nest site cover. I used an ANCOVA (PROC MIXED) to determine if overall constancy differed with nest site cover treatment size or nest site temperature change. I also used an ANCOVA (PROC MIXED) to determine if nest site temperature differed with nest site cover change. Included in both models as covariates were date and stage of incubation at the commencement of the treatment period. I used backward selection to remove any non-significant main effects ($\alpha < 0.05$) for both models to arrive at my final models.

RESULTS

I collected nest attendance data on 82 pintails (1094 days) and 94 mallards (761 days). Daily constancy was lower on days when an observer flushed the female, than on the day before the disturbance for pintails (43.38 ± 11.36; $P < 0.001$) and mallards (67.14 ± 16.40; $P < 0.001$), so those days were excluded from further analyses.

Incubation Constancy. -- Daily constancy was lower for pintails ($81.6 \pm 0.31\%$; range 7.3-100.0%) than mallards ($83.2 \pm 0.46\%$, range 0.0-100.0%; $F_{1,1821} = 4.85$, $P = 0.03$). For

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unmanipulated nests, daily constancy decreased with increasing nest site cover (lateral concealment) for females initiating nests early in the season, but constancy increased slightly with nest cover for late nesting pintails and mallards ($F_{1,1821}$ = 9.89, P < 0.01, Figure 2.1). Mallards selected nest sites with greater cover than pintails ($F_{1,171}$ = 12.66, P < 0.001), and both pintails and mallards selected nest sites in greater cover later in the season ($F_{1,171}$ = 27.31, P < 0.001).

Nest site cover manipulations (adding or removing vegetation) did not influence constancy in mallards ($F_{1,45}$ = 0.02, P = 0.89, Figure 2.2). Manipulation of nest site cover affected nest site temperature such that adding vegetation resulted in lower nest site temperatures ($F_{1,45}$ = 15.54, P < 0.001), but lower nest site temperatures associated with nest site cover change did not influence constancy ($F_{1,45}$ = 2.42, P = 0.13).

For nests with no vegetation manipulation, the effect of incubation stage was not consistent with species ($F_{1,1821}$ = 6.55, P = 0.01). Early stage pintails had lower constancy (-48 minutes per day) than late stage pintails (LSMEANS early 78.2%, late 81.5%; P < 0.01), and early stage pintails had lower constancy (-70 minutes per day) than early stage mallards (LSMEANS early pintails 78.2%, early mallards 83.0%; P < 0.01), however there was no difference in constancy between early and late stage mallards (LSMEANS early 83.0%, late 82.2%; P = 0.92). A significant stage of incubation by precipitation interaction ($F_{1,1821}$ = 5.44, P = 0.02) indicated that pintail and mallard females similarly responded to rain by spending 19 more minutes on the nest during late stages of incubation when it rained than when it did not rain (LSMEANS no rain late 81.2%, rain late 82.5%; P = 0.06). Nest site temperature did not influence incubation constancy ($F_{1,1702}$ = 0.19, P = 0.66) and was subsequently removed from the model during backward selection.
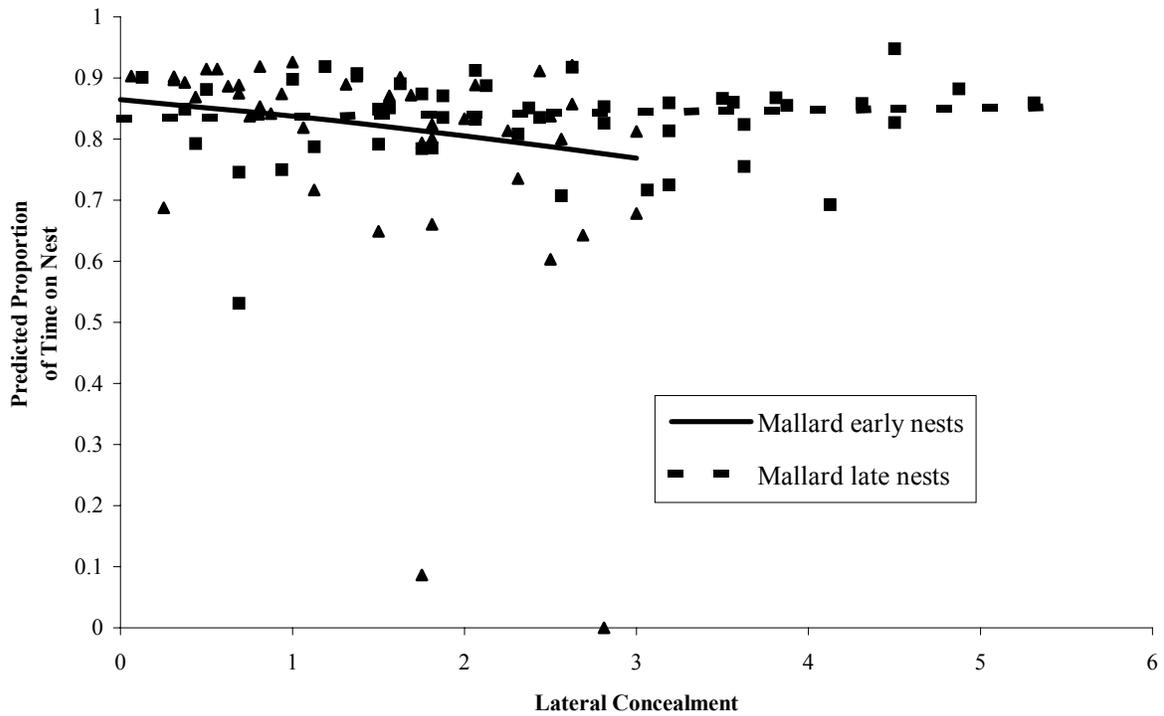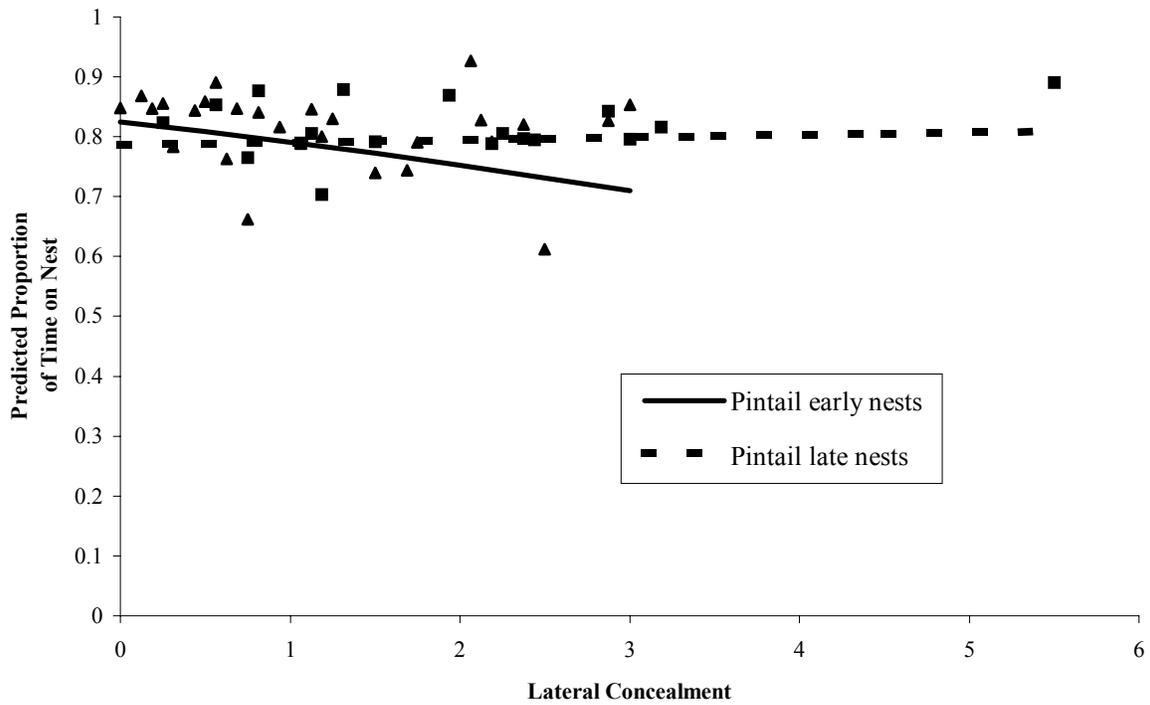
Figure 2.1. Relationship between predicted proportion of time on nest per day in relation to nest site cover for pintails (top figure) and mallards (bottom figure). In both figures the triangles represent the mean of daily incubation constancy at each level of lateral concealment for early nesting females; squares represent later nesting females.
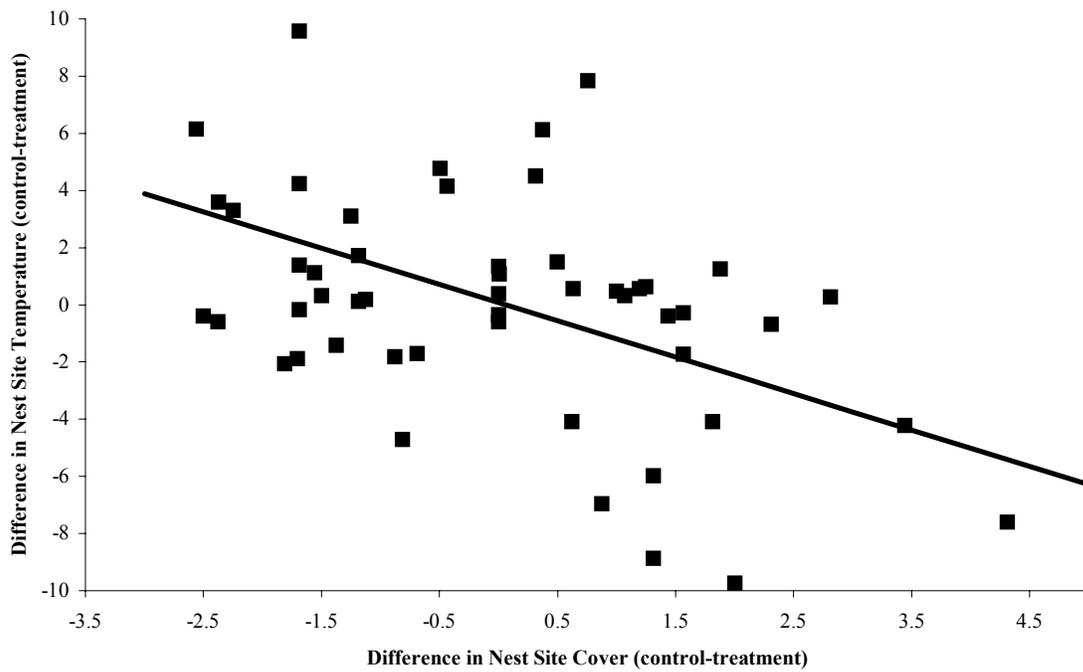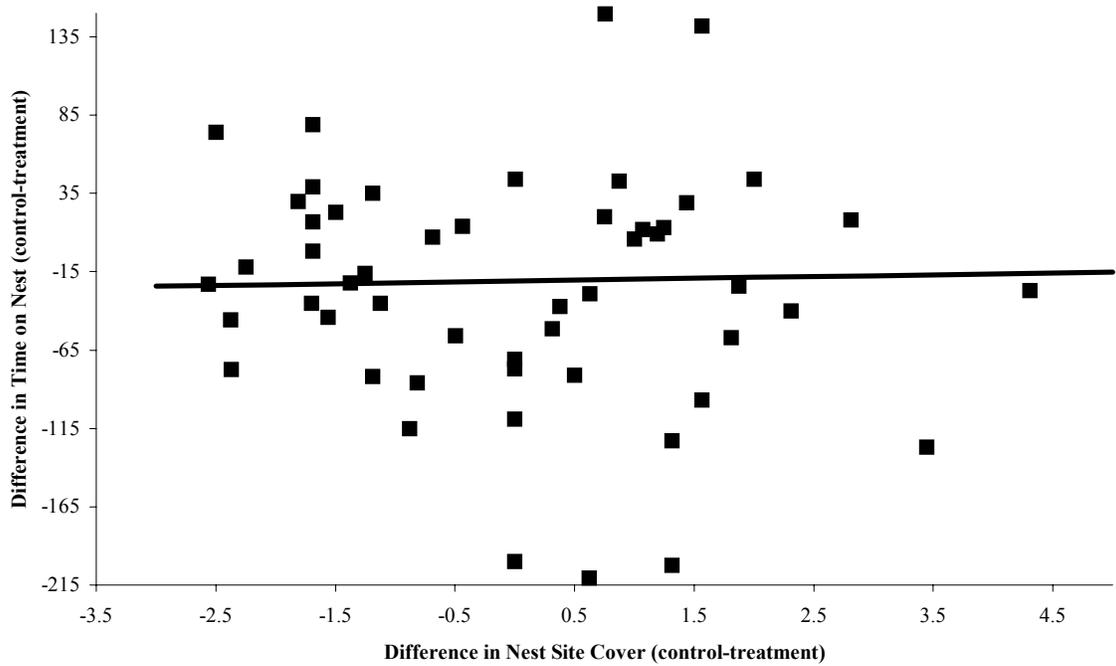
Figure 2.2. Relationship between nest site cover change to difference in time on nest (top figure) and nest site temperature (bottom figure).

Incubation Recesses. -- Mean recess duration was shorter for pintails (106.29 ± 87.08 minutes) than mallards (138.78 ± 104.81 minutes; $F_{1,1837} = 26.52$, $P < 0.001$). The effect of daily recess frequency on mean recess duration differed between species ($F_{1,1837} = 76.55$, $P < 0.001$, Figure 2.3), and pintails took more recesses per day than mallards (pintails 2.74 ± 0.04, range 0-8, mallards 1.72 ± 0.03, range 0-4). Pintails and mallards also differed in the distribution of the timing of recesses during the 4 segments of the day ($\chi^2_3 = 71.37$, $P < 0.001$, Figure 2.4). Pintails spread their breaks somewhat more evenly over the daylight period than mallards, which concentrated their breaks in the evening.

Incubation Period. -- I measured incubation period for 27 pintails and 11 mallards. Mean incubation period was shorter for pintails (23.00 ± 0.29 days) than mallards (24.10 ± 0.34 days). Incubation period was negatively related to overall constancy for pintails ($F_{1,24} = 9.51$, $P < 0.01$) but not for mallards ($F_{1,9} = 0.31$, $P = 0.59$, Figure 2.5).

DISCUSSION

Pintails nesting in North Dakota grasslands display a different incubation strategy than mallards. Pintails exhibited lower daily incubation constancy, and took 50% more recesses per day than mallards. These results are consistent with those reported for pintails (Afton 1978) and mallards (Caldwell and Cornwell 1975), although estimates of incubation constancy for both pintails and mallards from my study are lower than published reports. However, these differences may be due to small sample sizes in previous studies. My study was the first to document nest attendance patterns for pintails and mallards from a large sample of wild birds.

As predicted by the thermal-predation balance hypothesis, there was a negative relationship between nest site cover and incubation constancy for early season pintails and
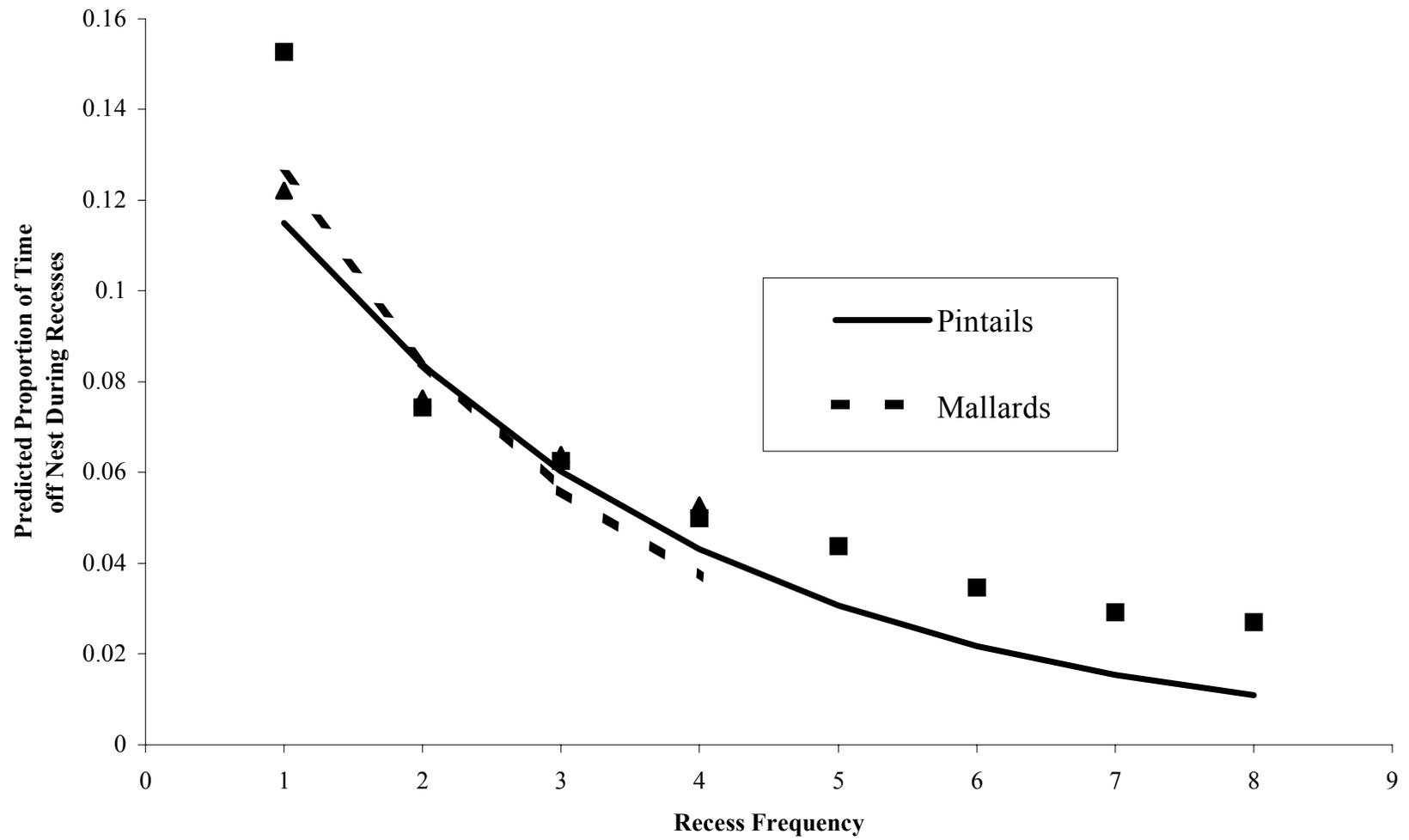
Figure 2.3. Relationship between predicted proportion of time off nest during recesses and recess frequency for pintails and mallards. The triangles represent the overall mean of mean recess duration at each level of recess frequency for pintails; squares represent mallards.
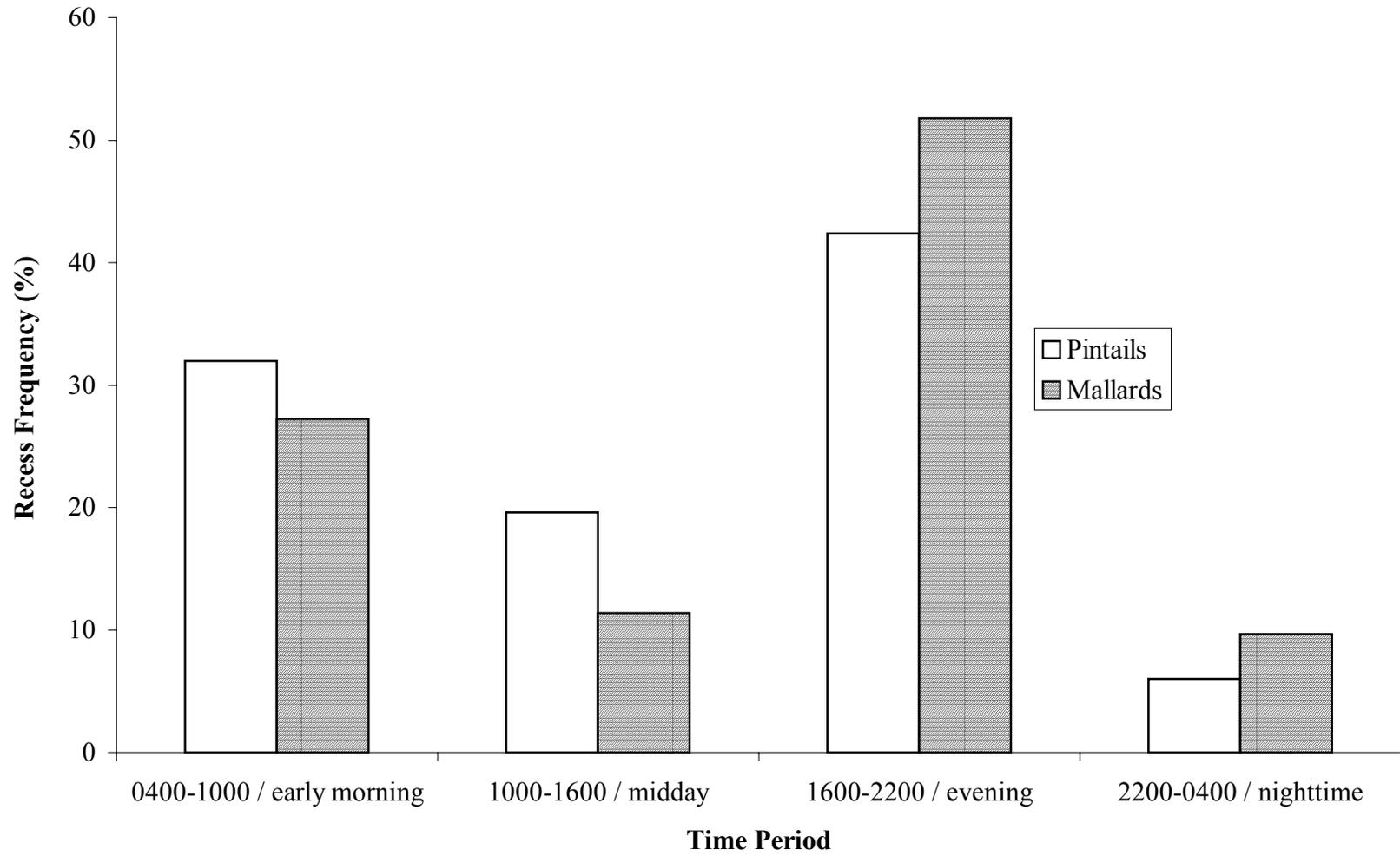
Figure 2.4. Distribution of recess initiation times by pintails and mallards.
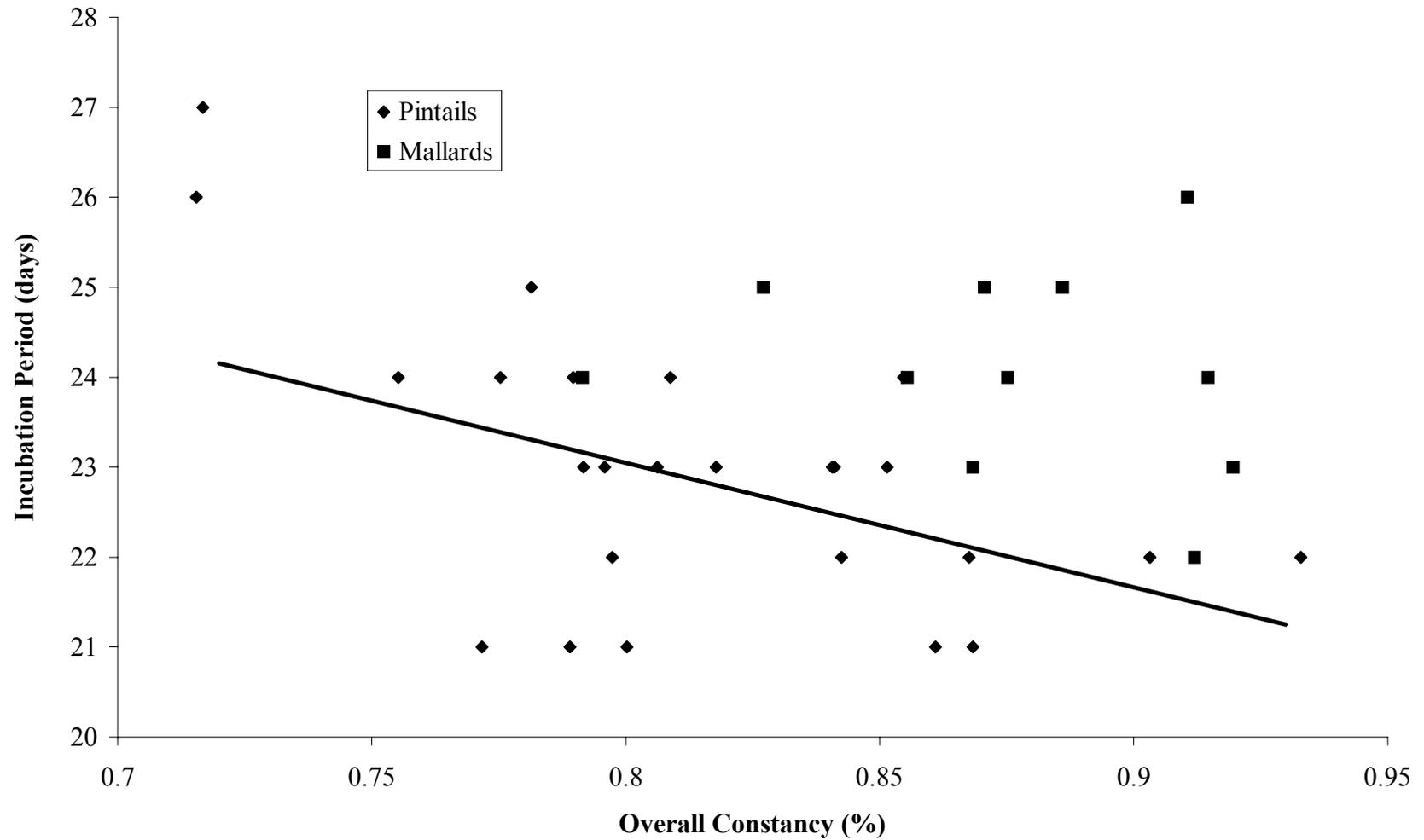
Figure 2.5. Relationship between incubation period by overall incubation constancy. Regression line for pintails is indicated by a solid line, and mallards did not show a significant relationship.

mallards. This relationship was not apparent for nests initiated after May 3. However, experimental manipulations of cover did not affect individual constancy. This leads me to question whether the descriptive results are simply consistent with the thermal-predation hypothesis, but caused by other factors. Loos (1999) proposed that a seasonal increase in incubation constancy in blue-winged teal is energetically driven. She suggested that frequent occurrence of cold temperatures early in the season may require females to spend more time off the nest feeding to meet energetic requirements during incubation. Conversely, warmer temperatures and perhaps greater food availability later in the year may result in females requiring less time off the nest to meet energetic requirements. This seasonal increase in incubation constancy could be present regardless of nest site cover. In addition, experimental results show that reducing nest site cover did influence the thermal environment as predicted, but temperature at the nest site did not affect incubation constancy. Guyn (2000) found that pintails selected nest sites that had lower temperatures than non-nest random sites and speculated that females exhibit nest site selection based on microclimate advantages especially later in the season. Perhaps nest site selection may be based on microclimatic features, but once the nest site was selected, females were unable to adapt their attendance patterns regardless of incubation costs for females.

As with the pintails in my study, several studies have shown a relationship of increased incubation constancy resulting in a shorter incubation period (Aldrich and Raveling 1983, Zicus et al. 1995, Yerkes 1998, Loos 1999). However, like the mallards in my study, some species do not exhibit shorter incubation periods with high constancy (Eichholz and Sedinger 1998, Flint and Grand 1999, Manlove and Hepp 2000). Perhaps the lack of relationship for mallards can be explained by the body size hypothesis (Afton and Paulus

1992). Mallards are a larger-bodied duck and rely more on endogenous reserves during incubation than smaller ducks (Gatti 1983). Flint and Grand (1999) concluded that the lack of relationship between incubation constancy and period suggests that recesses and egg cooling are not costly for egg development time in spectacled eiders. I suspect that recesses and egg cooling are costly for egg development time for mallards; but my sample size for this analysis was relatively small ($n = 11$) and there is not much variation in constancy between mallards and pintails.

Pintails spent more time on the nest as incubation stage progressed, but mallards did not show a similar effect. Other studies on prairie nesting ducks found an increase in incubation constancy with stage only in early nesting blue-winged teal (Loos 1999), or no change in daily constancy with stage (Afton 1980, Yerkes 1998). The effect of increasing stage also interacts significantly with the presence of precipitation for both pintails and mallards, such that females spend more time on the nest when it rains, especially in later stages of incubation. Developing embryos become less tolerant to cool temperatures as incubation progresses (Batt and Cornwell 1972). I expect that females are mitigating for effects of rapid cooling of eggs during rain events by remaining on the nest during those periods, especially later in incubation.

Waterfowl nesting on the prairies seem to show little variation in incubation constancy as can be illustrated by blue-winged teal (81.1%, Loos 1999), and pintails (81.6%) and mallards (83.2%) in my study. Interestingly, there are distinctive differences in daily recess frequency between blue-winged teal (3.0, Loos 1999), pintails (2.7), and mallards (1.8). I expect that the body size hypothesis Afton (1980) proposed would explain most differences in

recess frequency. Small-bodied teal, and intermediate-sized pintails likely require more recesses to feed because they do not use endogenous reserves as much as mallards.

Mallards use a significant amount of endogenous reserves during incubation (Gatti 1983). Surprisingly, Richkus (2002) found that pintails do not show a negative relationship between female condition and incubation stage. Richkus (2002) suggested that pintails might be maintaining a constant weight throughout incubation by exhibiting lower incubation constancy. My results suggest pintails increase recess frequency to maintain a more constant weight; presumably, taking more recesses per day increases foraging success. I would also speculate that taking more recesses per day assumes a greater risk of predation, such that pintails and mallards are balancing a trade-off between female requirements versus the survival of their nest (Afton and Paulus 1992).

Pintails and mallards initiated the greatest percentage of recesses in the evening and seldom took recesses during the nighttime, but pintails spread recesses more evenly throughout the day than do mallards (Figure 2.4). Afton (1980) proposed that females time recesses in response to 3 factors. Recesses taken just prior to or at sunrise and at sunset may be in response to increased food availability as zooplankton migrate towards the water surface in response to light conditions (Cushing 1951). In addition, recesses taken at these times may also be a predator aversion tactic, such that females leaving their nest in low light conditions reduce the risk of detection. Third, females may take recesses during the afternoon when temperatures are warm to minimize egg cooling. My data suggests that for pintails, timing of recesses is influenced by both food availability and a minimized risk of egg cooling, whereas for mallards, timing of recesses may only be influenced by food availability. If, as I proposed earlier, pintails take more recesses than mallards to maintain a more constant weight

throughout incubation, then logically, the timing of these recesses should coincide with high food availability and subsequently, a more efficient foraging regime. A high daily recess frequency suggests that pintails may have to mitigate for the negative effects of egg cooling resulting from frequent female absences by taking recesses during periods of the day when temperatures are warm. Perhaps nests in sparse cover, typical of pintails and small-bodied ducks that exhibit a high recess frequency, are benefiting from increased solar radiation such that egg cooling is less than nests in thicker cover, thus providing further evidence that females adopt incubation strategies that balance their own requirements with the survival of their nests.

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SUMMARY

Temperature data can be used with confidence to accurately determine female nest attendance on upland nesting waterfowl on the prairies. The camera system I developed to test the accuracy of using temperature data is relatively inexpensive (approximately $500 per unit), easy to set up in the field, durable during inclement weather, and provides a practical and viable option for recording a wide variety of parental behaviors at nests as well as reliably document predation events at nests.

Results from my study examining the influences on nest attendance in pintails and mallards indicates that although nest site cover may not be as influential in driving female nest attendance as I predicted, nest site selection may be driven by some expected set of environmental conditions for the female for the duration of the incubation period. Further insight into this question may be achieved by examining incubation rhythms of females in a variety of different habitat types and nest sites.

VITA

Andrea Kim Hoover was born on April 9, 1974, to parents Reg and Lenore Hoover. She grew up in Calgary, Alberta, and spent most summers during her childhood at the family cabin in Buffalo Lake, Alberta. It was at Buffalo Lake that she first learned of her love of the outdoors; perhaps partly due to the fact that the cabin did not have any running water and bathroom facilities were relegated to the outdoors. She graduated from Ernest Manning Senior High School in Calgary in June 1992, and moved shortly thereafter to Edmonton to attend the University of Alberta. It was during her third year at the U. of A. that she had her first job in the field as a summer field assistant for the Canadian Wildlife Service, discovering her passion for waterfowl and forever changing the course of her career. In 1996 she graduated with a Bachelor of Science degree in environmental and conservation sciences (wildlife and rangeland concentration). She worked for 3 years after graduation for the Canadian Wildlife Service and Ducks Unlimited Canada on as many waterfowl projects as she could before finally deciding in 1999 to pursue a master's degree. It was during the summer of 1999 while working for Delta Waterfowl and Wetlands Research that she met Dr. Frank Rohwer and eventually became a graduate student in the School of Renewable Natural Resources at Louisiana State University in 2000. The degree of Master of Science will be awarded in August 2002.