

THE INFLUENCE OF AGE, BODY MASS,
AND ENVIRONMENTAL VARIABILITY ON INDIVIDUAL VARIATION IN
REPRODUCTIVE BEHAVIORS OF FEMALE REDHEAD DUCKS

BY

TINA YERKES

A Thesis

Submitted to the Faculty of Graduate Studies
in Partial Fulfillment of the Requirements
for the Degree of

DOCTOR OF PHILOSOPHY

Department of Zoology

University of Manitoba

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Abstract. Variation in life history traits leads to variation in fitness among individuals. The objective of this research was to examine the influence of female age, body mass, and environmental variability on individual variation in incubation patterns, reproductive strategy choice, and brood ecology of female redheads (*Aythya americana*).

Redhead incubation constancy was the lowest reported among duck species. I proposed that incubation patterns are unusual due to prior parasitic behaviors, which result in a poor body condition. Constancy was higher for older hens, at higher ambient temperatures, and for lighter females at the end of incubation. End of incubation body mass may obscure this finding since mass loss relationships are unknown, but I proposed that heavier females at the beginning of season maintain higher constancy.

A dynamic state variable model was constructed to predict variation in strategy choice by age, body mass, food availability, and host availability. Model predictions were used to examine the occurrence of reproductive strategies on a population level. Strategy choice was influenced by body mass, age, and host availability, whereas food availability fine-tuned decision making. Predictions indicate that parasitism is exhibited in most situations, while nesting only is relatively rare.

A captive study was conducted to examine mass loss relationships and verify the predicted relationship between body mass and strategy choice. Body mass was significantly different at the beginning but not at the end of incubation. Thus, end of incubation body mass obscured the relationship between

constancy and mass. The predicted relationship between body mass and reproductive strategy choice was supported in captivity.

Finally, the influence of age and body mass on brood survival, habitat use, and brood movements was examined. Body mass influenced brood survival and brood movements among habitats, while age influenced only habitat use.

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CHAPTER ONE: GENERAL INTRODUCTION

The life history of an organism is the result of differential allocation of limited resources between the often conflicting demands of reproduction and survival (Roff 1992, Stearns 1992). Within a population, variation in life history traits leads to variation in fitness among individuals. Ultimately, each individual adopts an optimal life history such that lifetime reproductive success is maximized. Behavioral choices are often the mechanism by which variation is achieved. Age, body mass or condition, and environmental variability may influence choices that affect reproductive effort. Reproductive effort should increase with age (Trivers 1972, 1974), with body mass (Askenmo 1982, Moss and Watson 1984, Erikstad et al. 1993, Chastel et al. 1995, Winkler and Allen 1995), and in favorable environmental conditions such as increased food availability (Morton et al. 1972, James and Stugart 1974, Nolan and Thompson 1975).

Species of North American waterfowl (Family Anatidae) share several life history traits: they are migratory, exhibit some form of pair bond, and females lay relatively large, energy-dense eggs from which precocial young hatch after a period of incubation. Mortality is fairly high due to depredation and other natural occurrences, hunting, and is generally higher for females because of higher mortality on the breeding grounds (Sargeant and Raveling 1992). Waterfowl species meet the high energetic cost of reproduction in two fundamental ways. Geese (Subfamily Anserinae) are large-bodied waterfowl that exhibit permanent pair bonds, bi-parental care, and generally arrive on breeding grounds with

endogenous reserves adequate for the female to lay eggs and incubate (Ankney and MacInnes 1978, Raveling 1979, Ankney 1984, Ankney and Alisauskas 1991). Ducks (Subfamily Anatinae), in contrast, are small-bodied species that exhibit seasonal monogamy, female-only parental care, and arrive on the breeding grounds with fewer endogenous reserves than geese. Females rely on foraging for additional nutrients that are required for egg laying and subsequent incubation (Drobney 1980, Krapu 1981, Noyes and Jarvis 1985). Typical reproductive strategies of most North American ducks include producing their own clutch of large, high-energy, dense eggs that develop slowly (Alisauskas and Ankney 1992). Hens typically incubate their own nests over a period of 24 to 30 days and provide post-hatch care (Afton and Paulus 1992). Most female ducks have the choice within a season to breed or not and often renest if a nesting attempt fails.

Redheads (*Aythya americana*) are unusual among North American ducks because they exhibit a high frequency of facultative egg parasitism that extends their reproductive options within a season to include no breeding, parasitism, nesting, or a dual strategy. Sorenson (1990:82) described a 'dual strategy' "as a strategy that entails the separate and sequential utilization of two different reproductive strategies in which a female first lays a parasitic clutch and then lays her own clutch", the latter of which is subsequently incubated. If females lay eggs in their own nest, they must provide an adequate level of parental care to ensure survival of their offspring to fledging.

Behavioral decisions vary such that females have the ability to switch reproductive strategies from one season to the next. Saylor (1985) observed that in restricted environmental conditions, female Redheads employed a bet-hedging strategy and increased reproductive success by laying only parasitic eggs. Within a particular year, Sorenson (1990) attributed strategy variation in Redheads to a conditional strategy in which different reproductive decisions were made based on age and condition of the hen. The influence of and interaction between these factors are not well understood. Furthermore, females choosing more costly strategies, such as a dual strategy, may be energetically stressed and in poorer body condition, and thus the energetic investment to ensure reproductive success would be high. Factors that influence reproductive strategy choice and other behavioral patterns may include current or expected environmental conditions, hen age and body condition.

Incubation Behaviors

Although several studies have documented relationships between phenotypic and environmental variability and individual variation in clutch size (Rohwer 1992) and nest success of ducks (Johnson et al. 1992), few have examined variation in incubation behaviors. Furthermore, even though nest success is a direct reflection of successful incubation behavior, few studies have examined the factors related to intraspecific variation in behavior, such as incubation constancy. Only one study documented age effects on incubation constancy and demonstrated that young Canada Geese (*Branta canadensis*), incubating for the first time, exhibited lower incubation constancy (Aldrich and

Raveling 1983). The authors attributed the lower constancy to a lack of experience of young breeders. Redhead females that chose more costly strategies may be in poor condition and alter incubation patterns to allow greater foraging time.

A few studies have documented the effect of variation in body mass on incubation constancy. Heavier females were shown to be more successful incubators (Mallards *Anas platyrhynchos* and Northern Shovelers *Anas clypeata*, Gloutney and Clark 1991), exhibit higher incubation constancy (Canada Geese, Aldrich and Raveling 1983), and shorter incubation periods (Canada Geese, Aldrich and Raveling 1983; Common Eider *Somateria mollissima*, Erikstad et al. 1993). In contrast, Meade (1996) found no relationship between body mass and constancy in Canvasbacks (*Aythya valisineria*). Body mass may alter Redhead patterns, particularly if females are in poorer condition due to parasitic behaviors.

Environmental factors have also been shown to influence incubation constancy between years. Sayler (1985) documented the lowest incubation constancy of female Redheads during a drought year that was also a year of lowest female body masses. In another species, constancy of an individual female Ring-necked Duck (*Aythya collaris*) varied between years in response to water conditions, and thus food supply, and body mass (Hohman 1986).

Reproductive Strategy Choice

Facultative brood parasitism, an alternative female reproductive strategy, is often observed among waterfowl species, although the highest frequencies

are reported among Redheads. Several correlates have been proposed to account for the high frequency of parasitism observed in waterfowl: these include a large clutch size, a long egg laying period, and a long incubation period (for review see Sayler 1992). Parasitic frequencies also vary among waterfowl species and correlate with type of nest site used, degree of female philopatry, lack of territorial defense, degree of altricial-precocial development, cost/benefit to parent and cost/benefit to the parasite (Rohwer and Freeman 1989, Lyon and Eadie 1990, Sorenson 1992). Few studies have examined correlates of parasitism within species. In those which have, intraspecific variation in strategy choice and/or the occurrence of parasitism has been related to female age, body mass, density of nesting females, availability of nesting sites, and/or wetland water conditions. Additionally, Dugger (1996) suggests host density and the ratio of parasites to hosts can be an important factor that influences parasitic frequencies.

Lesser Snow Geese, which breed in the high arctic, rely heavily on endogenous reserves carried to the breeding grounds. Parasitic frequencies in Lesser Snow Geese have been attributed to nest site availability and female body condition (Lank et al. 1989, 1990). Lank et al. (1989) further hypothesized that parasitism was a poor reproductive tactic, but for females facing a high probability of nest failure the net reproductive benefit for parasitism may be higher than attempting to nest and therefore young females are more likely to switch between strategies.

In Common Eiders, which also nest in the arctic and exhibit colonial nesting, parasitic frequencies increase with increased nest densities (Robertson et al. 1992, Bjorn and Erikstad 1994). Robertson et al. (1992) proposed that nest density on initiation day mediated frequency of parasitism. Bjorn and Erikstad (1994) further attributed parasitism to immature females, those with a poor body condition, and/or those females whose attempts previously failed. In contrast, Robertson et al. (1992) found no evidence that parasitism was due to female condition or age.

Wood Ducks (*Aix sponsa*), which nest in cavities in the temperate zone, exhibit extensive parasitism. The frequency of parasitism has been attributed to nest site availability and population density. A lack of nest sites combined with an increase in population density produced high parasitic frequencies (Clawson et al. 1979, Haramis and Thompson 1985). Conversely, parasitic frequencies have been shown to be high even when a large number of unused nest sites were unoccupied (Semel and Sherman 1986, Semel et al. 1988a, b). In one study, higher parasitic frequencies were observed in nest boxes that were highly visible and clumped together as compared to nest boxes that were difficult to locate and more dispersed (Semel et al. 1988b).

Other cavity nesting species, such as Common Goldeneyes (*Bucephala clangula*), exhibit similar parasitic patterns. Nest site availability exerted the single greatest effect on the frequency of parasitism in Common Goldeneyes (Eadie 1991), while frequency of parasitism was not correlated with the number of host nests. In Barrow's Goldeneyes (*Bucephala islandica*), increased

parasitic frequencies were observed in years when population size was high and it was suggested that females may experience nest site limitations (Savard 1988).

In Redheads, which nest over water, parasitic frequencies are higher than in any other North American duck species. The occurrence of parasitism, as a reproductive strategy, has been attributed to hen age and body condition.

Parasitism is proposed to occur more often in young females (Sayler 1985, Sorenson 1990) and those females in poor body condition (Sorenson 1990).

The influence of water levels and food supply on the frequency of parasitism, however, is not clear. High parasitic frequencies have been attributed to water fluctuations and thus food supply (Low 1945, Erickson 1948). In other studies, no relationship has been found between environmental factors and frequency of parasitism (Olson 1964, Michot 1976, Joyner 1983, Sorenson 1990).

Additionally, Weller (1959) first stated that the most important factor influencing the degree of Redhead parasitism would relate to the density of parasites and hosts. No systematic study examining the influence of both phenotypic and environmental factors on the frequency of Redhead parasitism has occurred.

Brood Ecology

Nesting females must also invest in post-hatch care to ensure a reproductive payoff. Females enhance the survival of ducklings by 1) helping young to maintain body temperature until they can thermoregulate (Cain 1972, Seymour 1982), 2) selecting brood habitats (Inglis 1977, Ringelman and Longcore 1982), and 3) warning and protecting young against predators (Owen

1972, Ringelman et al. 1982). The critical period for care is the first two weeks after hatch when duckling mortality is highest (Afton 1984, Rhymer 1988, Rotella and Ratti 1992a). As female body mass is lower at the end of incubation than any other time of the year (Alisauskas and Ankney 1992), a hen must balance the needs of her brood with her own survival. Brood success is most often examined between years and related to the availability of quality habitat. Factors that influence success of individual females within a year, such as age and body mass, are rarely examined. Age did not influence brood survival in Lesser Scaup (*Aythya affinis*, Afton 1984) or Canvasbacks (Serie et al. 1992) and recruitment rates were not related to age in Barnacle Geese (*Branta leucopsis*, Forslund and Larsson 1991). However, recruitment rates were shown to vary with age in Lesser Snow Geese (*Chen caerulescens*, Ratcliffe et al. 1988). Only one study examined the relationship between female body mass and brood survival and found survival was not related to body mass in Canvasbacks or Redheads (Arnold et al. 1995).

Brood survival between years is often related to wetland density (Eldridge and Krapu 1988), variation in water levels (Rotella and Ratti 1992b), and factors relating to food availability (Kaminiski and Prince 1981, Murkin et al. 1982, Stoudt 1982, Talent et al. 1982). Individual differences in brood survival between years and environmental factors that may influence differences, for example variation in food availability across a landscape, have never been studied. Currently, little is known about Redhead brood survival and brood habitat use and how these may be affected by hen age and body condition.

The original objective of this study was to examine individual variation in parental care in the form of incubation behavior and brood ecology. This objective was expanded to include the prediction of variation in reproductive strategy choices. It was proposed that hen age, hen body mass, and environmental variability would influence behavioral variation within a population.

This study will document individual variation among female Redheads in incubation behavior, reproductive strategy choice, and brood ecology, and further document variation in individual success due to behavioral choices. Incubation patterns of female Redheads are examined in relation to ambient conditions, hen age, and hen body mass in Chapter 2. It is proposed that the differences observed in Redhead incubation patterns are due to energetic constraints imposed by prior parasitic behaviors of those females. Knowledge of individual reproductive strategy choices observed on a population level, however, is scant, thus Chapter 3 addresses this general lack of knowledge. A dynamic state variable model was developed to predict strategy choices under varying conditions of hen body mass and age, food availability, and host availability. The influence of each factor on strategy choice is discussed. Model predictions support the general hypothesis proposed in Chapter 2, which suggest that Redhead incubation patterns were unusual due to energetic constraints of parasitic behaviors. Chapter 4 reports the results of a captive study of female Redheads. The objectives are 1) to examine mass loss over the reproductive period and determine the relationship between body mass and

incubation constancy; 2) to confirm the relationship between strategy choice and body mass that is predicted in Chapter 3; and 3) to examine the relationship between mass, constancy, and strategy choice. In Chapter 5, variation in Redhead brood ecology is examined. Brood survival, the number of surviving ducklings, habitat use and brood movements are documented. Furthermore, the influence of hatch/initiation date, hen age, and body mass on survival, and habitat use and brood movements are examined. Chapter 6 summarizes factors found to influence individual variation in female Redheads.

CHAPTER TWO: FEMALE REDHEAD INCUBATION PATTERNS IN RELATION TO AMBIENT CONDITIONS, HEN AGE AND HEN BODY MASS

Birds exhibit a variety of incubation strategies (Skutch 1962, Drent 1975, Welty 1982). Shared incubation, in which both members of a pair cooperatively incubate, is the prevalent pattern (van Tyne and Berger 1959). In contrast, most North American duck species are female-only incubators that are forced not only to maintain an adequate environment for developing young but also to insure their own self-maintenance.

Incubation patterns vary among North American waterfowl species and are influenced by several factors. Interspecific differences in body size have been correlated with varying incubation patterns (Afton 1980). Large-bodied waterfowl, such as geese (Anserini), spend more time on the nest and rely heavily on endogenous reserves (Cooper 1978, Raveling 1979). In contrast, small-bodied ducks (Anatini, Aythyini) rely more on exogenous reserves, therefore, spending more time off the nest foraging (Krapu 1981, Drobney 1982, Barzen and Serie 1990). Among small-bodied duck species, incubation constancy (defined as the percent of time per day spent on the nest) also varies with body size. Representatives of large-bodied divers (Aythyini) and dabblers (Anatini), such as Canvasbacks and Mallards, exhibit an average incubation constancy of 87% and 89%, respectively (Gatti 1983, Meade 1996). In contrast, small-bodied divers and dabblers, such as Ring-necked Ducks and Blue-winged Teal (*Anas discors*), maintain a lower average constancy of 82% and 80%, respectively (Harris 1970, Hohman 1986). Afton and Paulus (1992) determined

that incubation constancy was positively related to body mass at the beginning of incubation for waterfowl species they compared ($n = 61$), although the relationship was strongest for geese and *Anas* species.

Ambient conditions, such as rainfall and ambient temperature, also influence interspecific differences in incubation patterns, particularly in small-bodied species. Large-bodied waterfowl have greater capacity for fat storage and thus rely on those reserves whereas small-bodied species cannot rely on endogenous reserves and must forage for exogenous nutrient sources (Afton 1980). Caldwell and Cornell (1975) and Afton (1980) demonstrated an increase in constancy in dabbling ducks with an increase in precipitation and decrease in temperature. Ambient temperature and/or precipitation did not influence incubation constancy of Ring-necked Ducks (Hohman 1986). Ring-necked females were observed to recess both in the middle of the night when temperatures were lowest and in the middle of the day when temperatures were highest (Hohman 1986).

Intraspecific differences in age and body condition may further influence incubation patterns. Currently, two prevailing and competing hypotheses are proposed to account for observed differences in reproductive effort in waterfowl by different age groups: restraint versus constraint (Rohwer 1992). The restraint hypothesis assumes 1) there is a tradeoff between the level of reproductive effort and subsequent survival, and 2) that birds' survival declines with age. This hypothesis predicts that reproductive effort should increase as an organism ages, up to a limit. The constraint hypothesis implies that young birds

are less capable of laying eggs and subsequently caring for them. At the end of egg laying, the restraint hypothesis predicts a higher reserve level in young birds because they hold back on reproductive effort. In contrast, the constraint hypothesis predicts a similar or lower reserve level in young versus older birds because they are presumably less proficient. Available studies support the constraint hypothesis. Aldrich and Raveling (1983) demonstrated that younger birds laid smaller clutches and were less attentive than experienced breeders. Yearling Mallards have lower reserves than adults at all stages of breeding (Krapu and Doty 1979). Further, Krapu and Doty (1979) suggest that clutch size of young Mallards in the wild is lower because they are ineffective at acquiring nutrient reserves for egg production. In captivity, where Mallards and Pintails (*Anas acuta*) were fed *ad libitum* and separated to eliminate competitive interactions, clutch size differences by age were not observed (Batt and Prince 1978, Duncan 1987a). In the wild, competitive interactions may occur and severely impact nutrient reserve acquisition. Nest success of Redheads has been shown to be influenced by age (Arnold et al. 1995) and this may be reflected by varying incubation patterns with age. Furthermore, constancy has been shown to be influenced by age in Canada Geese (Aldrich and Raveling 1983). Female geese nesting for the first time began incubation at a lower body mass and were less attentive than older, experienced females.

Intraspecific differences in body condition, often measured as body mass, may account for observed variation in constancy. Gloutney and Clark (1991) suggested that differences in body mass, and correspondingly nutrient reserves,

could explain intraspecific variation in incubation patterns. Additionally, Arnold et al. (1995) proposed that nutrient reserves, for temperate nesting waterfowl, are more likely to affect incubation behavior rather than the likelihood of nest abandonment. Gatti (1983) demonstrated that female Mallards in poor condition were less attentive (lower constancy) during incubation compared to those in better condition. Additionally, ducks that reneest and whose reserves may be further depleted, incubate less attentively (Afton 1980).

The objective of this study was to document Redhead incubation patterns and to examine interspecific and intraspecific differences in incubation behavior. Documentation of incubation patterns included incubation constancy, average recess number and duration, and the pattern of constancy over the incubation period. I propose that Redhead incubation patterns will be more similar to small-bodied duck species since Redheads may be energetically stressed due to prior parasitic behaviors. Furthermore, constancy should decline over the incubation period as female Redheads may require more time off the nest to forage for endogenous sources. Additionally, if reduced body condition affects incubation constancy in Redheads, the patterns should be influenced by ambient conditions much like small-bodied species. I further propose that intraspecific differences in incubation patterns will be attributed to female age and body mass such that older female Redheads will maintain higher constancy and heavier females will maintain higher constancy, as in other duck species.

Methods

Breeding Redheads were studied near Minnedosa, Manitoba, Canada (50°15'N, 99°50'W) during 1994 and 1995. The study area encompassed 143.4-km². The Minnedosa area is characterized by numerous seasonally- to permanently flooded wetlands, native aspen parkland vegetation and intensive agriculture (primarily small grains and oil seeds). Stoudt (1982) describes the study region in greater detail.

Redhead nests were located during daylight hours by over-water search techniques. If nests were located late in the laying stage (≥ 6 eggs) or during incubation, Hobo Temp XT remote temperature sensors (Onset Computer Co.), hereafter Hobos, were installed in the nest. A temperature sensitive probe was situated inside a 'dummy' egg in the middle of the nest. Probes were attached with silicon to the top of the egg, the location at which the closest contact between the probe and the hens' brood patch occurred. 'Dummy' eggs were constructed from hollowed out, large chicken eggs. Hollowed out eggs were reinforced internally with epoxy and attached to a rod stand, which extended perpendicular to the base of the egg. The rod stand secured the 'dummy' egg in the nest, which prevented the female from rolling the egg and prevented the egg from being ejected from the nest. Hobos were set to record temperature every 4.8 minutes, totaling 1800 data points in 6 days. Data from recorders were downloaded, generally in the afternoon, every six days.

Field candling (Weller 1956) determined stage of incubation. In 1995, one egg from each monitored female was collected and artificially incubated to

determine the exact date of hatch. In all cases of successfully hatched nests, artificially incubated eggs and wild clutches hatched on the same day. This monitoring method allowed accurate aging of nests that were abandoned or depredated.

At day 22-24 of incubation, hens were trapped on the nest to implant radio transmitters (see Chapter 5), and to assess age and body condition. Age of hen, classified as either yearling or adult, was determined by feather characteristics (Dane and Johnson 1975). Body mass was determined with a Pesola scale to the nearest 5 g and structural measurements of tarsus, culmen, and keel length were measured to the nearest 0.1 mm while right wing chord was measured to the nearest 1.0 mm. Body mass was used to indicate body condition (Appendix 1).

Weather data were obtained from Environment Canada. Weather information was recorded at Brandon Airport located 30 km southeast of the study site.

Data were collected from 71 hens in 1994 and 1995 totaling 446 incubation days. Days on which the hens were trapped or were disturbed by an investigator were excluded from analysis.

Statistical Analysis

Temperature data for each hen were visually scrutinized. A rise or drop in temperature of 3.0°C was defined as an 'on' or 'off' movement of the hen. If the drop in 3.0°C was not maintained for at least three time periods (14.8 minutes) the hen was scored as 'on' the nest but involved in a comfort

movement. Comfort movements, such as preening, were not considered as time off the nest. An individual recess was calculated as the total time the hen was recorded 'off' the nest to the time at which she was recorded as 'on' the nest.

Average recess frequency and duration were calculated for each hen.

Incubation constancy, defined as the percent of time the hen spent on the nest during a 24-hour period, was calculated for each hen. The relationship between daily average constancy, daily average recess number and daily average recess duration was examined with Pearson's correlation analysis. The pattern of recess frequency was examined over a 24-hour period by dividing the day into 24 1-hour time periods and correlating frequency with time of day. The relationship between daily average constancy and Julian date was examined by correlation.

To determine whether daily constancy changed over the incubation period and to determine the pattern of the change, daily constancy of individual hens was examined with a mixed linear model with repeated measures and linear, quadratic, and cubic contrasts (PROC MIXED, SAS). The influence of all potential main effects (age, mass, initiation day, incubation day, Julian date, maximum temperature, minimum temperature and precipitation) and significant two-way and three-way interactions on daily constancy were examined (PROC MIXED, SAS). During model development, non-significant 2- and 3-way interactions were eliminated and analysis was restricted to the main effects and significant interactions.

Results

Incubation constancy was calculated from 29 hens each with at least 8 days of incubation data totaling 348 hen-days (8 to 20 days per hen). Constancy was 0.819 ($SE \pm 0.007$) with a range of 0.751 to 0.897 . Redhead hens took an average of 7.2 ± 0.4 recesses per day for an average of 46.8 min. ± 2.3 . Average incubation constancy was significantly, negatively correlated with average recess number ($r = -0.57$, $P < 0.001$, $n = 29$), whereas average recess number was significantly, negatively correlated with average recess duration ($r = -0.57$, $P < 0.001$, $n = 29$). Recess frequency was not correlated with time of day, divided into 24 1-hour periods ($r = 0.29$, $P = 0.17$, $n = 24$)(Figure 2.1). Incubation constancy was not significantly different between females initiating nests early and late in the season, defined by average initiation date ($t = 1.06$, $P = 0.30$, $df = 27$).

The analysis of the pattern of incubation constancy over the 24 day incubation period indicated a daily decrease in constancy with increasing incubation day (Table 2.1). A mixed linear model with repeated measures revealed significant linear and quadratic trends and a marginally significant cubic fit (Table 2.1, Figure 2.2). These results indicate that constancy increased from day 1 to day 6, decreased between day 11 and 21, and increased slightly at the end of the incubation period.

The main effects of age, body mass, and maximum daily temperature and two-way interactions of initiation day by age and mass by Julian date

Figure 2.1. Timing of Redhead incubation recesses.

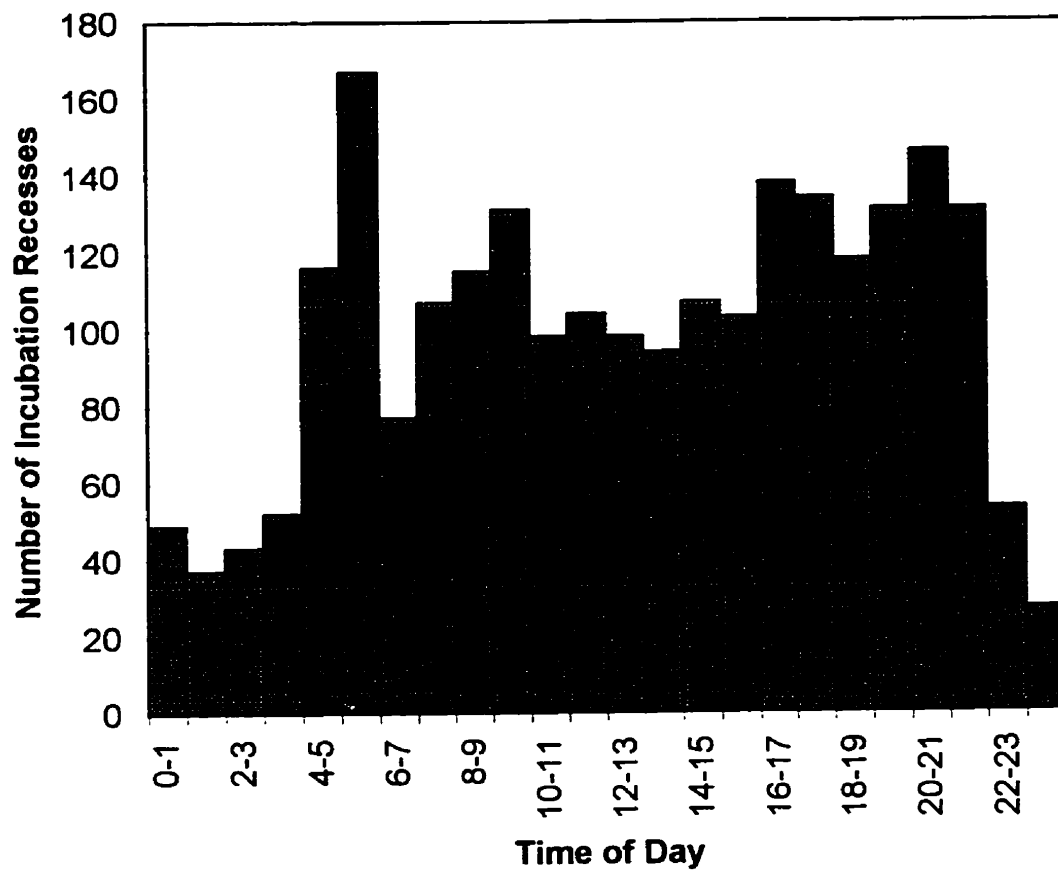


Figure 2.2. Curve fit of Redhead predicted incubation constancy over the incubation period and raw average constancy with standard error bars.

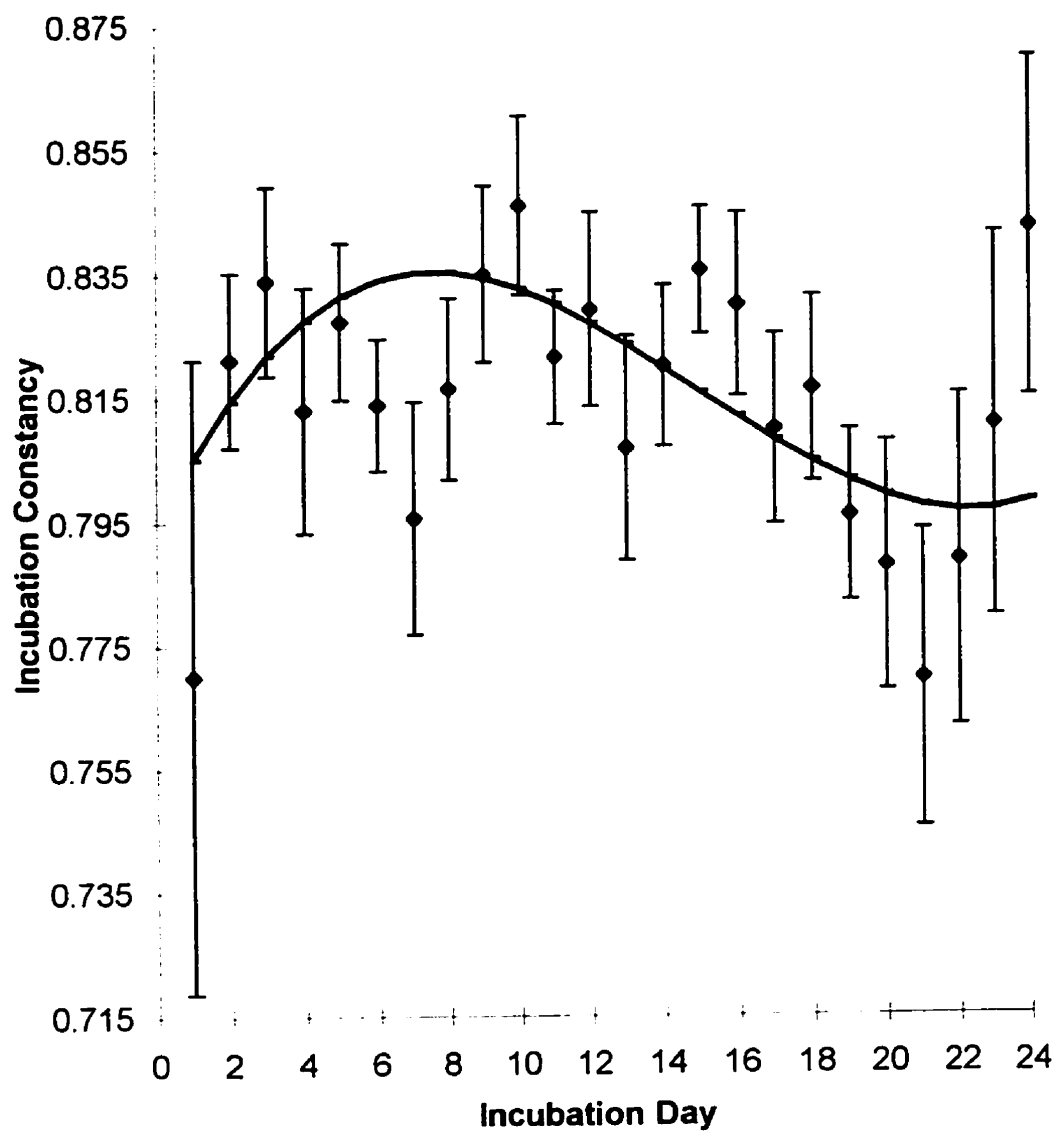


TABLE 2.1. The relationship between incubation day and daily incubation constancy of female Redheads.

Variable	Degrees of Freedom	t Value	P Value
Intercept	316	38.24	< 0.00
Linear Trend (incubation day)	316	2.13	0.03
Quadratic Trend (incubation day ²)	316	-2.16	0.03
Cubic Trend (incubation day ³)	316	1.86	0.06

significantly influenced daily incubation constancy (Table 2.2). Older hens exhibited higher average constancy (0.831 ± 0.009 , $n = 12$) than yearlings (0.811 ± 0.016 , $n = 8$). Lower constancy of yearlings was associated with more daily recesses (8.2 ± 0.9) of a shorter duration (42.9 ± 5.1) than adults (6.2 ± 0.5 ; 49.1 ± 3.0 , respectively). The interaction between initiation day and age indicated that yearling females tend to increase constancy late in the season compared to adults whose constancy tends to decrease with time (Figure 2.3). Constancy of adults is generally higher than yearlings early in the season. Initiation date was not significantly different between yearlings and adults ($t = -0.11$, $P = 0.46$, $df = 18$).

Females that ended incubation with a lower body mass maintained higher incubation constancy over the incubation period as compared to heavier females at the end of incubation (Table 2.2, Figure 2.4). Mass and Julian date also interacted to influence incubation constancy. Females that initiated clutches early in the season tend to exhibit decreased constancy with an increase in end-of-incubation body mass (Figure 2.5). Constancy of females initiating late in the season is fairly constant over the range of end-of-incubation body masses (Figure 2.5). Body mass did not influence initiation date ($R^2 = 0.002$, $F = 0.04$, $P = 0.85$, $df = 1, 18$).

Finally, as daily maximum temperature increased, daily constancy decreased (Table 2.2). Minimum daily temperature, daily precipitation, initiation day, incubation day, or Julian date (Table 2.2) did not influence constancy.

Figure 2.3. A comparison between age groups of the interaction of age and initiation date (first day of incubation) on incubation constancy.

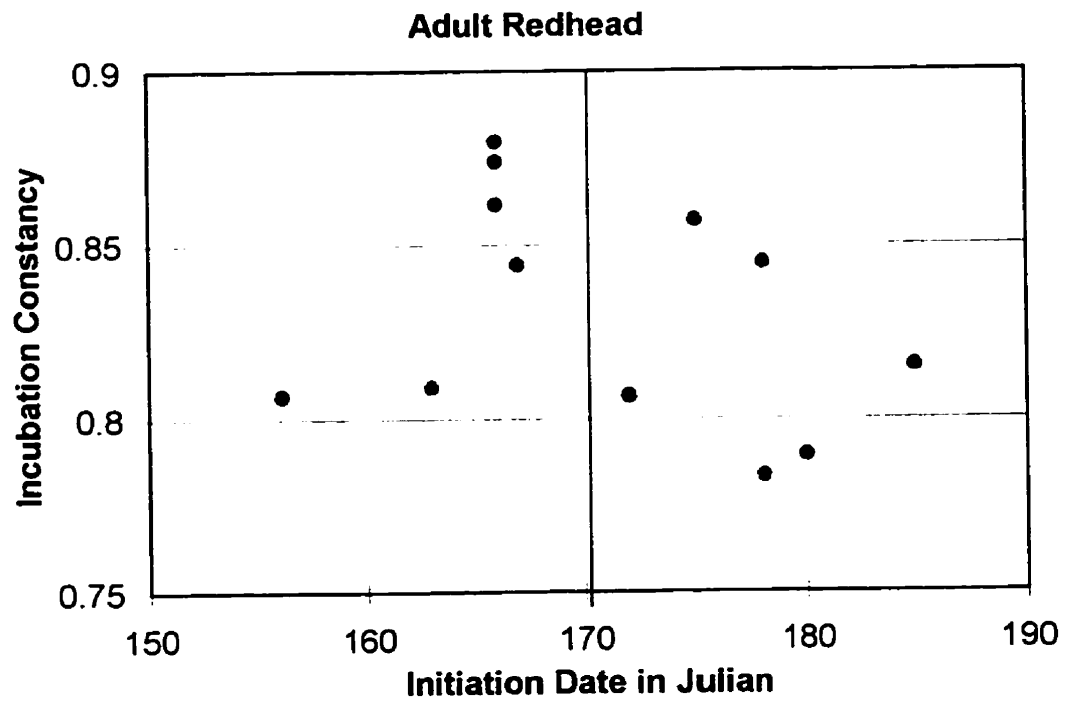
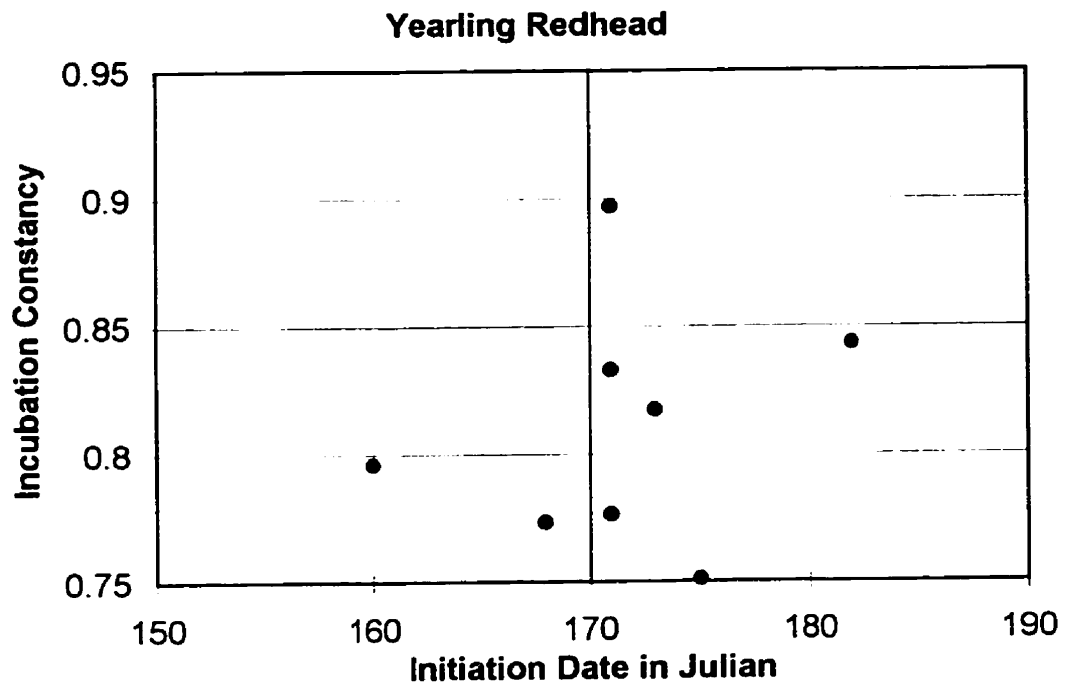


Figure 2.4. Scatter plot of Redhead body mass at the end of incubation and incubation constancy.

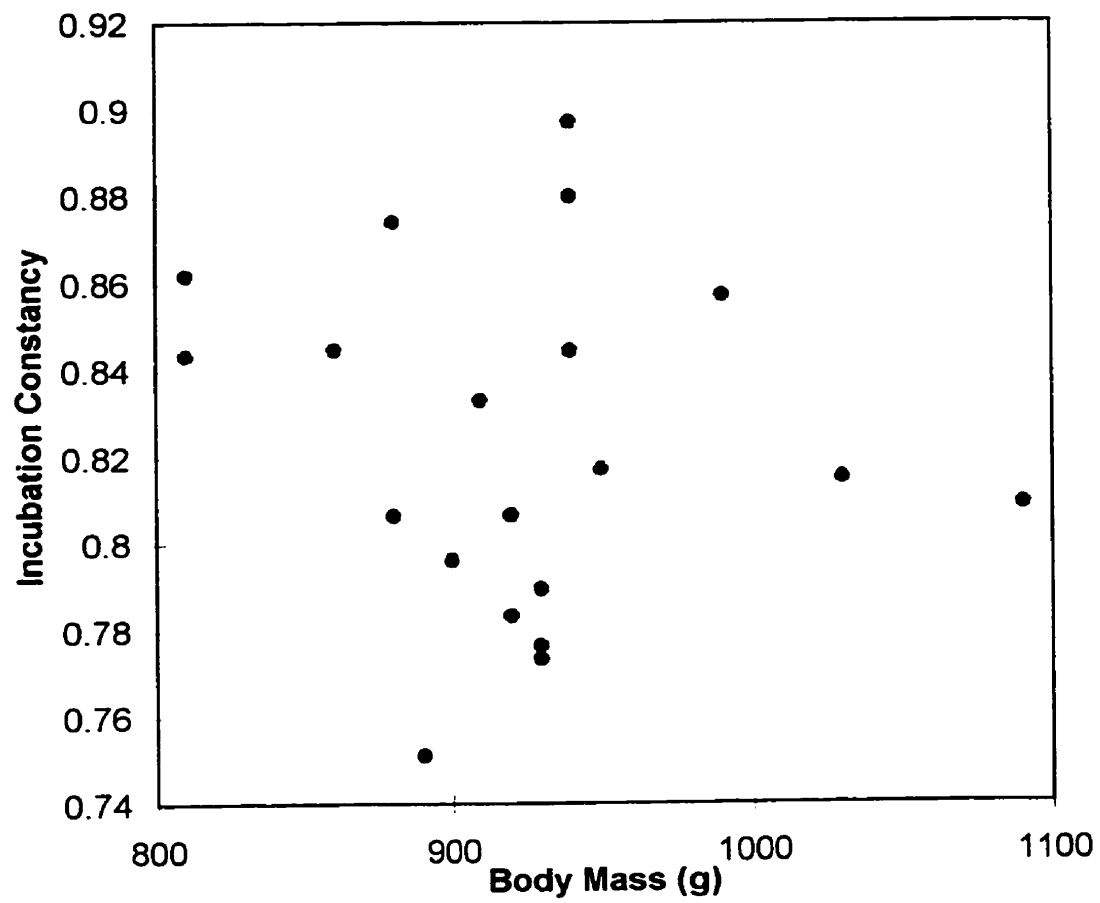
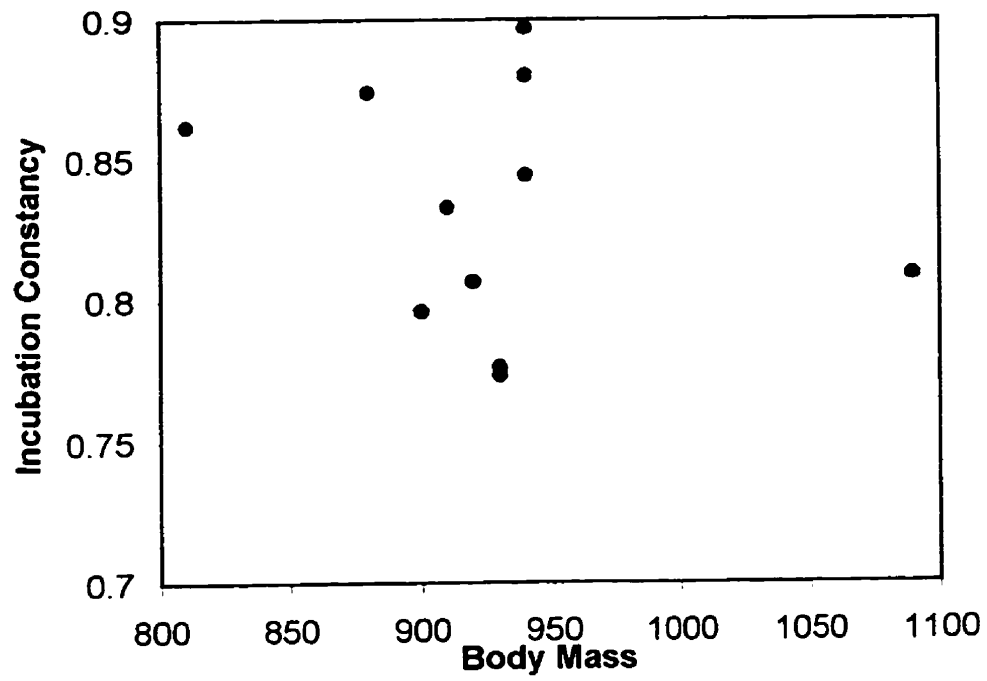


Figure 2.5. The interaction of Julian date and mass on incubation constancy. A) Female redheads that initiated early in the season (≤ 171 Julian) compared to B) females that initiated late in the season (> 171 Julian).

A



B

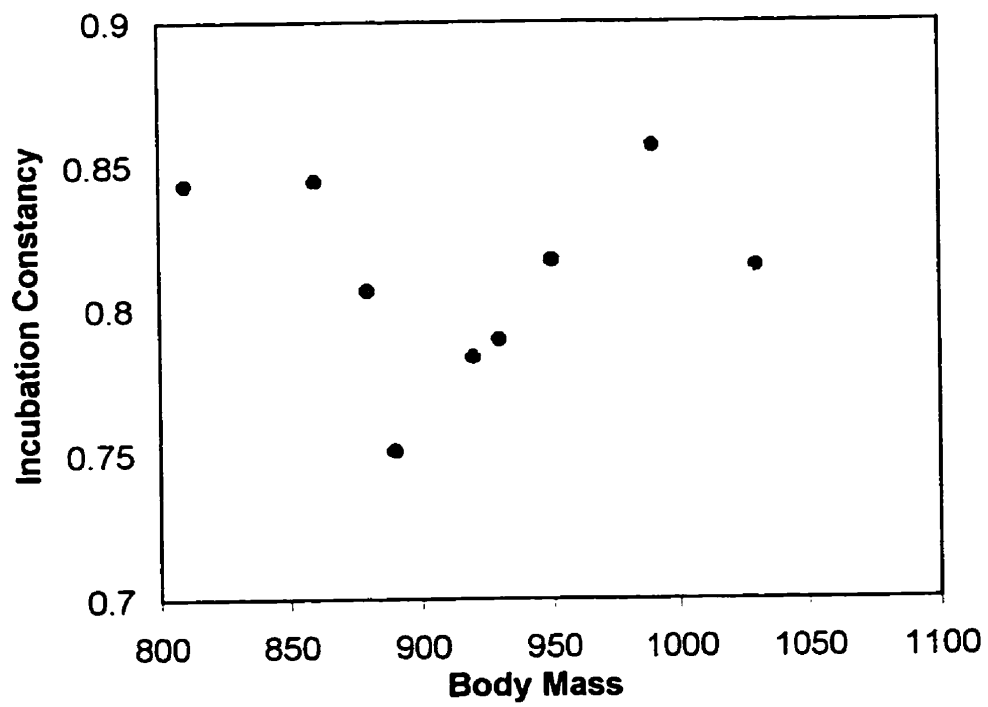


TABLE 2.2. The influence of the main effects and significant two-way interactions on Redhead incubation constancy.

Variable	Estimate	Degrees of Freedom	t Value	P Value
Age	-0.70528	234	-2.60	0.01
Mass	-0.00398	234	-2.29	0.02
Initiation day	-0.00173	234	-0.18	0.98
Incubation day	0.00026	234	-0.03	0.98
Julian date	-0.01974	234	-1.53	0.13
Maximum Daily Temperature	-0.00298	234	-2.55	0.01
Minimum Daily Temperature	0.00058	234	0.38	0.70
Precipitation	0.00241	234	0.82	0.41
Initiation Day x Age	0.00397	234	2.51	0.01
Mass x Julian Date	0.00002	234	2.25	0.03

Discussion

Interspecific Variation

Female Redheads exhibit unique incubation patterns both interspecifically and intraspecifically. Both for their size and in absolute terms, Redhead females maintain an average incubation constancy that is among the lowest of all waterfowl species and is the lowest reported for diver species (Table 2.3). Incubation constancy previously reported for Redheads ranged from 72% (Low 1945) to 85% (Sayler 1985). Low (1945) monitored only four hens and Sayler (1985) monitored hens only during daylight hours thus potentially overestimating constancy. Although large-bodied, Redheads exhibit constancy similar to small-bodied species, such as Blue-winged Teal (Harris 1970, Miller 1976) and Common Goldeneyes (Mallory and Weatherhead 1993). Afton (1980) and Afton and Paulus (1992) proposed and presented evidence for the incubation constancy – body size relationship in waterfowl, which proposed that constancy increases with body size. The relationship between body size and incubation constancy does not apply, without modification, to female Redheads. Furthermore, attempting to control for phylogenetic effects is difficult because data on most species are lacking.

High recess frequency and timing of recess initiations adds to the unusual incubation pattern observed in Redheads. Redheads take more recesses per day than any duck species previously reported (Table 2.3). Average recess duration, however, was not generally different because duration may be constrained by egg/embryo viability (Drent 1975, Webb 1987, Haftorn 1988)

TABLE 2.3. Incubation constancy, recess number, and recess duration for various waterfowl species.

	Body Mass (g)	Mean Incubation Constancy (%)	Average Recess Number (#/day)	Average Recess Duration (min.)
Anserini				
<i>Branta canadensis</i>	3721	97.5	2.8	13
<i>mofitti</i> ^{1,2}				
<i>B. c. minima</i> ³	1241	93.6	3.5	26
Anatini				
<i>Anas platyrhynchos</i> ^{4,5,6}	901	94.6	?	24
	982	89.2	?	?
<i>A. strepera</i> ⁷	642	84.7	1.9	118
<i>A. clypeata</i> ^{8,9}	518	84.6	2.3	94
<i>A. rubripes</i> ¹⁰	?	89.4	1.5	102
<i>A. discors</i> ^{11,12}	335	80	2.7	105

TABLE 2.3. Continued

	Body Mass	Mean	Average	Average
	(g)	Incubation	Recess	Recess
		Constancy	Number	Duration
		(%)	(#/day)	(min.)
Aythini				
<i>Aythya valisineria</i> ^{13,14}	1079	87	3.4	57
<i>A. americana</i> ^{15, 16, 17}	1051	82	7.22	47
		72		
		85		
<i>A. collaris</i> ¹⁸	630	85.2	3.4	67
<i>A. affinis</i> ¹⁹	629	85.1	2.8	76

1. Akesson and Raveling 1981; 2. Aldrich and Raveling 1983; 3. Raveling 1979; 4. Gatti 1983; 5. Krapu 1981; 6. Cornwell and Cromwell 1975; 7. Blohm 1979; 8. Ankney and Afton 1988; 9. Afton 1980; 10. Ringelman et al. 1982; 11. Harris 1970; 12. Miller 1976; 13. Barzen and Serie 1991; 14. Meade 1996; 15. this study; 16. Low 1945; 17. Sayler 1985; 18. Hohman 1986; 19. Afton and Ankney 1991

and/or by variance in incubation temperatures that may adversely affect incubation period (Wilson and Verbeek 1995). Redheads initiate recesses with equal frequency during all daylight hours and occasionally initiate at night, unlike other species that exhibit either a uni- or bimodal recess pattern during daylight hours (Caldwell and Cornell 1975, Afton 1980, Brown and Fredrickson 1987, Mallory and Weatherhead 1993, Meade 1996). Nocturnal recesses of significant duration are uncommon for ducks (Ringelman et al. 1982).

Redhead incubation constancy decreased over the incubation period, a pattern that is observed in many duck species (Afton 1980, Brown and Fredrickson 1987, Mallory and Weatherhead 1993), but may not be common in other birds (Drent 1970). This pattern has often been attributed to increasing ambient temperature with increasing incubation period (Mallory and Weatherhead 1993), an increase in embryonic heat production (Drent 1970), and/or energetic constraints on the female (Afton and Paulus 1992). Although increased ambient temperatures were proposed to explain decreased constancy in Goldeneyes (Mallory and Weatherhead 1993), temperature over the incubation period did not influence Redhead patterns because Julian date and daily constancy were not related. Redhead females may be responding to an increase in embryonic heat production as proposed by Drent (1970), however, this effect was not assessed in the present study. Energetic constraints, in the form of declining endogenous reserves as incubation progresses, may force females to acquire more exogenous nutrient sources thus resulting in decreased attendance at the nest (Afton and Paulus 1992). This pattern has also been

documented in Canada Geese (Aldrich and Raveling 1983, Murphy and Boag 1989).

Ambient conditions, within a particular day, may also account for interspecific variation in incubation constancy because behaviors vary among species. Redhead females apparently respond only to maximum daily temperature, like Goldeneyes (Mallory and Weatherhead 1993), decreasing daily constancy on days with higher maximum temperatures. In others, constancy often increases as ambient temperature decreases and during rain (Caldwell and Cornell 1975, Afton 1980). Some large bodied species, such as Canvasbacks (Meade 1996) and White-winged Scoters (*Melanitta deglandi*) (Brown and Fredrickson 1987) modify patterns in response to daily precipitation only. Some species, however, do not respond to either temperature or precipitation (Ringelman et al. 1982, Hohman 1986).

Several hypotheses have been offered to explain the low incubation constancy and unusual incubation patterns exhibited by Redheads: (1) excessive disturbance at the nest (Low 1945), (2) reduced maternal investment (Low 1945), and (3) energetic constraints on the female (Sayler 1985). If excessive disturbance at the nest due to parasitic behaviors of other hens significantly reduces constancy, one would expect females nesting early in the season, those nesting during peak parasitic events, to exhibit lower constancy than later nesters because Redhead females parasitizing other Redheads encounter an incubating host as much as 71% of the time (Sayler 1996). In this study, constancy of females nesting early and late in the season was not

significantly different. Reduced maternal investment in the clutch seemingly would not account for lower constancy of Redheads because hatch success is not significantly lower than other diving ducks (Bellrose 1980) and is not decreased in other parasitized species (Morse and Wight 1969, Bouffard 1983, Eadie and Lumsden 1985). Rather than reduce hatch success, parasitized females are more likely to abandon excessively parasitized clutches (Clawson et al. 1979, McCamant and Bolen 1979, Andersson and Eriksson 1982, Haramis and Thompson 1985, Rohwer and Freeman 1989, Dugger 1996; but see Eadie 1989) or abandon if parasitized early in their laying sequence (McRae 1995).

Finally, energetic constraints imposed by prior parasitic behaviors may account for the low constancy exhibited by Redheads. Redhead body condition may indeed override the relationship between body size and incubation constancy, much like that proposed for Black Ducks (*Anas rubripes*), which face energetic constraints due to low densities of aquatic invertebrate prey (Ringelman et al. 1982). Additionally, Noyes and Jarvis (1985) demonstrated that female Redheads used most of their stored lipids during laying (46%) and continued to deplete lipid reserves during incubation, investing 30% of their remaining reserves. They attributed the large amount of lipid reserves lost during the laying period by females to both parasitic laying and the laying of a nested clutch. Frequency of parasitism was 65% in their study and, although prior parasitic behaviors of hens in this study were not known, Redheads parasitized 85% of Canvasbacks nests indicating that many Redheads parasitized prior to nesting.

Intraspecific Variation

Energetic constraints, coupled with age/experience, account for intraspecific differences observed in female Redheads. Adult female Redheads exhibited higher constancy with fewer recesses of longer duration than yearlings, however, prior experience of adults is unknown. Higher constancy may increase nest success, given that nest success has been shown to be influenced by age in Redheads (Arnold et al. 1995). Captive Canada Geese (Aldrich and Raveling 1983) and Goldeneyes (Mallory and Weatherhead 1993) provide additional evidence for the influence of age on constancy. Adult females may be more efficient competitors and foragers, thus more capable of maintaining sufficient nutrient reserves allowing a higher incubation constancy.

Hen age and initiation date interact to further influence Redhead incubation constancy. In most ducks, young hens often initiate clutches later than adults. In Redheads, yearlings often initiate nests earlier or at the same time as adults (Sorenson 1990). In this study, initiation dates between age groups were not significantly different. The effect of the interaction between initiation date and age on Redhead constancy indicated that young hens initiating later in the season maintained higher average constancy than older hens that initiated late in the season. Given similar nest initiation times, this relationship may represent young hens that have nested compared to older hens that have employed a dual strategy, leaving young hens with greater residual reserves than they would have had if they too had followed a dual strategy. Older hens employing a dual strategy may be in a compromised body condition

due to parasitic behavior and therefore forced to maintain lower incubation constancy. The converse is also true, when both age groups initiated nests early in the season, a time when parasitism was not likely to have occurred, adults maintained higher constancy than yearlings, which potentially represents an advantage gained through experience or greater body reserves.

Body mass further explains intraspecific variation in incubation patterns of Redheads. Although variance was large in this study, heavier female Redheads, weighed at the end of incubation, maintained lower incubation constancy than lighter hens. In this study, however, mass taken at the end of incubation may obscure this comparison because in other species heavier hens at the beginning of incubation lose more mass over the incubation period than lighter hens (Harvey et al. 1989, Hepp et al. 1990). If this mass loss relationship prevails in incubating Redheads, hens finishing incubation at a lighter body mass, which exhibited higher constancy, may have begun incubation at a heavier body mass and therefore heavier females may incubate at a higher constancy. Evidence in support of this interpretation is presented in Chapter 4. Additional evidence for this relationship is provided by Aldrich and Raveling (1983) and Reed et al. (1995), in which heavier female geese at the beginning of incubation exhibited higher nest attentiveness. Between years, Hohman (1986) observed a single female to exhibit the lowest incubation constancy during a year in which she entered reproduction in a reduced body condition.

The interaction between body mass and Julian date also influences Redhead constancy. Females incubating early in the season exhibit higher

constancy and end incubation at a lower body mass versus females incubating later in the season which exhibit lower constancy and ended incubation at a higher body mass. If heavy females lose more mass than light females, as suggested above, heavy females as compared to light females that initiate early, maintain higher constancy and end incubation at a lower body mass as indicated by the interaction above. This may further suggest that females that initiated nests early at high body mass are non-parasitic females (nesters only) and those that initiate later at lower masses are parasitic females (dual strategists). Thus, body mass and reproductive strategy choice may indeed interact to influence incubation constancy.

Female Redheads exhibit unique patterns that are not generally predicted given their body size. Large-bodied female Redheads should exhibit a comparatively high incubation constancy, however, they exhibit one of the lowest reported coupled with one of the highest recess frequencies. The conclusions of this chapter are based on two premises. First, the majority of nesting Redheads parasitized prior to nesting, and thus began incubation in a reduced body condition. Second, the relationship between incubation constancy and mass, inversely related in Redheads, is obscured by using the end-of-incubation body mass because heavier females at the beginning of incubation may lose more mass than lighter cohorts. Two additional studies were designed to determine the validity of these assumptions. First, a dynamic state variable model was constructed to predict the reproductive strategy choices of female Redheads and examine the prediction that most nesting females participated in parasitic events

prior to nesting. The results of this model are discussed in Chapter 3. Second, a captive study was designed to examine mass loss relationships of incubating female Redheads. Results of this study are discussed in Chapter 4.

CHAPTER THREE: FEMALE REDHEAD REPRODUCTIVE STRATEGY CHOICES: A PREDICTIVE MODEL.

Reproductive strategy choices weigh the costs and benefits of producing offspring against parental survival. Strategy choices are assumed to have been selected to maximize fitness by maximizing lifetime reproductive success.

Choosing among alternate reproductive strategies often results in variation in reproductive success among individuals. In all animal populations studied thus far, individuals vary greatly in the number offspring produced over a life span (Clutton-Brock 1988). Variation in reproductive behavior may be contingent upon the environment or upon phenotypic characteristics such that reproductive effort may increase when environmental conditions are favorable, increase with age to a limit and increase with body mass. Several studies have shown that some bird species regulate the level of reproduction relative to the amounts of energy they have available to them (Morton et al. 1972, James and Stugart 1974, Nolan and Thompson 1975). Age of parent may also influence strategy choice (Trivers 1972, 1974). Lastly, although the influence of body mass on strategy choice has never been assessed in birds, body mass has been shown to influence other reproductive parameters. Body mass influences clutch and brood sizes in a variety of avian species (Askenmo 1982, Moss and Watson 1984, Erikstad et al. 1993, Chastel et al. 1995, Winkler and Allen 1995).

Among North American waterfowl, Redheads are unusual in their extensive use of inter- and intraspecific hosts and their high frequency of facultative parasitic egg laying. Redheads may adopt this behavior as an

additional strategy to increase reproductive success. However, the occurrence of alternate strategies on a population level within and between years and the possible factors that influence strategy choice are not well documented or understood.

Annual variation in reproductive tactics chosen by female Redheads appears to be influenced by annual variation in environmental conditions, especially wetland and water conditions. Sayler (1985) compared the frequency of parasitism between a drought year and a 'good' year and found the frequency of parasitism to be 51-61% versus 27%, respectively. In drought years many non-breeders were present in the population and nest success was lower (16%) compared to 'good' years (88%). Sayler (1985) attributed a low nesting frequency and increased costs to Redheads in drought years to lower water levels, which may have reduced food abundance. Increased parasitism in drought years represented lower reproductive effort by avoiding reproductive costs of incubation and brood rearing. Thus, in restricted environmental conditions, some females may lack sufficient endogenous reserves and foraging time to both lay and incubate eggs. Sayler (1985) concluded that Redhead hens employed a bet-hedging strategy by increasing production of parasitic eggs under environmental conditions less favorable to reproductive success, such as during drought.

In a later study, Sorenson (1990) attributed within-year variation among individual Redhead females to a conditional strategy in which different reproductive choices were observed by hen age and physical condition. Age

appeared to affect individual choices in that adults were most often observed employing a dual strategy, whereas yearlings either parasitized or nested only. Young may acquire resources less proficiently, which results in higher costs of reproduction, lower probability of success and/or greater likelihood of constraints. Young may invest less in reproduction because they have higher residual reproductive value (Pianka and Parker 1975). In waterfowl, young lay fewer eggs, nest later in the season, and are more likely not to breed or reneest (Krapu and Doty 1979, Afton 1984). Additionally, in Redheads, Sayler (1985) found decoy trapped hen mass to be lowest in drought years when the frequency of parasitism was highest.

Variation in reproductive strategy choice among individual female Redheads has been documented both within and among years. Previous research (Weller 1959, Sayler 1985, Sorenson 1990) alludes to the importance of environmental conditions within and among years and the influence of individual female age and body condition on variation in reproductive strategy choice. Long-term studies, however, have not been conducted to determine the influence of these different factors on variation in strategy choice. Further, the variation of observed strategies within a year, on a population level, is not well documented since obtaining this information in the wild is difficult. To predict strategy choice on a population level and the influence of female body mass, female age, and environmental variability on strategy choice, a dynamic state variable model was developed (Mangel and Clark, 1988). I attempted to

determine whether females that were observed to nest in the wild were also likely to have parasitized prior to nesting, as assumed in Chapter 2.

Model Description

To model the reproductive strategy decisions of female Redheads, a dynamic state variable model was constructed (see Table 3.1 for a list of the model parameters and values). Environmental variability was divided into the probability of finding food and the probability of finding a host nest. Age of hen was defined as the probability of surviving to the next breeding season, whereas body mass ranges were obtained from a wild population of female Redheads. This model runs over one breeding season, which was split into seven time steps ($T = 7$) representing approximately 10 days each. Laying eggs is restricted to the first three time periods and the reproductive options available include: forego breeding in that season, parasitize either inter- or intraspecifically, lay a nest of eggs and provide the appropriate care, or employ a dual strategy. By definition, the options to nest or brood parasitize are available only during the first three time periods of the breeding season which represent time constraints experienced by wild breeding female Redheads. If females do not lay or parasitize early in the breeding season, there may not be adequate time for the ducklings to mature before fall migration. The termination of nesting may reflect a point where payoffs for late nesters are below survival costs to late nesting females (Dobson 1987, Rohwer 1992). When a female nests she must incubate the eggs for three time periods in this model, which represent the approximate incubation period of a wild Redhead. She must then

TABLE 3.1. Description of the model parameters and values used in the basic model.

Parameter	Values	Description
T	7	The final time step (time horizon)
t	---	The current time step for all $t < T$
x	---	The current body condition (a state variable)
x_c	800	Critical (minimum) body mass
x_m	1200	Maximum body mass
n	---	Current number of nested eggs (a state variable)
p	---	Current number of eggs laid parasitically (a state variable)
e_n	10	Expected number of nested eggs
e_p	10	Expected number of parasitically laid eggs
λ	0.8	Probability of finding food per t
Y	10	Benefit to body mass of finding food
α	---*	Cost to body mass of option i
β	---*	Offspring mortality associated with decision i
ϕ	0.25, 0.2, 0.15	Survival rate of parasitic eggs laid at $t = 1, 2$, or 3
ε	0.5	Over-winter survival
γ	0.5	Probability of finding a host nest

* See Table 2 for specifics on these values

invest further to rear the ducklings for an additional time period. After this point the offspring are considered to be independent and do not require further parental care. The female has the option to abandon the nest at any point in this process, which results in the loss of all eggs laid in the nest.

Parasitic eggs, in this model, only require the energetic investment associated with formation of eggs. Costs, such as locating host nests and vigilance against depredation are not included here or elsewhere in the model. If a female decides to parasitize early in the season (the first time period), there is the possibility for a second parasitic clutch to be laid or for the female to subsequently nest. The female, however, must take one time period off between her initial decision to parasitize and subsequent decision to parasitize or nest. This time period represents the hypothetical time (approximately 10 days) required to regain an appropriate amount of nutrient reserves to lay another clutch of eggs (Sorenson 1990).

Decisions made at each time period are based on three state variables: body mass of the female (x), the number of nested eggs (n), and the number of eggs laid parasitically (p). Each of these state variables is influenced by the decisions made by the female at each time step, and the current environmental conditions. Fitness is calculated at the end of the season based on the final values of these three state variables. Behavioral decisions available include 1) sitting out/abandon, 2) parasitize, 3) nest, 4) incubate time one, 5) incubate time two, 6) incubate time three, 7) rear, and 8) finish the season (Figure 3.1).

Figure 3.1. Potential pathways and the resulting reproductive strategy choice of female redheads. Reproductive options include O = sit out, P = lay 10 parasitic eggs, N = lay 10 nested eggs, I = incubate in three time periods, and R = rear young. A female can abandon at any time by choosing option O. A decision to nest or parasitize must be made in the first three time periods; before the vertical line.

T	1	2	3	4	5	6	7	Strategy
	O	O	O	O	O	O	O	No Reproduction
	P	O	O	O	O	O	O	Lay One Parasitic Clutch
	O	P	O	O	O	O	O	Lay One Parasitic Clutch
	O	O	P	O	O	O	O	Lay One Parasitic Clutch
	P	O	P	O	O	O	O	Lay Two Parasitic Clutches
	P	O	N	l_1	l_2	l_3	R	Dual Strategy
	N	l_1	l_2	l_3	R	O	O	Nest
	O	N	l_1	l_2	l_3	R	O	Nest
	O	O	N	l_1	l_2	l_3	R	Nest

Finishing the season represents a time when brood rearing has been completed and the female can molt and forage in preparation for the fall migration.

Body mass is affected by the probability of finding food (λ), the benefit of finding food (Y) expressed as body mass gained, and the cost of each decision (α) expressed as body mass lost. Costs (Table 3.2), in terms of body mass lost, for parasitizing, nesting, and incubating were determined from a captive study of breeding Redheads (Appendix 2). Although captive females do not face the same pressures of wild hens, i.e. finding and obtaining food and avoiding depredation, mass loss patterns over the reproductive season are similar between wild and captive females (Appendix 3). The cost of rearing a brood is arbitrary, but assumed to be small. There are no body mass costs associated with sitting out/abandon or finish the season. The value of Y (10 g) was chosen so that Y and α together roughly conformed to those data obtained in captivity. Since studies that address mass gain with food availability are nonexistent, I varied the value of Y to examine its influence on strategy choice. Values of 20g and 40g (average mass gain observed over 10 day periods in captivity from 20 to 60 days prior to egg laying) exerted an influence on the proportion of strategies observed, but predictions were often unrealistic or contrary to those observed in the wild (Sayler 1985, Sorenson 1990). For example, at base levels ($\lambda = 0.8$, $\gamma = 0.5$, $\varepsilon = 0$), all females chose a dual strategy (Table 3.3). Furthermore, the proportion of costly strategies increased as the benefit of finding food increased. Therefore, a value of 10g was used for all runs of the model.

TABLE 3.2. Parameter values specific to each reproductive strategy.

Strategy (i)	Energetic Cost (α_i)	Mortality of Nested Offspring (β_i)
Sit out/ Abandon	0	1
Parasitize	20	1
Nest	40	0.1
Incubate 1	40	0.075
Incubate 2	40	0.1
Incubate 3	40	0.125
Rear	20	$1 - ((-12 + 0.018x)/10)$
Finish the Season	0	0

TABLE 3.3. The proportion of strategy choices predicted when the benefits of finding food (Y) vary.

Parameter				Strategy choice				
value								
Food	Age	Host	Y	No	Parasitize	Double	Nest	Dual
(λ)	(ϵ)	(γ)		breed		Parasitize		Strategy
0.8	0	0.5	10	0	0.02	0	0.02	0.92
			20	0	0.01	0	0	0.98
			40	0	0	0	0	1.0
	1		10	0	0.39	0	0.04	0.57
			20	0	0.16	0	0	0.84
			40	0	0	0	0	1.0
	0	0.25	10	0.03	0	0	0.96	0
			20	0	0	0	1.0	0
			40	0	0	0	0.62	0.28
	0	0.75	10	0	0	0.09	0	0.90
			20	0	0	0.02	0	0.98
			40	0	0	0	0	1.0

During each time step, body mass changes depending upon the behavioral decision. If the individual chooses option i and finds food, body mass in the next time step will be:

$$x' = x - \alpha_i + Y. \quad (1)$$

If no food is found, however, body mass at time $t + 1$ will be:

$$x'' = x - \alpha_i. \quad (2)$$

To be consistent with wild populations, body mass ranges are bound by an upper maximum of 1200 g, x_m , and a minimum critical level of 800 g, x_c . Body mass increases in discrete steps of 10 g. At any time, if female body mass falls below a minimum level, x_c , the female dies and all nested eggs are lost.

The number of nested eggs is affected by the rate of offspring mortality (β). Offspring mortality (Table 3.2) was subdivided into the nesting phase (one time period), the incubation phase (three time periods), and brood rearing phase (one time period). Mortality experienced during the incubation period varied among phases one, two, and three. Most waterfowl studies do not differentiate between mortality experienced during nesting and incubation, but lump the two events into a single measure of nest success. Generally, the survival probability of nested eggs in waterfowl species decreases with laying date. For Redheads, average nest success is approximately 60% (Weller 1959, Sayler 1985, Sorenson 1990, Yerkes, pers. obs.). Although an average mortality value (0.4) was used for all runs of the model, I tested extreme values of 0.8, 0.6, and 0.0 and found that a wide range of mortality rates resulted in practically no difference in reproductive strategy choice predictions. Only at extremely low

values of offspring mortality (0), values that are not biologically realistic, were predictions drastically altered.

Brood mortality during rearing is based on the body mass of the female at the time of hatch and was derived from a study on wild brood rearing females. A significant relationship was found between female body mass at hatch and the number of ducklings that survived to 30 days post-hatch ($R^2 = 0.19$, $P = 0.007$, $df = 35$; Chapter 5).

The nested eggs state variable will be affected by choice i so n at time $t + 1$ will be:

$$n' = \begin{cases} (1 - \beta_i)n + e_n & \text{if } i = \text{nest} \\ (1 - \beta_i)n & \text{otherwise} \end{cases} \quad (3)$$

where e_n is the number of nested eggs a female gains by nesting.

The number of parasitic eggs is affected by the probability of finding a host nest of any species in which to lay a parasitic egg (γ) and the survival rate of eggs laid in a host nest (ϕ). The survival probability of parasitic eggs varies in the wild averaging 0.20, but generally decreases with time (Sayler 1985, Sorenson 1990). Therefore, I used the average survival of parasitic eggs (0.2), but reflected decreasing survival with time so that earlier laid eggs experienced higher survival (0.25) compared to parasitic eggs laid later (0.15). At time $t + 1$, the number of parasitic eggs will be:

$$p' = \begin{cases} p + \phi_i \gamma e_p & \text{if } i = \text{parasitize} \\ p & \text{otherwise} \end{cases} \quad (4)$$

where e_p is the number of parasitic eggs gained by brood parasitism, ϕ_t is the survival rate of parasitic eggs, and γ is the probability of finding a host nest in which to lay parasitic eggs.

A female Redhead's expected fitness from time t to the horizon, T , given x energy reserves, n nested eggs, and p parasitically laid eggs is defined by:

$$F(x, n, p, t, T) = \lambda F(x', n', p', t+1, T) + (1-\lambda) F(x'', n', p', t+1, T) \quad (5)$$

where x' , x'' , n' and p' are defined by equations (1), (2), (3), and (4) respectively.

The female Redhead chooses the option i , at each time step to maximize $F(x, n, p, t, T)$.

At the horizon, T , individual female fitness is based on the number of surviving nested and parasitic eggs, as well as a future reproductive component defined as a function of body mass at the end of the breeding season and over-winter survival (ϵ). Body mass at the end of the season has been shown to influence reproductive performance in the following year (Lessels 1986). Additionally, body mass during winter influences reproduction and survival in captive studies (Dubovsky and Kaminiski 1994) and in the wild (Porter et al. 1993, Jeske et al 1994). Thus, the terminal fitness function (TFF) is defined as:

$$F(x, n, p, T, T) = \begin{cases} 0 & \text{if } x < x_c \\ n + p + 5\epsilon (1 - e^{-0.0001(x - x_c)^2}) & \text{if } x \geq x_c \end{cases}$$

The optimal decision at each time step was determined by backward iteration, and predictions about reproductive behavior of Redheads were generated through forward iterations of the model (Mangel and Clark, 1988). The forward iterations were initially run with a uniform distribution of mass categories (1000 females per mass category) to determine the possible strategy choice outcomes and then run with a normal distribution of individual mass categories to determine the proportion of strategies that may be observed on a population level. The normal distribution of mass categories was derived from wild female Redheads trapped in early spring at Minnedosa, Manitoba ($\bar{x} = 1051 \text{ g} \pm 77.23 \text{ SD}$, $n = 25$; Figure 3.2).

Model Predictions

Body Mass

The model predicts a general distribution of strategy choice by mass category (Figure 3.3). Females in lower mass categories are restricted to no breeding and parasitizing either once or twice depending on specific situations reported below. Females in higher mass categories choose more costly strategies, nesting and dual strategy, but incur a higher payoff. In all situations, threshold mass levels at which switches occur from 'low' to 'high' cost strategies exist between approximately 900 g and 1060 g. The general mass distribution pattern and threshold levels were not influenced by a normal distribution of individuals in mass categories at the beginning of the breeding season.

Figure 3.2. The normal distribution of mass categories used in the forward iteration of the model. The horizontal line represents the number of females present in the uniform distribution of mass categories.

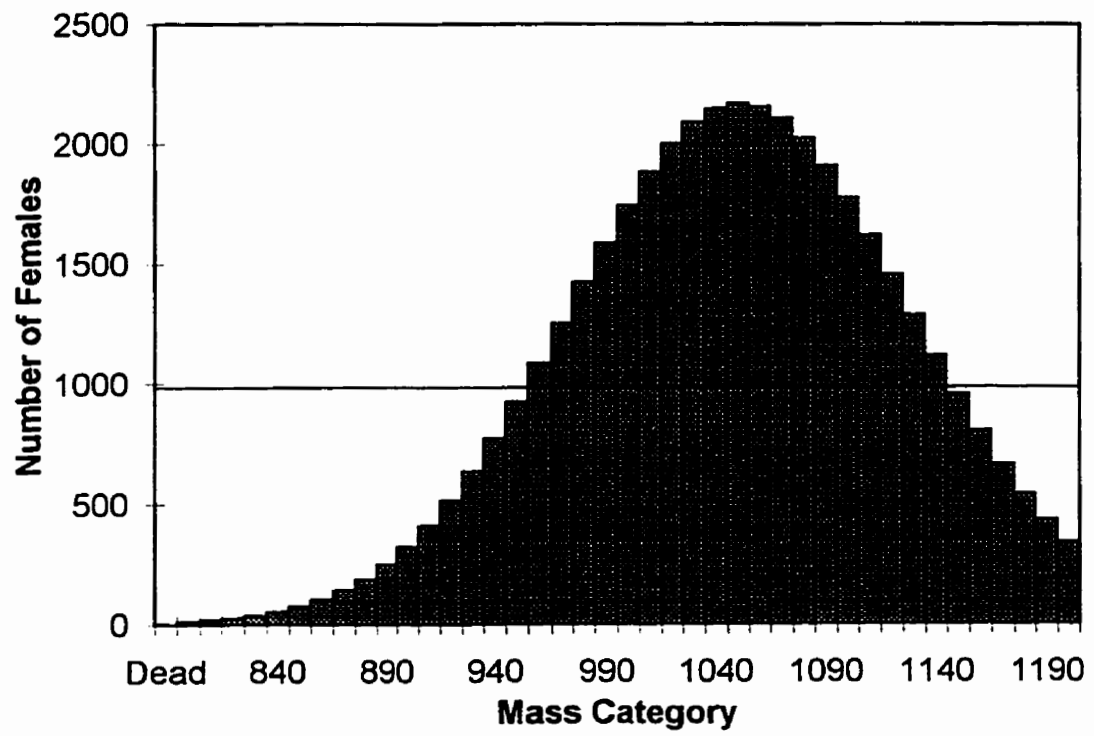
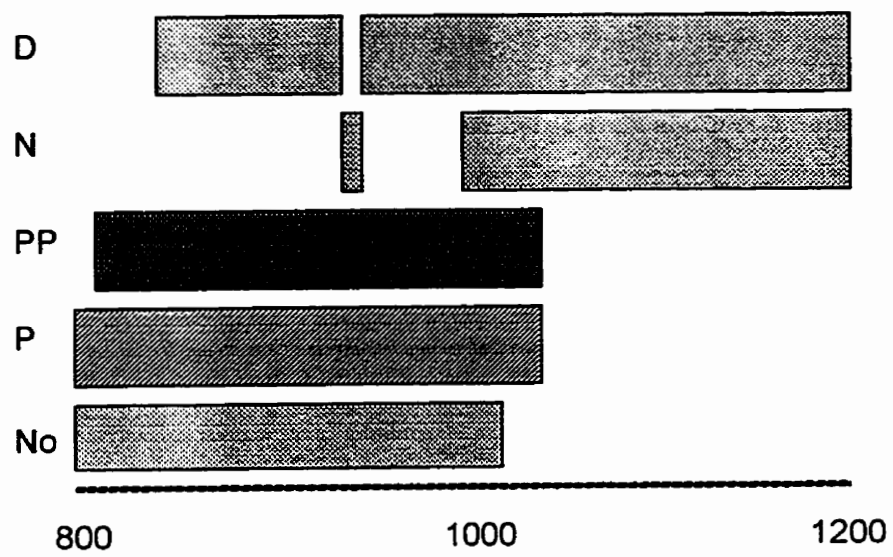


Figure 3.3. The range of body masses that exhibit a particular reproductive strategy across a wide variety of parameter values.



Over-winter Survival

The probability of survival to the next breeding season (based on a function of body mass) has a significant effect on strategy choice (Figure 3.4a). As the probability of survival decreases, females at the lower end of the mass threshold choose more costly strategies. Therefore, the proportion of dual strategists observed in a population increases among the females at lower mass categories. Choosing more costly strategies, in this situation, results in more deaths at lower mass categories due to the gamble of investing heavily. Under a normal distribution of individuals within each mass category, the population level pattern discussed above holds true. The distribution results in more females at middle mass categories choosing more costly strategies that result in greater proportions of more costly strategies observed on a population level (Figure 3.4b, Table 3.4).

Food Availability

The general mass distribution described above (Figure 3.3) is slightly influenced by the probability of finding food (Figure 3.5). As the probability of finding food increases, females at lower mass categories begin to choose more costly strategies that result in a population level shift in the proportion of strategies observed. When the probability of finding food is high, more females in the population choose dual strategies over parasitism only. Predictions based on model runs with a normal distribution of individuals within mass categories resulted in a higher proportion of females, on a population level, choosing more costly strategies with fewer females dying and forego breeding (Figure 3.5a).

Figure 3.4. The influence of the probability of surviving to the next breeding season on strategy choice when using an initial A) uniform distribution and a B) normal distribution of mass categories.

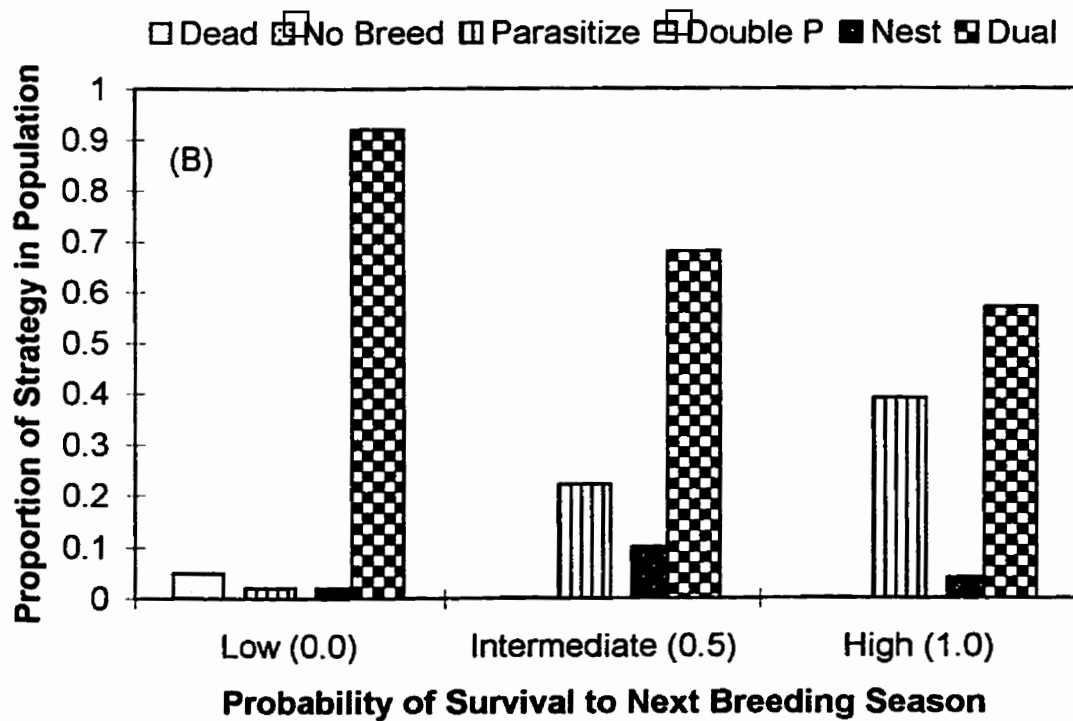
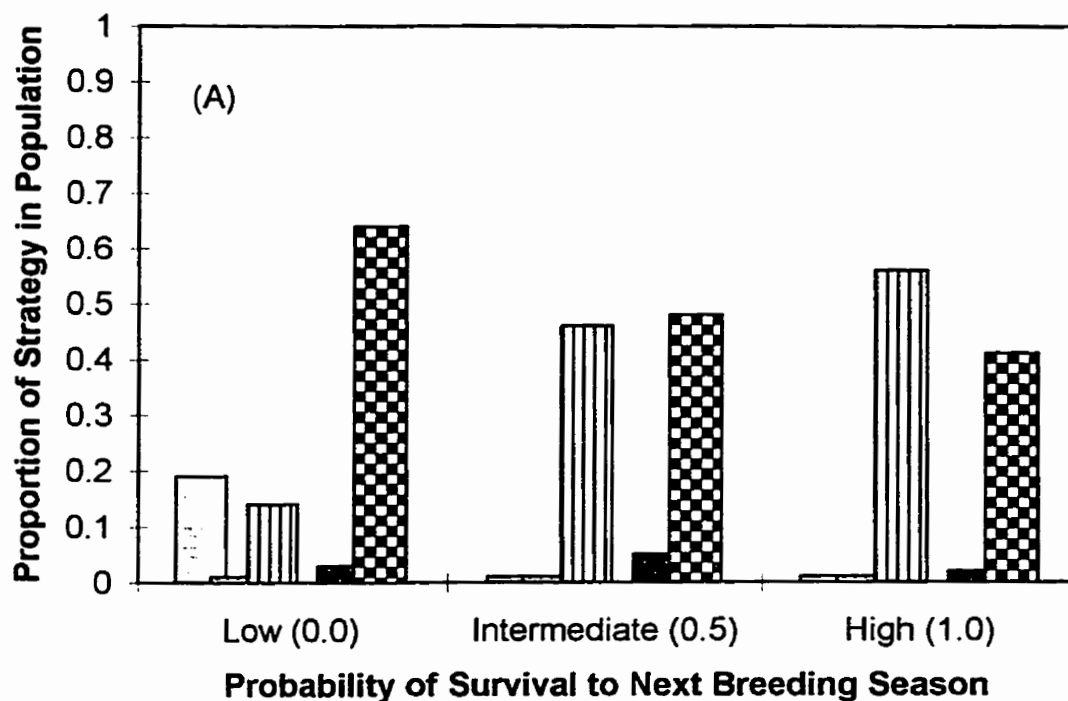


Figure 3.5. The influence of the probability of finding food on strategy choice when using an initial A) uniform distribution and a B) normal distribution of mass categories.

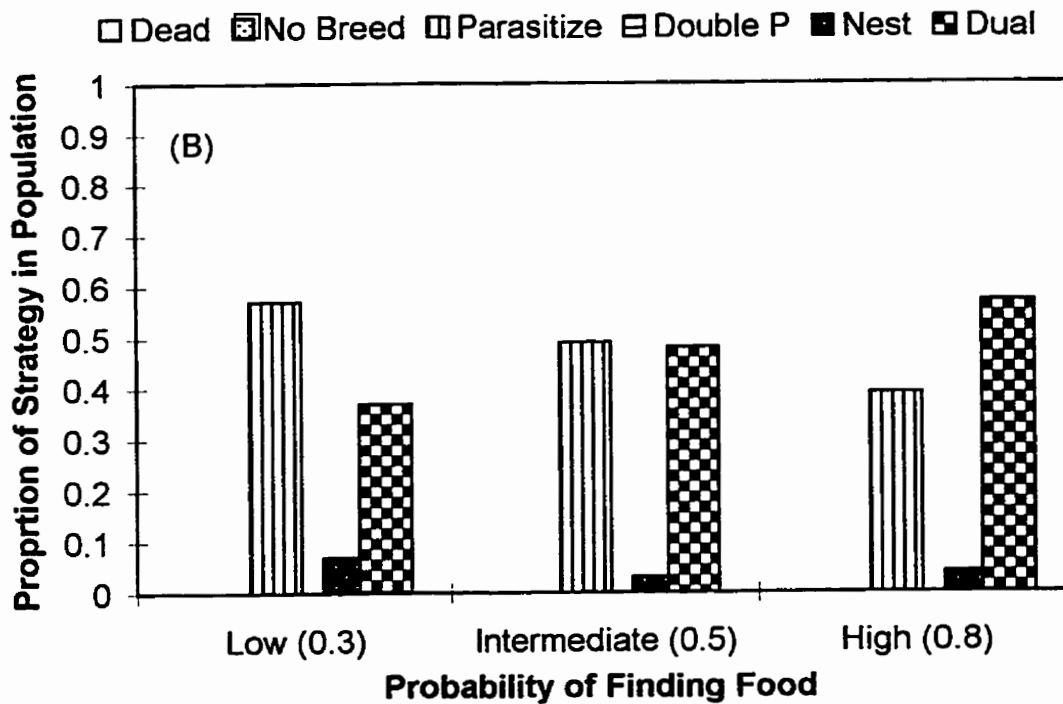
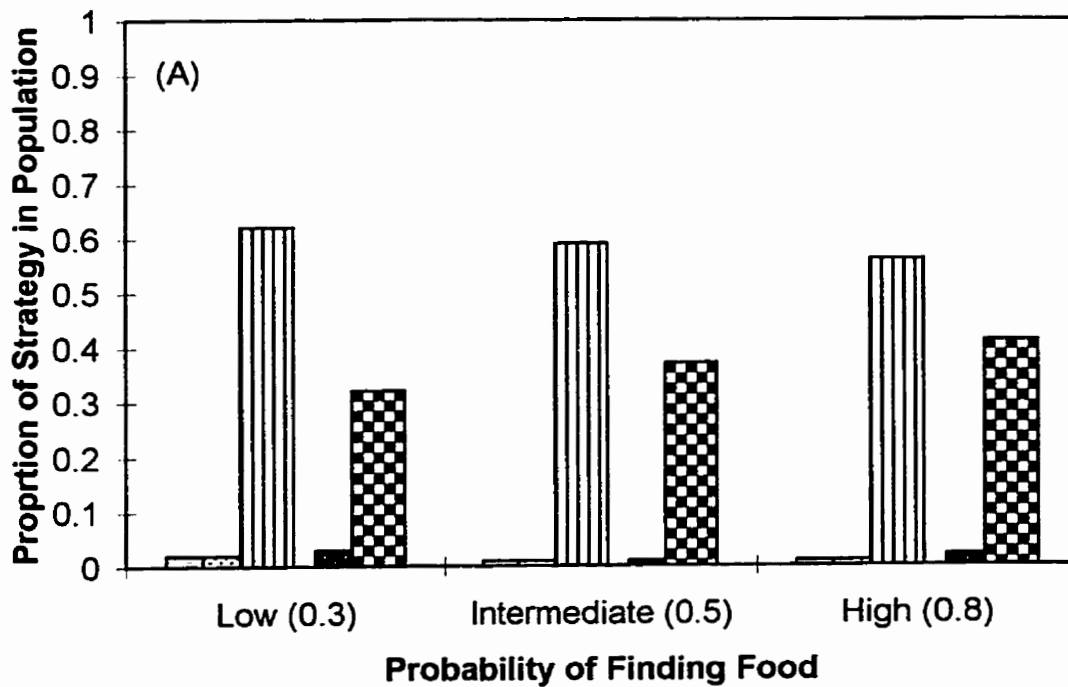


TABLE 3.4. The proportion of strategies predicted when survival to the next breeding season varies ($\lambda = 0.8$, $\gamma = 0.5$).

	Uniform			Normal		
	Distribution			Distribution		
Probability of	0	0.5	1	0	0.5	1
Surviving to the Next Breeding Season						
Strategy						
Dual Strategy	0.64	0.48	0.41	0.92	0.68	0.57
Nest	0.03	0.05	0.02	0.02	0.1	0.04
Parasitize Twice	0	0	0	0	0	0
Parasitize Once	0.14	0.46	0.56	0.02	0.22	0.39
No Breeding	0.01	0.01	0.01	0	0	0
Dead	0.19	0.01	0.01	0.05	0	0

When comparing both the uniform distribution predictions and the normal distribution predictions, the probability of finding food exerts a greater influence on the observed proportions of each strategy within the normal distribution population (Figure 3.5b, Table 3.5). One would expect to observe a distribution of strategies in the wild that was more similar to the predictions from the normal distribution results.

Host Availability

The probability of finding a host nest has a strong effect on overall strategy choice (Figure 3.6a). When the probability of finding a host is very low, only pure nesting and non-breeding are viable options. At intermediate host availability levels, single parasitic events and dual strategists are common, while pure nesting accounts for a very small proportion of the population. At intermediate levels, the overall probability of a parasitically laid egg surviving to fledge is 0.10, as the survival probability of parasitic eggs is 0.20 and probability of finding a host is 0.50. At low host levels the overall probability of surviving to fledge is 0.05 while at high host levels it is 0.15. At high levels of host availability, double parasites and dual strategists account for the majority of the population. Again, pure nesting is relatively insignificant. Predictions from normal distribution are parallel to those discussed above because more females in middle mass categories are laying two clutches of parasitic eggs and choosing to be dual strategists (Figure 3.6b, Table 3.6).

Figure 3.6. The influence of the probability of finding a host on strategy choice when using an initial A) uniform distribution and a B) normal distribution of mass categories.

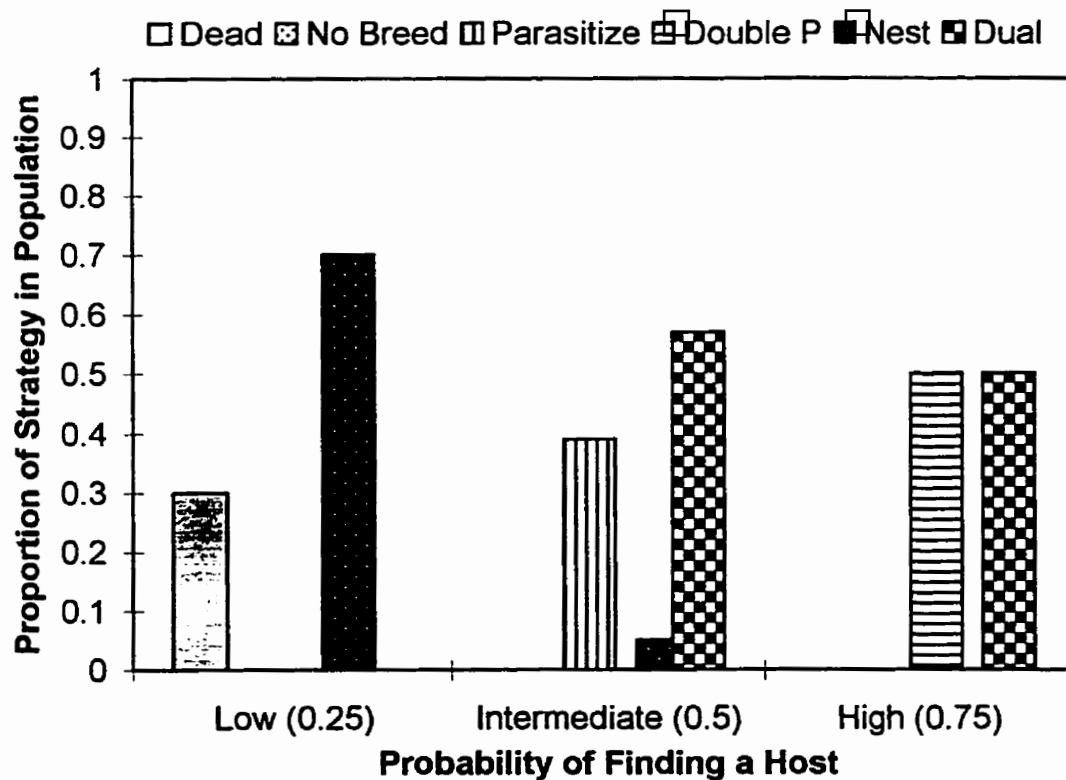
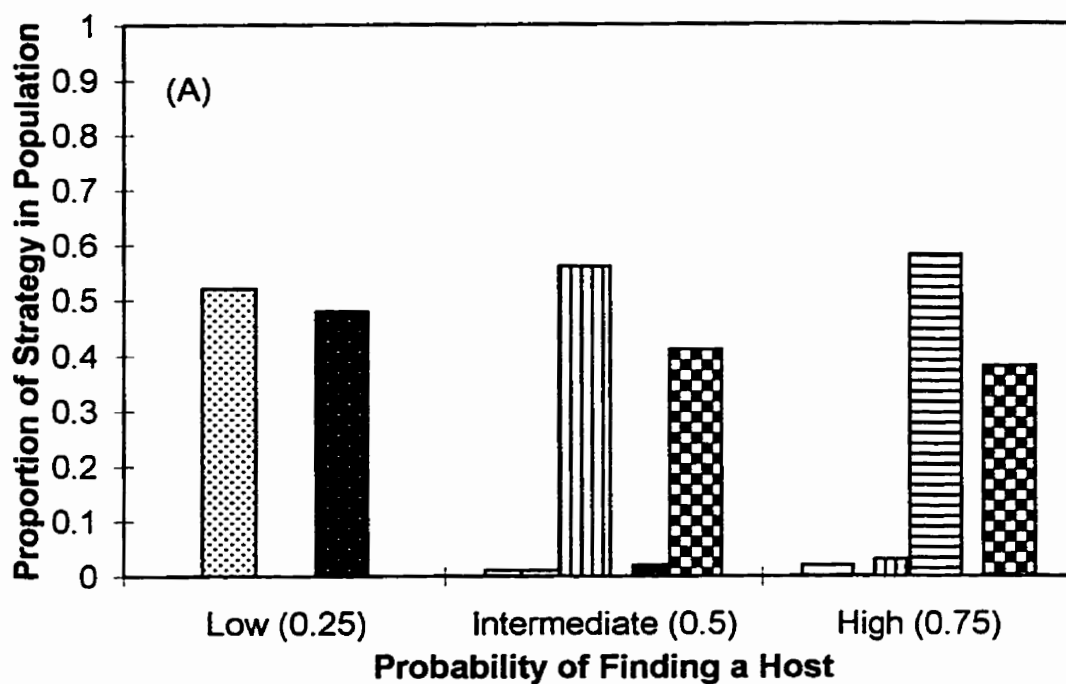


TABLE 3.5. The proportion of strategies predicted when food availability varies ($\varepsilon = 1$, $\gamma = 0.5$).

	Uniform			Normal		
	Distribution			Distribution		
Probability of	0.3	0.5	0.8	0.3	0.5	0.8
Finding Food						
Strategy						
Dual Strategy	0.32	0.37	0.41	0.37	0.48	0.57
Nest	0.03	0.01	0.02	0.07	0.03	0.04
Parasitize	0	0	0	0	0	0
Twice						
Parasitize	0.62	0.59	0.56	0.57	0.49	0.39
Once						
No Breeding	0.02	0.01	0.01	0	0	0
Dead	0.02	0.01	0.01	0	0	0

TABLE 3.6. The proportion of strategies predicted when the probability of finding a host varies ($\lambda = 0.8$, $\varepsilon = 1$).

	Uniform			Normal		
	Distribution			Distribution		
Probability of	0.25	0.5	0.75	0.25	0.5	0.75
Finding a						
Host						
Strategy						
Dual strategy	0	0.41	0.38	0	0.57	0.5
Nest	0.48	0.02	0	0.7	0.04	0
Parasitize	0	0	0.58	0	0	0.5
Twice						
Parasitize	0	0.56	0.03	0	0.39	0
Once						
No Breeding	0.52	0.01	0.001	0.3	0	0
Dead	0	0.01	0.01	0	0	0

Discussion

In general, one would expect an animal to be able to adjust reproductive behavior each breeding season to phenotypic and environmental variability that they face so that within a season reproductive success and lifetime reproductive success is maximized. The model predicts that female body mass and age and environmental variability influence variability of within season strategy choice.

Body Mass

Redhead body mass was an important determinant, along with other factors, in reproductive strategy choice. This relationship supports the conditional strategy proposed by Sorenson (1990). Evidence provided from Sorenson's (1990) work demonstrates that nesters were heavier than females that did not nest. He further suggested the existence of a threshold level of phenotypic and environmental condition where females switched from one strategy to another. This is also predicted by the model and, with the parameter values used, this threshold occurs between 900 g and 1060 g.

Body mass has also been shown to be an important correlate of several reproductive parameters in other species. Female mass, or body condition, is often correlated with clutch size (Ankney and MacInnes 1987, Erikstad et al. 1993, Chastel et al. 1995, Winkler and Allen 1995) and brood size (Askenmo 1982, Moss and Watson 1984) such that heavier females or females in better condition produce more offspring. Females in better condition also survive better (Reid 1987, Nur 1984). Body condition also influences some reproductive decisions, specifically abandonment of offspring. Monaghan et al. (1980) found

Arctic Terns (*Sterna paradisaea*) in poor condition abandon clutches more often.

In another study, Kehoe (1986) found that female Common Eiders in poor condition often abandoned care of their offspring to other females.

Over-winter Survival

Several studies on birds have demonstrated a relationship between reproductive effort and age with reproductive effort generally increasing with age (Bryant, 1988; Newton, 1988; Scott, 1988). This relationship has also been shown for several duck species (Afton 1984, Cowardin et al. 1985; Heusmann 1975; Krapu and Doty 1979; Ratcliffe et al. 1988). In the model, age was not explicitly included, instead the probability of survival to obtain future reproduction was used. This could represent age, suggesting that female Redheads are increasing reproductive effort with age. Sorenson (1990) and Sayler (1985) both suggested that older females tend to exhibit nesting and dual strategies while young females were restricted to parasitic events. The model does not support this qualitative difference in strategy choice by age predicted by Sorenson (1990). Instead, it predicts that females of all ages choose a variety of strategies. Older females are not restricted to nesting or dual strategies while young are not limited to parasitism, but instead survival probabilities exert an influence on the mass category at which a female switches from low to high cost strategies. At low survival probabilities, females at lower mass categories invest more heavily in the current season by choosing more costly strategies.

The model does not directly assess the cost of reproduction on future survival or fecundity. I attempted to control for this through the use of a future reproductive component in the calculation of fitness. Each female receives a value of future expected eggs based on her body mass at the end of the current season such that lower masses equal fewer eggs in the future. Although the costs associated with reproduction are controversial, several studies have correlated various aspects of reproductive performance in the current season with future survival and fecundity (Nur 1984, 1988, Reid 1987, Dijkstra et al. 1990).

Environmental Variability: Food and Host Availability

The probability of finding food had a comparatively smaller influence on Redhead strategy choice than intuitively expected. In birds, productivity has been shown to increase in years with increased food availability or when food quality was better or supplemented (Morton et al. 1972, Nolan and Thompson 1975). In waterfowl, drought has a major effect on reproductive performance of prairie-nesting ducks (Olsen 1964, Rogers 1964, Stoudt 1971, Afton 1984, Sayler 1985).

Previous field studies of Redhead reproductive strategies under varying environmental conditions have produced mixed results. In one of the earliest comprehensive studies, Weller (1959) stated that parasitic behavior of Redheads was inherent and not modified by the physical environment. In contrast, other studies attributed parasitic laying to fluctuating water levels (Low 1945, Erickson 1948). Giroux (1981) attributed low parasitism in a dry year to

low population levels of Redheads. Lastly, Olson (1964), Michot (1976), Joyner (1983), Stoudt (1971), and Sorenson (1990) found no association between water levels and frequency of parasitism on their study areas. These authors proposed a) that parasitism was a low cost alternative to nesting in poor environmental conditions, in other words, a best-of-a-bad job strategy, and b) that parasitism functioned to increase fecundity when environmental conditions were good. Few of these studies, however, examined the occurrence of pure nesting and dual strategies.

Sayler (1985) found great differences in the parasitic frequencies between 'good' and 'bad' years. During drought, or 'bad' years, parasitic frequencies were 51-61% as opposed to wet, or 'good' years, when frequencies were only 27%. Although proportions predicted by the model of different strategies on a population level cannot compare directly to parasitic frequency, the overall proportion of individuals that laid parasitically should reflect the number of parasitic eggs found in other species nests, which is defined as parasitic frequency. Predictions of this model support Sayler's (1985) trends of lower parasitic frequencies in 'good' years. At extremes, when the probability of finding food is very low (0.30), the total proportion of individuals that laid parasitic eggs is 0.94 (parasites = 0.57 added to dual strategist = 0.37). When the probability of finding food is very high (1.0), however, 0.79 of the population laid parasitic eggs. This suggests that food availability exerts some control over strategy choice, however, it does not produce a large disparity in the proportions of different strategies observed on a population level, as one would predict.

The model predicts Redhead females vary reproductive effort by availability of food resources and parasitism is a viable reproductive strategy in all situations except when host availability is very low. Based on model predictions, I propose an alternative explanation for the previously conflicting and non-consistent relationships observed between the frequency of parasitism and fluctuating water levels. I propose that female Redheads assess the 'host environment' prior to making decisions regarding strategy choice. Although the model does not include assessment per se, the predictions indicate that this occurs. Therefore, host availability, and not food variability per se, drives the frequency of parasitism and other strategies on a population level. This is particularly true with a nesting only strategy, which is relatively uncommon except when survival probability of parasitic eggs are very low (0.5) or the probability of finding food is very high (1.0).

Data provided by Sayler (1985), support this contention, although Sayler drew different conclusions. In four years, the frequency of parasitism, the number of Redhead eggs per host nest, and the number of Redhead and Canvasback nests varied (Table 3.7). The lowest parasitic frequencies were recorded in the wettest year, which also was the year when the fewest host nests (Canvasback) were found and presumably available. Further, the frequency of parasitism was highest in the year when the most host nests were found. Similar data obtained from Sorenson (1990), however, are not as clear (Table 3.8). In all years of his study, host availability was similarly high. Thus, one would predict comparatively high parasitic and nesting frequency for all years. The

TABLE 3.7. Canvasback and Redhead nesting and parasitic egg laying data obtained from Sayler (1985).

Year/Habitat Conditions	Number of Canvasback Nests Found	Number of Parasitic Redhead Eggs Found	Average Number of Redhead Eggs Per Canvasback Nest	Number of Redhead Nests Found	Relative Assignment of Food and Host Availability
1977 - Dry	15	116	7.73	3	Low Food High Host
1978 - Dry	17	194	11.41	13	Low Food High Host
1979 - Wet	10	33	3.3	35	High Food Low Host
1980 - Dry	13	99	7.6	14	Low Food Low Host

TABLE 3.8. Canvasback and Redhead nesting and parasitic egg laying data obtained from Sorenson (1990).

Year/Habitat	Number of	Average	Number of	Relative
Conditions	Canvasback	Number of	Redhead	Assignment of
	Nests Found	Redhead	Nests Found	Food and
		Eggs Per		Host
		Canvasback		Availability
		Nest		
1986 - Wet	55	4.64	20	High Food
				High Host
1987 - Wet	66	2.9	9	High Food
				High Host
1988 - Dry	58	3.53	4	Low Food
				High Host

lowest parasitic frequencies, however, occurred during a wet year when the most host nests were available. Sorenson (1990) attributed the low parasitic frequencies to a low density of Redheads on his study site. Although both data sets (Sayler 1985, Sorenson 1990) are generally consistent with the above hypothesis, neither is a strong test. I would therefore make the following general statement: following the assessment of the 'host environment', the availability of food would encourage or discourage selection of more costly strategies at lower mass categories. Specifically, I would predict that parasitism, on a population level is common when host availability is high, regardless of food availability. Conversely, parasitism would be low in years when host availability was extremely low. Table 3.9 presents model predictions obtained when various levels of host availability and food availability are examined. Parasitic frequencies increase as host availability increases from low to intermediate, then food availability determines which strategies (P, PP, or D) contribute to high frequency of parasitism. This supports the idea that host availability determines the decision to parasitize or not, and then food availability 'fine tunes' strategy choice (or the proposal that food affects strategy subject to the constraint of host availability).

Conclusions

I propose, based on the predictions derived from the model, that females arriving on the breeding ground simultaneously assess three factors prior to making reproductive strategy choices. They assess the 'host environment', their own body mass and their age or residual reproductive value. Food availability

TABLE 3.9. Predicted proportions of Redhead reproductive strategies given different levels of food availability and host availability.

Food Availability	Host Availability	Strategy					Relative Prediction
		No Breeding	Single Parasitism	Double Parasitism	Nest	Dual Strategy	
High (0.8)	Low (0.25)	0.3	0	0	0.7	0	No Parasitism
Low (0.3)	Low (0.25)	0.45	0	0	0.55	0	No Parasitism
High (0.8)	Intermediate (0.5)	0	0.39	0	0.04	0.57	High Rates of Parasitism
Low (0.3)	Intermediate (0.5)	0	0.57	0	0.07	0.37	High Rates of Parasitism, not Significantly Different From Above
High (0.8)	High (0.75)	0	0	0.5	0	0.5	Highest Rates of Parasitism
Low (0.3)	High (0.75)	0	0.01	0.65	0	0.34	Highest Rates of Parasitism, not Significantly Different From Above

functions to fine-tune this assessment. Based on this assessment, reproductive effort is adjusted to maximize fitness while balancing the number of young produced within season with the future potential for survival and future reproduction. I further suggest that parasitic females make a secondary decision, based on the same three factors, to either parasitize again, nest or sit the rest of the season out. Therefore, there appears to be a simple decision rule: if an adequate number of hosts exist and body mass is adequate, parasitize instead of nest. If enough hosts exist after parasitizing, the female should either parasitize again, nest or sit out depending on the combination of age and body mass.

In general, nesting was not a popular strategy choice except when the overall survival probability of parasitic eggs was very low (0.05). Previously, in Chapter 1, the assumption was made that most, if not all, wild Redhead hens that were observed nesting parasitized prior to initiating their own nest. Predictions from the model support this assumption, in most cases.

CHAPTER FOUR: THE INFLUENCE OF BODY MASS ON STRATEGY CHOICE AND INCUBATION CONSTANCY IN CAPTIVE FEMALE REDHEADS.

Reproductive effort models of life history evolution are based on the assumption that reproducing individuals incur costs (Partridge and Harvey 1988). Trends in body mass change may provide an index to physiological demands of reproduction (Harris 1970, Krapu 1981) and an indirect measure of such costs. In waterfowl, females lose mass from laying through incubation in many species (Krapu 1981, Drobney 1982, Ankney and Afton 1988, Murphy and Boag 1989, Barzen and Serie 1990, Parker and Holm 1990, Gloutney and Clark 1991, Mallory and Weatherhead 1993). Mass loss patterns vary both inter- and intraspecifically and may be related to several factors. Absolute mass loss has been related to stage of incubation and hen experience in Mallards (Gatti 1983) and Wood Ducks (Harvey et al. 1989), but was not related to age. Mallard hens that initiated nests early, weigh more and lose more mass than later nesting females (Gatti 1983, Pattenden and Boag 1989). Further, heavier Wood Ducks not only nested earlier and lost mass at a greater rate than lighter hens, but also were more likely to return to the area in the following year (Harvey et al. 1989, Hepp et al. 1990). In larger waterfowl, experienced Canada Goose hens lost more mass than inexperienced hens, although both ended incubation with similar body mass (Aldrich and Raveling 1983). Additionally, length of incubation was influenced by female mass in Canada Geese (Aldrich and Raveling 1983).

The influence of female Redhead body mass on incubation constancy and reproductive strategy choice was documented in Chapters 2 and 3. Although mass had a significant influence on incubation constancy, the nature of the relationship was not entirely clear because the use of end-of-incubation body mass may have obscured the relationship. I proposed in Chapter 2 that heavier Redhead females, weighed at the beginning of incubation, may maintain higher incubation constancy and lose significantly more mass compared to females that were lighter at the beginning of the reproductive period. Therefore, one objective of the captive study was to examine mass loss over the reproductive period for female Redheads and to determine the relationship between body mass and incubation constancy. Females that are heavier at the beginning of the season should lose more mass than lighter females and heavier females should maintain higher incubation constancy compared to lighter females.

Body mass was predicted to be an important factor in reproductive strategy choices in Chapter 3. The second objective of the captive study was to examine the relationship between body mass at the beginning of the season and subsequent reproductive strategy choice. As predicted by the model, body mass should be positively correlated with strategy choice: lighter females should choose less costly strategies of non-breeding or parasitism compared to heavier females that should choose the more costly strategies of nesting or a dual strategy.

The third objective was to explore the potential relationship between strategy choice, mass loss, and incubation constancy by examining differences

between nesting females and dual strategists. In Chapter 2, it was proposed that heavier females maintain higher constancy compared to lighter females, however, significant interactions suggested that strategy choice may alter this pattern. Results in Chapter 2 indicate that early incubators, potentially nesting females, maintained higher incubation constancy and ended incubation at a lower body mass compared to late incubators, potentially dual strategists, which maintained lower constancy and ended at higher body masses (see Chapter 2, Results). Thus, within strategy, heavier females may maintain higher constancy, but between strategy, nesters may exhibit higher constancy because they lose relatively less mass due to the lower investment of nesting only.

Methods

During 1996, 22 pairs of seven-year-old Redheads were housed at the Conservation Research Center, in Front Royal, Virginia. Females were weighed with pesola scales to nearest 5 g every second day from 13 April to 6 July, a period covering prelaying to the end of incubation for the last nesting female. As in Chapter 2, body mass alone was used as a comparative measure among hens. Birds were fed *ad libitum*.

Throughout the study, two pairs of Redheads were housed together in an individual pen with a pair of Cinnamon Teal (*Anas cyanoptera*) to act as hosts for parasitic egg laying of the Redhead females. Eggs found in pens and in nests were counted. In all cases, the first to lay of the two females housed together could be identified as the layer by the presence of a hard shell egg in the oviduct.

Hens were classified into reproductive strategy choices based on their reproductive activities. Strategy classifications included no reproduction (O), parasitic layer only (P), parasitic layer that laid two clutches (PP), nester only (N), semi-dual strategist (SD) and dual strategist (D). A semi-dual strategist was defined as an individual that laid between 1 and 3 parasitic eggs before initiating her own nest. A dual strategist laid a clutch of at least 6 parasitic eggs before initiating her own nest.

Statistical Analysis

To document mass loss patterns, individual mass loss was examined using regression lines and predicted mass values. Predicted values were used for comparisons due to daily variation in hen body mass. Mass loss values used to establish regression equations were obtained from individual hens from one day before the first egg was laid to the last day of incubation. Fifteen hens that attempted incubation were used for this analysis. Females that did not incubate, parasites, lost mass (Appendix 3), whereas a single female that exhibited no reproductive activity did not lose mass ($R^2 = 0.002$, $P = 0.77$, $df = 39$).

To compare mass loss differences, 11 successful incubators were divided into 'heavy' and 'light' groups based on initial body mass obtained from regression equations and mean body mass ($x = 1055$ g). Hens classified in the 'heavy' group ($x = 1128.2$ g \pm 17.4, $n = 5$) had significantly higher body mass at the beginning of laying than hens classified in the 'light' group ($x = 994.9$ g \pm 12.2, $n = 6$) ($t = 6.43$, $P < 0.000$, $df = 9$). Difference in mass change between

groups was examined with an F test of sample variance followed by the appropriate t-tests.

Incubation constancy for individual hens completing incubation was determined as described in Chapter 2, Methods. Incubation constancy was compared between heavy and light groups of females with a t-test.

The influence of initial body mass on strategy choice was examined using 21 hens and Spearmans' correlation coefficients. Initial body masses obtained during the first day of the study (13 April) were used to relate body mass to subsequent strategy choice, which was ranked by presumed energetic cost. Predicted mass values obtained from regression equations were used to calculate mass loss of individual hens which was then used to compare mass loss and strategy choice.

Differences in strategy choice, mass loss and incubation constancy between nesting females and dual strategists were examined with t-tests.

Results

Female Redheads in captivity chose the following reproductive strategies: no reproductive activity (n = 1), parasitic layer (n = 3), double parasitic layer (n = 2), nesting only (n = 7), semi-dual strategist (n = 5), and dual strategist (n = 4).

Two nests were depredated by rodents: one a nester only and one a dual strategist. Of the remaining nesters (n = 13), three abandoned nests after 3 to 7 days of incubation. Egg laying dates ranged from 22 April to 18 June whereas nest initiation dates ranged from 29 April to 12 June.

Mass loss of individual hens was significant over the reproductive period from beginning of laying to the end of incubation (Table 4.1). Hens that abandoned nests prior to completion of incubation still lost mass but exhibited lower R^2 values (Table 4.1).

Body mass at the end of incubation was not significantly different between 'heavy' ($842 \text{ g} \pm 25.1$) and 'light' groups ($799 \text{ g} \pm 19.2$) ($t = 1.38$, $P = 0.20$, $df = 9$). However, mass loss over the laying and incubation period was significantly different between 'heavy' ($286 \text{ g} \pm 13.9$) and 'light' hens ($195.9 \text{ g} \pm 13.1$) ($t = 4.7$, $P < 0.000$, $df = 9$) (Figure 4.1). Proportional mass loss was also significantly different between 'heavy' (0.25 ± 0.001) and 'light' females (0.20 ± 0.001) ($t = 2.86$, $P = 0.02$, $df = 9$).

Incubation constancy between 'heavy' (0.877 ± 0.013 , $n = 5$) and 'light' hens (0.887 ± 0.015 , $n = 3$) was not different ($t = -0.50$, $P = 0.32$, $df = 6$). The power of this test was limited by low sample sizes (0.07). Furthermore, there was no significant correlation between: (1) body mass at the beginning of incubation and incubation constancy ($r = 0.008$, $P = 0.99$, $n = 8$); (2) body mass at the end of incubation and incubation constancy ($r = 0.365$, $P = 0.37$, $n = 8$); or 3) mass loss and incubation constancy ($r = -0.39$, $P = 0.337$, $n = 8$).

Body mass at the beginning of the reproductive period was related to subsequent strategy choice ($r = 0.46$, $P = 0.038$, $n = 21$) (Figure 4.2). Mass change over the reproductive period (all but two lost mass) was also correlated to reproductive strategy choice ($r = -0.46$, $P = 0.04$, $n = 20$) (Figure 4.3).

Figure 4.1. A comparison of mass at the beginning of reproduction, end of reproduction, and mass loss for 11 female redheads. (The top five females were classified as 'heavy' and the bottom 6 were classified as 'light'. Strategy choice indicated in parentheses.)

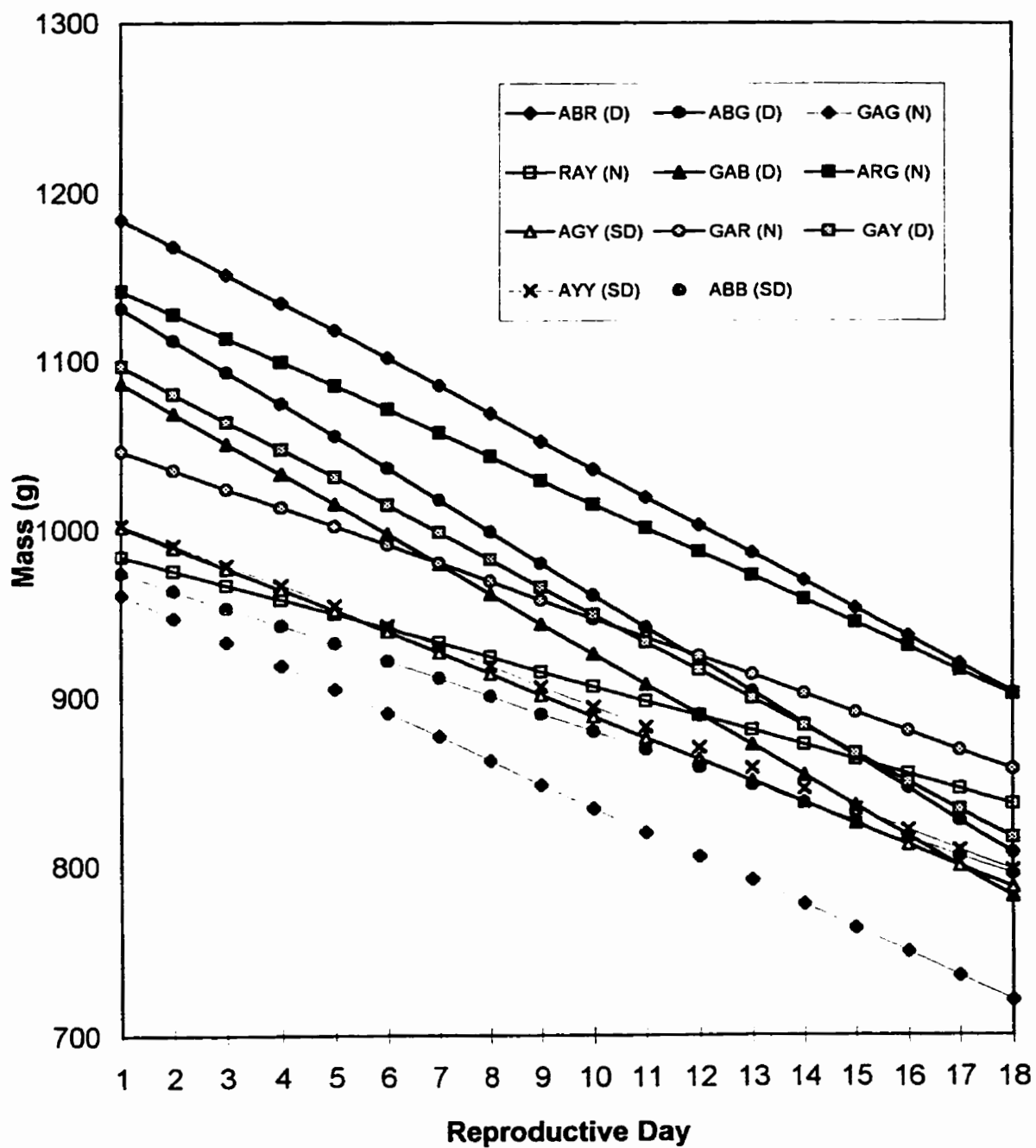


Figure 4.2. Relationship between mass at the beginning of the reproductive cycle and strategy choice. (Strategies ranked by presumed energy costs, 1 = no breeding, 2 = lay one parasitic clutch, 3 = lay two parasitic clutches, 4 = nesting, 5 = semi-dual strategist, 6 = dual strategist.)

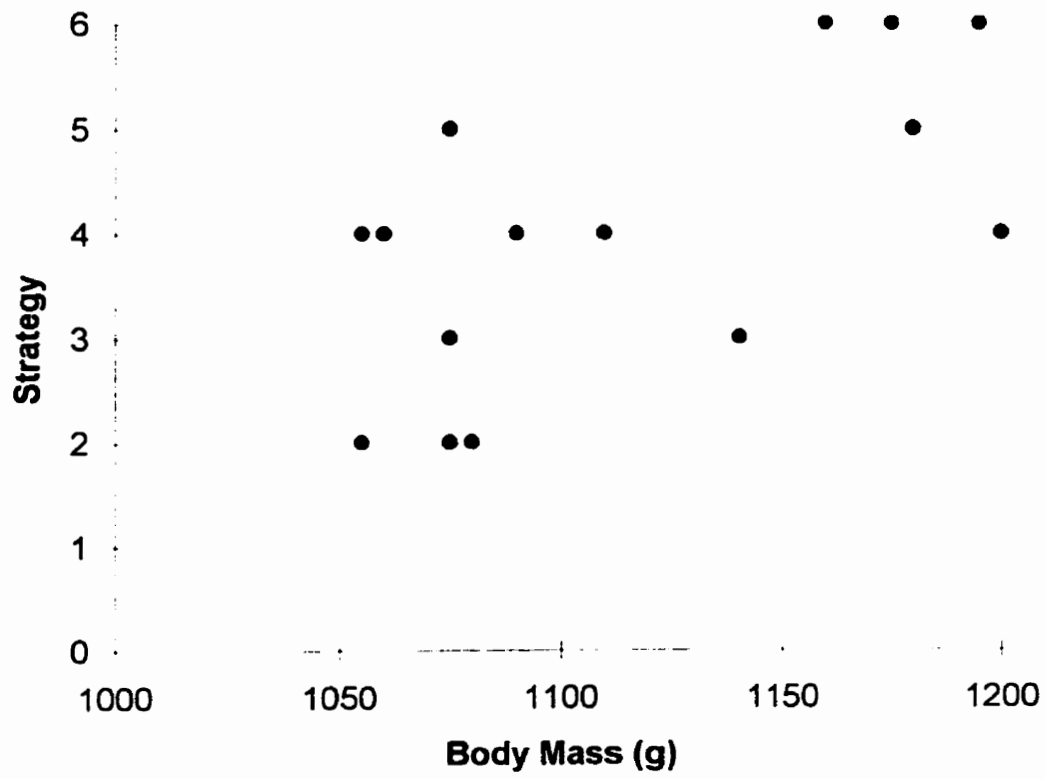


Figure 4.3. Relationship between mass change and reproductive strategy choice. (Strategy categories identical to Figure 4.2)

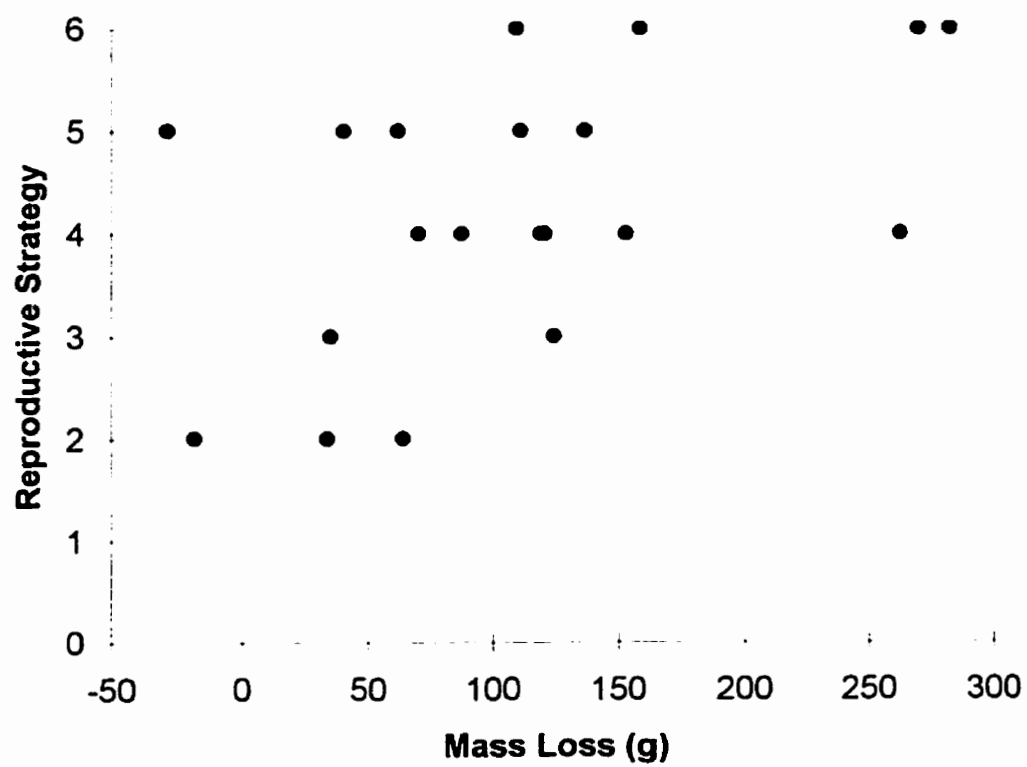


TABLE 4.1. Regression values for captive females from the first egg laid to the end of incubation.

Hen ID	# Mass Days	R ² Value	P Value	Strategy
ABR	18	0.62	<0.000	Dual
ABG	18	0.92	<0.000	Dual
ABY	18	0.51	0.0009	Nest, Abandoned
GAG	18	0.83	<0.000	Nest
RAY	18	0.71	<0.000	Nest
GAB	18	0.75	<0.000	Dual
AYB	18	0.55	0.0004	Semi-Dual, Abandoned
ARY	18	0.43	0.003	Semi-Dual, Abandoned
ARG	18	0.67	<0.000	Nest
AGY	18	0.64	<0.000	Semi-Dual
BAB	18	0.44	0.003	Nest, Abandoned
GAR	18	0.52	<0.000	Nest
GAY	18	0.88	<0.000	Dual
AYY	18	0.53	<0.000	Semi-Dual
ABB	18	0.61	<0.000	Semi-Dual

Mass loss, both absolute and relative, was significantly different between nesting females and dual strategists. Incubation constancy was similar between the reproductive strategies (Table 4.2a), but higher in nesting females than dual strategists. Constancy varied within strategy (Table 4.2b). A single semi-dual strategist maintained incubation constancy at 0.9069

Discussion

Many duck species lose mass during the breeding season (Ankney and Afton 1988, Barzen and Serie 1990, Parker and Holm 1990), a trend that is also observed in captive breeding Redheads. Females that participated in reproductive activities lost a significant amount of mass averaging 22.3% for nesters, semi-dual, and dual strategists. Noyes and Jarvis (1985) reported a 22% mass loss for wild female Redheads collected in Nevada. Similar mass loss trends were also observed in wild females in Minnedosa, Manitoba, however, individual mass loss data were not obtainable (Appendix 3).

Heavier female Redheads, at the beginning of reproduction, lost more mass compared to lighter females, although the groups were not different in mass at the end of incubation. This relationship suggests that end-of-incubation body mass, which was used in Chapter 2, is not a good indicator of mass at the beginning of reproductive activity for Redheads.

Redhead incubation constancy was not different between females classified as 'heavy' and 'light', however, this result was limited by low sample sizes. Results in Chapter 2 suggest that heavier females, as compared to lighter females, potentially maintain higher incubation constancy. Therefore, the

Table 4.2. Comparison of mass loss and incubation constancy A) between nesting females and dual strategists and B) initial mass and constancy within strategy.

A			
Strategy	Average Absolute Mass Loss	Average Relative Mass Loss	Average Incubation Constancy
Dual Strategy (n = 4)	297.4 ± 10.3 g	0.26 ± 0.01	0.866 ± 0.009
Nest (n = 3)	209.3 ± 31.1 g	0.20 ± 0.03	0.890 ± 0.018
	t = 3.07, P = 0.01, df = 5	t = 2.21, P = 0.04, df = 5	t = -1.34, P = 0.12, df = 5
B			
Strategy	Mass at the Beginning of Reproduction (g)	Incubation Constancy	
Dual Strategy	1184.1	0.871	
	1131.2	0.886	
	1097.6	0.843	
	1086.4	0.865	
Nesting	1141.6	0.918	
	983.8	0.895	
	961	0.858	

relationship between Redhead incubation constancy and body mass is unresolved.

A positive relationship between body mass and reproductive strategy choice in captivity indicated that heavier females tended to choose more costly strategies. Furthermore, females choosing more costly strategies lost significantly more mass than those that parasitized only. Whether or not heavier females choosing more costly strategies, lost more mass simply because they were more physiologically able or because more costly strategies require more lipid reserves, i.e. body mass, is unclear. Mass loss may, however, come with consequences. Females that lose proportionately large amounts of mass during incubation may abandon their clutches (Korschgen 1977), die (Harris 1970, Korschgen 1977) or may not survive to the next breeding season.

The influence of body mass and strategy choice on incubation constancy was first proposed in Chapter 2. Constancy, however, was not significantly different between nesting females and dual strategists in captivity, although dual strategists lost more mass than nesting females. Trends in constancy within each reproductive strategy suggest that heavier dual strategists maintain higher constancy than light dual strategists, although definitive conclusions are limited by sample size. Work in captivity therefore suggests the relationship between mass and constancy is influenced by strategy choice, as proposed in Chapter 2. Since heavier females choose dual strategies, exhibit higher relative and absolute mass loss, constancy may be lower when compared to lighter females

that nested and lost less mass. In this study, a trend for nesters to maintain a higher average constancy than dual strategist exists, although not significant.

CHAPTER 5: REDHEAD BROOD ECOLOGY

North American waterfowl species produce precocial young with parents providing post-hatch care. Parental care often involves brooding the young (Koskimies and Lahti 1964, Afton and Paulus 1992), protection from predators (Lazarus and Inglis 1978), and selection of brood rearing habitats and food locations within those areas. Early parental care also allows for proper imprinting (review in Smith 1983). In duck species, post-hatch care is critical during the first and second weeks of life when mortality is highest (Ball et al. 1975, Savard et al. 1991, Mauser et al. 1994). However, time spent in brood care may conflict with the physiological demands of the female, as females try to enhance their physical condition after losses in body mass resulting from laying and incubation in order to molt and participate in fall migration. Variation in care may result in lower brood survival because reduction in care often comes at the cost of increased mortality of the young (Ball et al. 1975, Talent et al. 1983). Several factors may influence variation in care and/or success: initiation/hatch date, hen age and body mass, habitat use and brood movements.

In waterfowl, parental care patterns vary with initiation/hatch date, hen age and body mass, although Redhead brood ecology is essentially unknown. In some species, late-hatched broods have a lower survival rate (Orthmeyer and Ball 1990, Rotella and Ratti 1992a, but see Savard et al. 1991, Mauser et al. 1994), which is potentially due to several factors. Late-hatched brood rearing conflicts with time needed by the female to regain mass lost during laying and incubating. Late-season females appear to spend more time feeding and less

time in parental care activities, which possibly reduces survival of the brood (Rushforth Guinn and Batt 1985). Additionally, declining wetland density as the season progresses (Eldridge and Krapu 1988) may influence late-hatch broods. Finally, late-nesting females may be young, inexperienced or in poor condition, and therefore less attentive to broods (Krapu 1981, Ringelman and Longcore 1982) or be renesters (Doty et al. 1984, Swanson et al. 1986). Redheads, however, are known to renest only in one isolated population outside the normal breeding grounds (Alliston 1979)

Hen age may influence brood care and ultimately survival. Theoretically, older hens should exhibit greater levels of parental investment than younger hens (Trivers 1972, 1974). Further, older hens may provide better care due to experience gained from raising previous broods (Carlisle 1982). A study on Lesser Scaup provides weak support of the influence of age on parental investment (Afton 1984): time spent in brood care increased and self-maintenance decreased from one to three year old hens. However, care and self-maintenance of Scaup females four years and older were similar to yearlings.

Body condition of females may also affect brood care and survival. Female Redheads that invested heavily in reproductive activities, especially dual strategists, may be in a compromised body condition. In other species, such as the Common Eider, hens in poorer condition were more likely to abandon care of their young to other females (Bustnes and Erikstad 1991). White-winged Scoter

females in poorer condition, however, did not abandon their young more frequently than other females (Kehoe 1986).

Habitat requirements during brood rearing are important since they may influence pre-fledging survival (Rotella and Ratti 1992b). Pre-fledgling survival has been determined to be a major component of recruitment (Cowardin and Johnson 1979). Feathersone (1975) and Woodin (1987) demonstrated the importance of relatively small, semipermanent wetlands for breeding Redheads. No studies have examined brood rearing habitat use of Redheads even though wetland abundance and density have been shown to be important for diving duck species (Smith 1971, Stoudt 1971).

Although some dabbling and a few diving duck species have been studied during brood rearing, little is known about Redhead brood ecology. The first objective of this study was to document Redhead brood survival and the number of surviving ducklings and examine the influence of initiation/hatch date and hen age and body mass on individual variation in survival. The second objective was to document Redhead habitat use and its influence on brood survival and to examine the influence of hen age on habitat use. The final objective was to document brood movements and their influence on brood survival and to examine the influence of hen age and body mass on brood movements.

Methods

Redhead females found late in incubation or monitored during incubation (see Chapter 2) were trapped between 22 and 24 days of incubation, aged (Dane and Johnson 1975), weighed and surgically implanted with radio

transmitters (ATS, Inc.). Surgical procedures followed Korshgen et al. (1984) using a portable surgical lab at the trap site.

Hens with broods were located daily with either a truck-mounted 2-antenna, 4-element system or by 3-element hand held antennas. Ducklings in each brood were counted every day or as often as they were visible within a wetland. Twice, the number of ducklings in a brood could not be determined because visibility was impaired on the wetland where they were located due to 100% cover of vegetation. Broods were monitored for a maximum of 30 days post-hatch.

A brood was considered to have survived if at least one duckling survived to 30 days post-hatch (Klett et al. 1986). Brood survival was measured as the proportion of broods that survived to 30 days. The maximum number of ducklings observed and the last number of ducklings observed were recorded. The last known number of ducklings was used as a measure of the number of surviving ducklings from a brood since observations on females were not equal. This number, however, should be interpreted with caution as one egg from each clutch was removed to determine hatch date (see Chapter 2). Females that experienced total brood loss prior to 30 days received a duckling value of 0. Redhead broods did not amalgamate in this study.

Habitat use and availability were determined by classifying all wetlands within 0.8-km of the nest site. Habitats were classified using the system developed by Stewart and Kantrud (1971) for prairie pothole habitats (see Appendix 4 for summary of habitat classification).

Brood movements were measured on aerial photographs as straight-line distances between the center of wetlands used by broods. A brood was considered to have moved only when it was observed on a new wetland or, in the case of 100% vegetative cover, when a female remained on the wetland for at least three consecutive days of monitoring. Occasionally, females left broods unattended and flew to nearby wetlands. This movement by a female did not constitute a brood movement. Brood activity was monitored daily with telemetry equipment. The exact wetland location of the brood was verified daily by visual observation and/or using hand-held telemetry equipment.

Statistical Analysis

Brood Survival

Brood survival estimates were calculated as the proportion of surviving broods out of the total radioed females that successfully hatched eggs ($n = 40$). The average number of surviving ducklings, however, was calculated using only 36 of the 40 females because predators killed two and two other broods were never observed due to the use of wetlands with 100% vegetative cover. Correlation coefficients were used to examine the influence of hatch date on brood survival.

A chi-square test was used to determine whether brood survival was different between age groups. The influence of hen age on the number of surviving ducklings was first analyzed with an F-test for equal variances followed by the appropriate two-tailed t-test, unless otherwise noted. The relationship between hen body mass and brood survival was examined using the same

procedure. Simple linear regression was used to examine the relationship between the number of surviving ducklings and hen body mass at the end of incubation.

Habitat Use

Habitat use versus availability was examined using Johnson's (1980) Preference Test. This technique results in the ranking of habitats on the basis of preference and allows for significance tests of the ranking. This test has the advantage of producing comparable results whether doubtful habitats are included or excluded. Johnson's (1980) test initially produces a ranking of habitats according to selection and a ranking of habitats according to availability. Substantial differences in these rank orders causes rejection of the null hypothesis that all habitats are equally preferred. If the null hypothesis is rejected, habitats used are compared with the multiple comparison procedure of Waller and Duncan incorporated into the procedure of Johnson (1980).

Average use patterns were examined for 39 radioed females that hatched eggs with use days per female ranging from 2 to 30 days. General use patterns were examined and habitats that were never chosen, although available, were excluded from analysis. The method developed by Johnson (1980) is relatively insensitive to inclusion/exclusion of doubtful components (habitats).

The full data set of 39 hens was subdivided into surviving and non-surviving broods and the Johnson's (1980) Preference Test was performed on both to examine use/preference differences between the groups. The same procedure was applied to subgroups of yearling and adult hens with broods.

Brood Movements

Brood movement measures (the average number of movements, distance of the first move, the distance of the longest move and the total distance moved) were calculated from the entire data set of 40 radioed females and correlated to examine inter-relationships. For tests of brood survival, a subset of 38 hens was used because predators killed two hens. Further, a subset of 36 hens was used for tests of the number of surviving ducklings, because predators killed two hens and two hens with broods that were never observed.

The difference in brood movement measures between surviving and non-surviving broods was examined with ANOVA, whereas a multiple regression was used to determine the influence of brood movement measures on survival. A multiple regression was used again to examine the relationship between brood movement measures and the number of surviving ducklings.

An ANOVA was used to examine brood movement differences between yearling and adult hens. The influence of hen body mass on brood movements was examined with individual simple linear regressions.

Results

Forty broods were monitored from hatch to a maximum of 30 days during 1994 ($n = 12$) and 1995 ($n = 28$). Brood survival averaged 55% ($n = 40$). The average number of surviving ducklings was 4.2 ± 0.4 ($n = 36$) with a range of 0 to 9. Hatch dates ranged from 161-202 Julian (10 June to 21 July) for 1994 and 169-209 Julian (18 June to 28 July) in 1995. Brood survival was not correlated

with hatch date ($r = -0.23$, $P = 0.16$, $n = 38$). The number of surviving ducklings was also not correlated with hatch date ($r = 0.13$, $P = 0.44$, $n = 36$).

Age of the brood hen did not influence brood survival. There was no significant difference between survival of broods of yearling hens (56.25%, $n = 16$) and adult hens (59.09%, $n = 22$) ($\chi^2 = 0.95$, $P = 0.33$, $df = 1$). Also, the number of surviving ducklings was not significantly different between age groups ($t = 0.51$, $P = 0.61$, $df = 34$). Lastly, hatch date was not significantly different between yearling hens and adult hens ($t = -1.30$, $P = 0.20$, $df = 36$).

In contrast, brood survival and the number of surviving ducklings were both influenced by hen body mass. Body mass of hens with successful broods (937.7 ± 12.3 , $n = 22$) was significantly higher than for unsuccessful brood hens (905 ± 12.7 , $n = 16$) ($t = -1.82$, $P = 0.04$ (one-tailed), $df = 36$). The number of surviving ducklings increased significantly with increasing hen body mass ($R^2 = 0.19$, $F = 8.19$, $P = 0.007$, $df = 35$) (Figure 5.1). The number of ducklings observed within one week of hatch, an early indication of survival, was not correlated with hen body mass ($r = 0.25$, $P = 0.14$, $n = 36$).

Habitat Use

Habitats 4-3, 4-2, and 3-3 were used most often, based on the habitat ranks (Table 5.1). Habitat types 3-4, 2-3, 2-4, 1-1, 1-2, 1-3, and 1-4 were never chosen by female Redheads and were excluded from analysis (Table 5.1).

The average difference between ranks of wetland use and ranks of wetland availability are reported in Table 5.2a. The null hypothesis that each habitat was equally preferred was rejected ($F = 16.78$, $df = 8, 31$, $P = < 0.000$).

Figure 5.1. Relationship between hen body mass at the end of incubation and the number of surviving ducklings per brood.

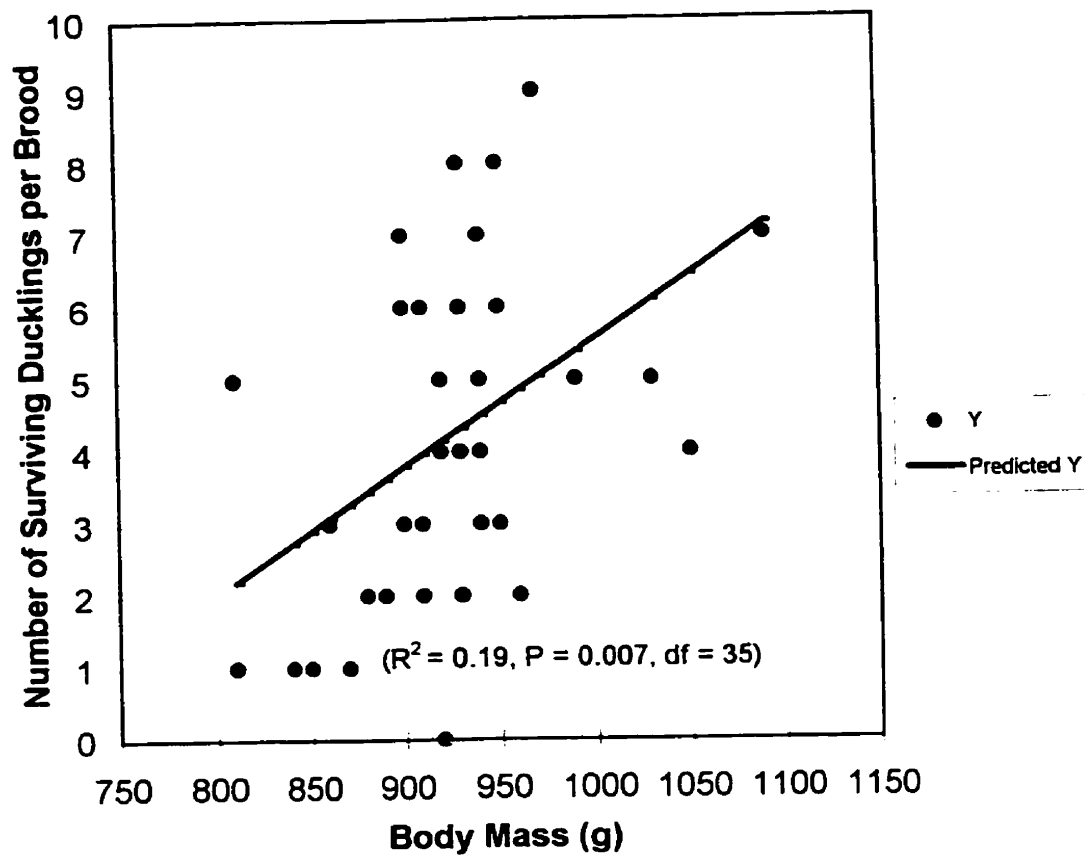


TABLE 5.1. The percent of all female Redheads that used a particular habitat type compared to the percent of those females that had a particular habitat available to them.

Habitat Type	Percent Use	Percent Availability
4-1	10	69
4-2	31	85
4-3	87	100
4-4	5	36
3-1	10	87
3-2	3	85
3-3	31	69
3-4	0	5
2-1	8	95
2-2	5	64
2-3	0	26
2-4	0	13
1-1	0	41
1-2	0	8
1-3	0	0
1-4	0	5

TABLE 5.2. The A) habitat ranks and B) habitat preferences of females

Redheads. Habitat types indicated are preferred (>) over other indicated habitat types and types not indicated are chosen equally with all others.

A) Habitat Type	T bar	Rank
4-4	-1.92	1
3-3	-0.96	2
4-1	-0.51	3
4-2	-0.48	4
2-2	-0.14	5
3-1	0.06	6
4-3	0.31	7
3-2	1.54	8
2-1	2.24	9

B)	Habitat Preferences
	4 - 4 > 4 -1, 4 -2, 4 -3, 3 -1, 3 -2, 3 -3, 2 -1, 2 -2
	4 -1, 4 -2, 4 -3 > 3 -2, 2 -1
	3 -3 > 4 -3, 3 -2, 2 -1
	3 -1 > 2 -1
	2 -2 > 3 -2, 2 -1

Habitat types 4-4, 4-1, 4-2, 4-3, and 3-3 were selected out of proportion to their availability (Table 5.2b). The use of habitat type 4-4, although significant by the test results, was used by only two females of the total tested (Table 5.1).

Although rank differences between surviving broods and unsuccessful broods were similar (Table 5.3a), habitat types were not chosen equally in either group: successful ($F = 10.11$, $P < 0.000$, $df = 8, 14$) and unsuccessful broods ($F = 3.75$, $P = 0.04$, $df = 8, 9$). Significant preferences existed in both groups, however, the surviving brood hens appeared to have stronger preferences exhibited by specific habitat usage (Table 5.3b).

The number of wetlands available to brood hens per brood study site (wetland density) did not differ between successful broods and unsuccessful broods ($t = 0.598$, $P = 0.55$, $df = 37$). Further, the average proportion of each habitat type available within a 0.8-km radius did not differ between successful and unsuccessful broods (Table 5.4).

The average difference in rank use/availability for yearlings and adults was similar for the most and least preferred habitats, but quite different for all others (Table 5.5a). Yearlings chose habitats out of proportion to their availability only marginally ($F = 3.33$, $P = 0.06$, $df = 8, 8$) whereas adults chose habitats significantly out of proportion to their availability ($F = 9.4$, $P < 0.005$, $df = 8, 15$). Adults preferred habitats 4-4, 4-1 and 3-3 most often and habitat types 3-2 and 2-1 least often (Table 5.5b).

TABLE 5.3. The A) rank differences and B) habitat preferences of successful and unsuccessful broods. Habitat types indicated are preferred (>) over other indicated habitat types and types not indicated are chosen equally with all others.

A) Rank	Successful Broods	Unsuccessful Broods
1	4-4	4-4
2	3-3	3-3
3	4-2	4-1
4	4-3	2-2
5	4-1	4-2
6	3-1	3-1
7	2-2	4-3
8	3-2	3-2
9	2-1	2-1

B)	Successful Brood Habitat	Unsuccessful Brood Habitat
	Preferences	Preferences
	4-4 > 4-1, 4-2, 4-3, 3-1, 3-2, 2-1, 2-2	4-4 > 4-3, 3-2, 2-1
	3-3 > 3-2, 2-1, 2-2	3-3, 2-2 > 3-2, 2-1
	4-2, 4-3 > 3-2, 2-1	4-1, 4-2 > 2-1
	4-1, 4-2, 3-1 > 2-1	

TABLE 5.4. Proportion of different habitat types available to successful and unsuccessful broods.

Habitat	Successful Broods	Unsuccessful Broods	t Value	P Value	df
4-1	0.082	0.075	-0.212	0.42	37
4-2	0.094	0.096	0.059	0.48	37
4-3	0.289	0.335	1.14	0.13	37
4-4	0.008	0.015	1.19	0.12	37
3-1	0.095	0.067	-1.0	0.16	37
3-2	0.103	0.102	-0.02	0.49	37
3-3	0.066	0.07	0.14	0.44	37
3-4	0.001	0.001	0.13	0.45	37
2-1	0.144	0.145	0.04	0.49	37
2-2	0.079	0.051	-0.93	0.18	37
2-3	0.006	0.006	0.15	0.44	37
2-4	0.001	0.003	0.98	0.17	37
1-1	0.031	0.029	-0.06	0.48	37
1-2	0.002	0.004	0.80	0.22	37
1-3	0	0	-	-	37
1-4	0.001	0.001	0.22	0.41	37

TABLE 5.5. The A) rank differences and B) habitat preferences between yearling and adult female Redheads. Habitat types indicated are preferred (>) over other indicated habitat types and habitat types not indicated are chosen equally with all others.

A) Rank	Yearling	Adults
1	4-4	4-4
2	4-2	3-3
3	2-2	4-1
4	3-3	3-1
5	4-3	2-2
6	4-1	4-2
7	3-1	4-3
8	3-2	2-1
9	2-1	3-2

B) Yearling Habitat Preferences	Adult Habitat Preferences
4-4 > 3-2, 2-1	4-4 > 4-1, 4-2, 4-3, 3-1, 3-2, 2-1, 2-2
4-3, 4-2, 3-3, 3-1, 2-2 > 2-1	3-3 > 4-2, 4-3, 3-2, 2-1, 2-2
	4-1, 4-2, 3-1, 2-2 > 3-2, 2-1

Brood Movements

Brood movements as indicated by the average number of movements, distance of the first move, the longest distance moved, and the total distance moved are reported in Table 5.6a. All movement measures are highly correlated (Table 5.6b). In an ANOVA with survival as dependent factor, all movement measures are significantly different between successful broods and unsuccessful broods (Table 5.7). In a multiple regression model, the first distance moved is the only measure that significantly influences survival (Table 5.8). A multiple regression of the number of surviving ducklings with brood movement measures indicates that only the first distance moved marginally influenced the number of surviving ducklings (Table 5.9, Figure 5.2).

Lastly, brood movement measures were not significantly different between yearling and adult brood hens (Table 5.10). Using individual regressions, only the distance of the first movement was marginally (although not at 0.05 level of significance) influenced by hen body mass (Table 5.11, Figure 5.3).

Discussion

Variation in parental care by female Redheads influenced brood survival. Although brood survival was generally high, it was influenced by variation in female body mass but not age or differences in initiation/hatch date. Habitat use patterns were different between successful and unsuccessful females and were influenced by female age. Finally, variation in brood movements influenced brood survival and were influenced by female body mass but not age.

Figure 5.2. Relationship between the number of surviving ducklings per brood and the distance of the first brood movement.

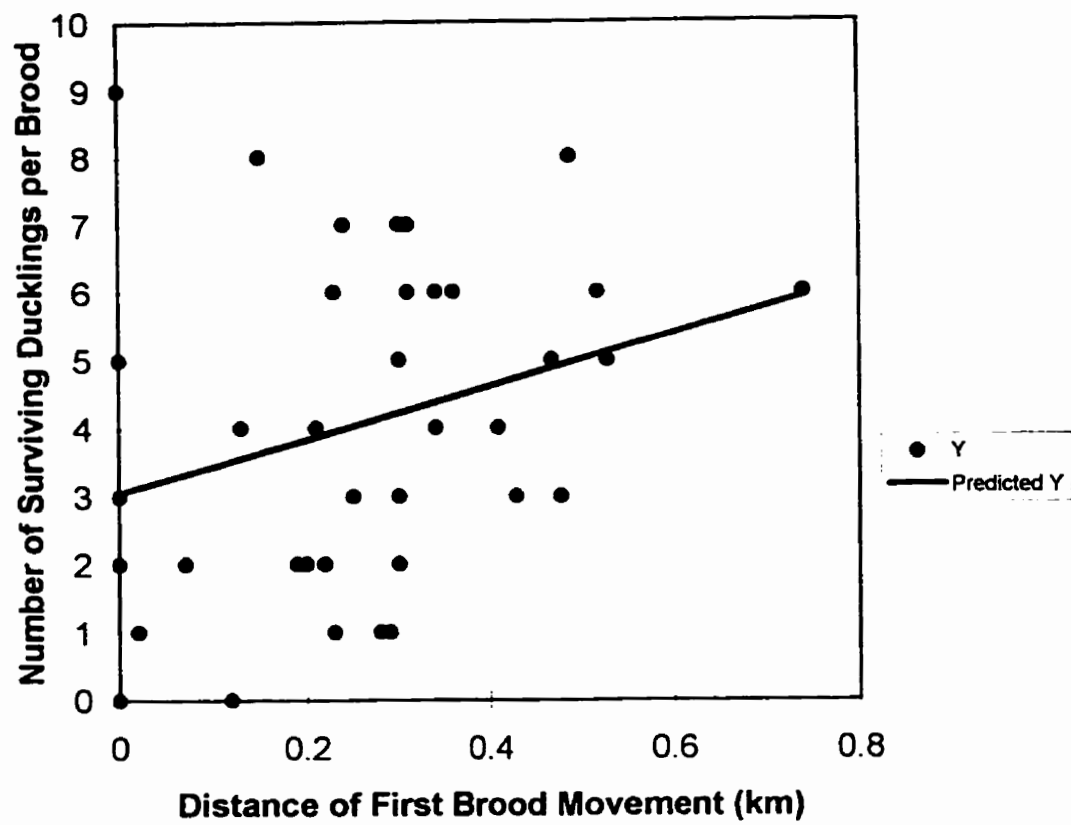


Figure 5.3. Relationship between hen body mass at the end of incubation and the distance of the first brood movement.

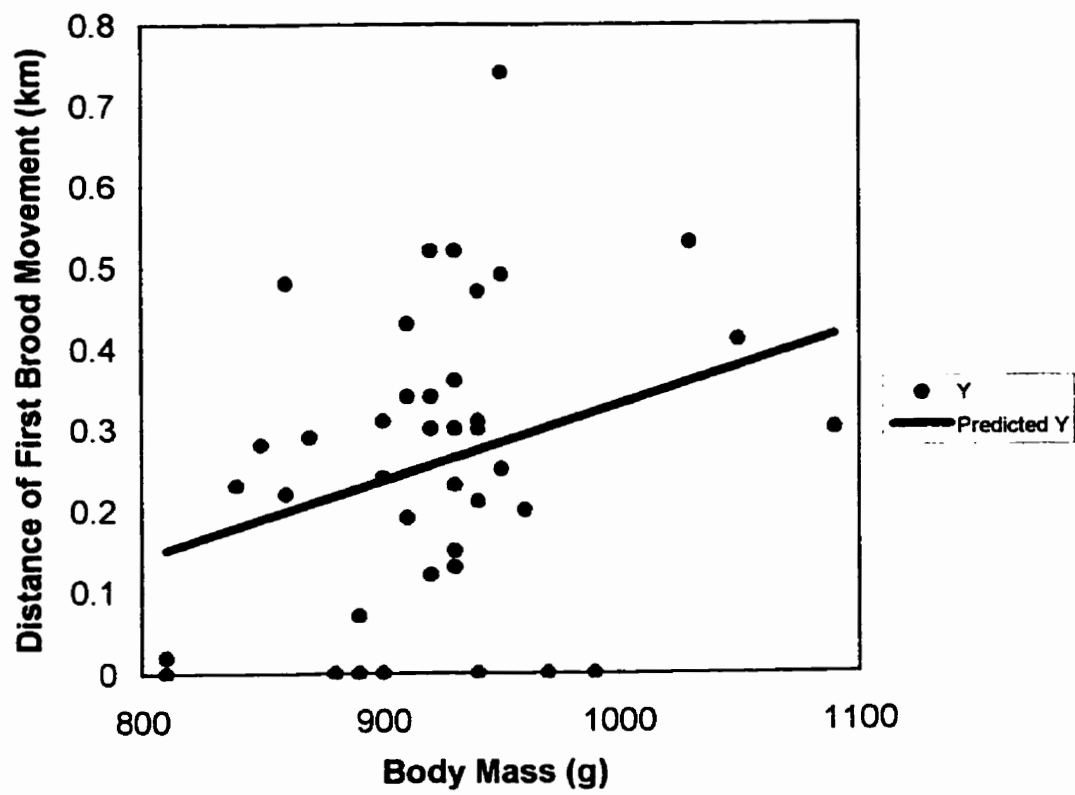


TABLE 5.6. A) Brood movement measurements and B) correlation between measures.

A)			
Total Number of Movements	Distance of First Movement (km)	Distance of Longest Movement (km)	Total Distance Moved (km)
(mean \pm SE, range)			
2.5 \pm 0.34, 0 - 9	0.244 \pm 0.029, 0 - 0.74	0.351 \pm 0.042, 0 - 1.14	0.779 \pm 0.122, 0 - 3.55
B)			
	Distance of First Movement	Distance of Longest Movement	Total Distance Moved
Total Number of Movements	R = 0.403, P = 0.01	r = 0.619, P = 0.000	r = 0.922, P = 0.000
Distance of First Movement		r = 0.702, P = 0.000	r = 0.496, P = 0.001
Distance of Longest Movement			r = 0.805, P = 0.000

TABLE 5.7. ANOVA of brood movement measurements between successful and unsuccessful broods.

ANOVA	F Value	P Value	df
Total Number of Movements	4.816	0.034	39
Distance of First Movement	12.377	0.001	39
Distance of Longest Movement	8.61	0.006	39
Total Distance Moved	7.387	0.01	39

TABLE 5.8. Multiple regression of the influence of brood movement measurements on brood survival.

ANOVA	F Value	P Value	df
Regression	3.468	0.017	4
Residual			35
Total			39

Model, Brood Survival as the Dependent Variable	t Value	P Value
Constant	1.463	0.152
Total Number of Movements	-0.463	0.646
Distance of First Movement	2.094	0.044
Distance of Longest Movement	-0.419	0.678
Total Distance Moved	0.831	0.411

TABLE 5.9. Multiple regression of the influence of brood movements on the number of surviving ducklings.

ANOVA	F Value	P Value	df
Regression	1.136	0.356	4
Residual			33
Total			37

Model, Number of Surviving Ducklings as the Dependent Variable	t Value	P Value
Constant	3.851	0.001
Total Number of Movements	-0.486	0.63
Distance of First Movement	1.796	0.082
Distance of Longest Movement	-0.324	0.748
Total Distance Moved	0.177	0.860

TABLE 5.10. ANOVA of brood movement measurements of yearling and adult hens.

ANOVA	F Value	P Value	df
Total Number of Movements	1.469	0.229	39
Distance of First Movement	1.367	0.25	39
Distance of Longest Movement	1.002	0.323	39
Total Distance Moved	0.905	0.347	39

TABLE 5.11. Individual regressions of the influence of body mass on brood movement measurements.

Variable	R ² Value	F Value	P Value	df
Total Number of Brood Movements	0.002	0.061	0.807	39
Distance of First Brood Movement	0.086	3.57	0.066	39
Distance of Longest Brood Movement	0.033	1.31	0.26	39
Total Distance of Brood Movements	0.003	0.104	0.749	39

Brood Survival

Redhead brood survival was found to be 55% and was similar to survival estimates available for diving ducks in the same area (Bellrose 1980). Brood survival was not influenced by hatch date, although several other studies have reported lower brood survival of late hatched broods (Bengston 1971, Orthmeyer and Ball 1990, Rotella and Ratti 1992b). Savard et al. (1991) demonstrated yearly effects of hatch date on survival of Goldeneyes but found no relationship between hatch date and brood survival of Buffleheads. Other studies, such as Mauser et al. (1994), demonstrated no difference in brood survival between early and late hatch Mallard broods and attributed high survival of late broods to a corresponding peak hatch of Gadwall (*Anas strepera*) nests, which potentially provided an alternative prey source reducing depredation on Mallard ducklings. Redheads may not exhibit differential brood survival with hatch date because their breeding season may be more restricted due to a later nest initiation, as compared to some duck species.

Although hen age may be important since young are inexperienced or could be in poor condition and therefore less attentive to broods (Krapu 1981, Ringelman and Longcore 1982), hen age did not influence Redhead brood survival. Age has been shown to influence nest initiation date, clutch size, and the number of young raised in some waterfowl species (Krapu and Doty 1979, Raveling 1981, Afton 1984, Duncan 1987a,b), but no studies have examined the influence of age on brood survival in dabbling and diving ducks.

In this study, hen body mass influenced Redhead brood survival. Hens that were heavier at the end of incubation exhibited higher brood survival and produced more ducklings per brood than lighter hens. This relationship cannot be attributed to heavier hens initially producing more eggs and thus hatching more ducklings because body mass at the end of incubation was not related to the number of ducklings that hatched. These findings are in contrast to those of Arnold et al (1995) who demonstrated that late incubation body mass was unrelated to brood and duckling survival in both Redheads and Canvasbacks. In this study, females in better condition at the beginning of the brood care phase may have been able to devote more time to brood care activities than females which were of a lighter body mass. Females in a compromised or of a lighter body mass would be required to devote a large amount of brood rearing time to self-maintenance. Time budget studies of female waterfowl in varying body condition states during the brood rearing phase are non-existent. In general, however, time budget studies have shown that brood rearing females devote approximately 50% of their time to self maintenance (mostly feeding) and that females with broods spend less time feeding than females without broods (Scott 1980, Afton 1984, Giroux et al. 1986). Variability of time spent feeding by hens during brood rearing is likely to be influenced by body condition.

Habitat Use

Habitat use during brood rearing is important because habitat conditions may influence pre-fledgling survival (Rotella and Ratti 1992b). In my study, Redhead brood hens exhibited strong preferences for certain habitats that were

selected out of proportion to their availability and used many habitats that were equally available. Hens used semi-permanent and seasonal wetlands with up to 95% open water and a band of at least 2 m of emergent vegetation in proportion to their availability (4-3 and 3-3). Furthermore, hens selected semi-permanent and seasonal wetlands with greater than or equal to 95% open water and with the existence of a band of emergent vegetation out of proportion to their availability (types 4-4 and 3-3). Temporary and seasonal wetlands with less than 5% open water and less than 95% open water, respectively, were often avoided.

Successful and unsuccessful brood hens selected habitats differently, although the density and proportion of available wetland classes did not differ between groups. Successful females selected semi-permanent wetlands with greater than 2 m of emergent cover (4-4) and seasonal wetlands with 5-95% open water (3-3) over all other types available. Unsuccessful hens exhibited less preference, selecting 4-4 and 3-3 with all other types equally, with exception of 4-3, 3-2 and 2-1. Unsuccessful hens choosing habitats 4-1, 4-2, 3-1 and 2-2, which are entirely or partially covered by emergent vegetation and correlated with shallow water conditions, may have experienced greater brood loss due to depredation. Shallow water habitats are easily utilized by mammalian predators, such as raccoons (*Procyon lotor*) and skunks (*Mephitis mephitis*).

Yearlings and adults also exhibited different habitat selection strategies. Yearlings did not select habitats out of proportion to their availability while adults preferred 4-4 and 3-3 to most habitats and avoided 3-2 and 2-1. Preferences

may reflect previous experience with the brood rearing range since Redhead females exhibit strong nest site fidelity from year to year (T. Yerkes, pers. obs.). Redhead hens may acquire valuable knowledge and fitness advantages from such behavior.

Brood Movements

Brood movements influence redhead brood survival. Specifically the distance of the first movement influenced survival and the number of surviving ducklings per brood. Although brood movements are negatively correlated with brood survival in Mallards and Wood Ducks (Ball et al. 1975, Rotella and Ratti 1992b, but see Evans and Black 1956, Duncan 1986, Mauser et al. 1994), this relationship is opposite in Redheads. The first distance moved was positively correlated with brood survival and the number of surviving ducklings per brood. Brood movements are common in other duck species (Dzubin and Gallop 1972, Ringelman and Longcore 1982, Talent et al. 1982, Duncan 1987c, Gauthier 1987). These possibly occur in response to low invertebrate numbers (Talent et al. 1982, Gauthier 1987) or to avoid wetlands lacking a zone of emergent vegetation (Evans et al. 1952, Keith 1961). This may reflect strong preference for specific wetland types by Redheads even though it requires longer overland movements to reach those areas, thus potentially demonstrating that Redheads may have specialized requirements. Elsewhere, I have documented differential use of nesting and brood rearing habitats, such that Redheads switch from relatively small wetlands used for nesting to larger, semipermanent wetlands for brood rearing (unpubl. data).

CHAPTER SIX: CONCLUSIONS - FACTORS THAT INFLUENCE INDIVIDUAL VARIATION IN REPRODUCTIVE PARAMETERS OF FEMALE REDHEADS

The overriding objective of my research was to examine individual variation in Redhead reproductive behaviors and determine the factors that influence variation in success. I found that variation in incubation behaviors, brood rearing success and reproductive strategy choices of individual females is the result of female age and body mass and several environmental factors. More importantly, this research has demonstrated variable consequences of reproductive strategy choice and how choice is influenced by parameters such as age and mass. I proposed that strategy choice also influences subsequent behavior later in the season, such as incubation constancy and brood rearing.

Incubation Constancy

I found that female Redheads, although relatively large-bodied, exhibit one of the lowest incubation constancy's reported among duck species. This relationship is in contrast to Aftons' (1980) proposal, which states constancy among species should be positively related to body size. I proposed that low constancy is a result of the preponderance of parasitism prior to nesting, a strategy uncommon in other ducks. High frequency of parasitism may reduce body condition of nesting females and result in the low constancy observed. Furthermore, I found that hen age and mass resulted in variation among females. Older female Redheads exhibited, on the average, higher incubation constancy than yearlings. Although the prior breeding history of adult Redheads in my study was unknown, prior experience potentially influenced incubation

patterns of adult females. I found that body mass also exerted an influence on incubation constancy. Although the relationship between body mass and constancy was not entirely clear due to use of mass at the end of incubation, I proposed that heavier females at the beginning of incubation were capable of maintaining higher constancy, on the average, as compared to light females. I propose that heavier females would be able rely more on endogenous reserves thus be capable of maintaining higher constancy.

In captivity, I determined that the use of end-of-incubation body mass is not a good measure for examining the relationship between mass and constancy because females that were significantly heavier at the beginning of incubation were not significantly different from lighter females at the beginning of incubation. Heavy and light females did not differ in incubation constancy as proposed, however, this test was restricted by small sample sizes. Because significant interactions were found in the wild between mass and Julian date, I suggest that mass and strategy choice may interact to influence incubation constancy.

In most studies of waterfowl incubation constancy, variation has been attributed to female age and body mass. In general, and in my study, older, experienced females maintain higher constancy (Aldrich and Raveling 1983). It has been proposed that experience mediates this relationship and not age per se. Furthermore, I found that heavier females maintain higher constancy than their lighter cohorts, results similar to others (Aldrich and Raveling 1983, Gloutney and Clark 1991, Erikstad et al. 1993). Heavier females are able to rely

more on endogenous reserves and thus maintain higher constancy while foraging less as compared to lighter females.

I also found that ambient conditions exerted an influence on incubation constancy. Constancy of female Redheads was lower on days with higher maximum temperatures. Constancy did not increase in response to colder ambient temperatures or precipitation. I propose that females in a reduced body condition may not be able to respond to decreasing temperatures by increasing constancy beyond some maximum level constrained by their current body condition. Females may, however, respond to the opposite scenario. At higher ambient temperatures, females may take advantage of favorable ambient conditions to increase foraging time and thus decrease constancy.

Although ambient temperature and precipitation have been found to influence constancy, this influence varies greatly among species. Some species increase constancy in response to decreasing ambient temperatures and precipitation (Caldwell and Cornell 1975, Afton 1980). Others increase constancy only in response to increasing temperatures (Malloy and Weatherhead 1993) or precipitation events (Brown and Fredrickson 1987, Meade 1996), whereas others do not respond to temperature or precipitation (Ringelman et al. 1982, Hohman 1986). Body size and variation in nutrient storage capabilities among species mediate this relationship. Species that are capable of responding to colder temperature by increasing constancy may be able to do so due to stored reserves. Others, like Redheads, may be

maintaining constancy at a physiological maximum dictated by nutrient reserves and thus can only take advantage of higher ambient temperatures.

Finally, I found significant interactions between age and initiation date and mass and Julian date on incubation constancy. Early in the season, before parasitism has occurred, yearling females maintain lower constancy than adults whereas, later in the season yearling constancy is higher than adults. I propose that this interaction shows an influence of age on strategy choice which subsequently effects incubation constancy, such that yearling females that nest late in the season may only have nested compared to adults which may have chosen dual strategies and hence maintained lower incubation constancy.

Additionally, I propose that strategy choice and mass may also interact to influence constancy. I found that early season nest initiators maintained higher constancy and ended incubation at lower body masses than late season initiators that maintain lower constancy by ended with higher body masses. I proposed that early initiators are nesters only and later initiators are dual strategists, and hence mass and strategy choice influence constancy such that nesting females maintain higher constancy as compared to dual strategists.

Reproductive Strategy Choice

As predicted by the dynamic state variable model that I developed, reproductive strategy choices of female Redheads were influenced by age, body mass, and environmental variability in the form of food availability and host availability. I found that body mass determined strategy choice resulting in a distribution from most to least costly, whereas age shifted the mass distribution

up or down depending on the survival probability. For example, females with a low probability of survival to the next breeding season, therefore an old female, chose more costly strategies at lower body masses. These findings support my predictions of the influence of mass and age on strategy choice. In all cases, I would predict that nesting only was rare, while parasitism and dual strategies were common. The positive correlation between body mass and reproductive strategy choice that I found in captivity supports the model conclusions based on mass.

The availability of food exerted a slight influence on strategy choice, whereas host availability exerted a strong influence on choice. When food availability was high, slightly higher proportions of more costly strategies were observed in a breeding population. In contrast, when host availability changed, the profile of reproductive strategies observed in a population changed dramatically. At extremely low host availability, I would predict only non-breeding and pure nesting, whereas at all other levels of host availability, parasitism and dual strategies are predicted but no pure nesting

Based on the combined results of the incubation studies and the model predictions, the interaction I proposed between mass, age, and strategy choice that influence behavior, such as constancy, is strengthened. I propose that heavier and/or older females invest heavily in costly strategies at the expense of body mass and constancy, but realize higher expected fitness values as predicted by the model. Lighter females, in contrast, choose a less costly strategy, nesting, and consequently maintain higher constancy. I found support

for this relationship in captivity. These data suggest that dual strategists, compared to nesters, maintained higher constancy and lost more relative and absolute mass. I also found that within each strategy, heavier females tended to maintain higher constancy than lighter females.

Studies of alternative reproductive strategies in waterfowl have attributed parasitic frequencies to many factors (for review see Sayler 1992). Species that nest in northern latitudes, such as Lesser Snow Geese, increase the frequency of parasitism in response to limited nest sites, poor female condition and/or age and thus are purportedly making the best-of-a-bad job (Lank et al. 1989, 1990). Eiders (Robertson et al. 1992, Bjorn and Erikstad 1994) and cavity nesters (Clawson et al. 1979, Haramis and Thompson 1985, Savard 1988, Eadie 1991) respond to the availability of nest sites and population levels, such that lack of nest sites and increased population levels increase the frequency of parasitism. I would predict that Redheads, which nest over water and rarely experience nest site limitations, respond strongly to host availability mediated by female age and body mass.

There are two broader conclusions that can be made from these findings: 1) Redheads increase reproductive effort with age and 2) host availability is very important in Redhead reproductive strategy choice. As I predicted, females Redheads increase reproductive effort with age. This relationship is further influenced by mass. Earlier researchers suggested a qualitative difference in strategy choice by age, such that yearlings were restricted to parasitism and older females chose to nest or dual. My work does not support a qualitative

difference, but predicts that survival probabilities exert an influence on the mass category at which females switch from low to high cost strategies.

More interestingly, the model results predict that host availability has a stronger influence on strategy choice than food availability. Previous results of field studies under varying environmental conditions produced conflicting and mixed results: in some cases the environment modified strategy choice whereas others found no influence. I propose an alternative explanation for these mixed findings: Redhead females assess the "host environment" in addition to their own age and mass, prior to making a strategy decision. Food availability functions to fine-tune this assessment, by either encouraging or discouraging more costly strategies at lower mass categories.

Brood Rearing

Variation in brood success can also be attributed to phenotypic variation and environmental factors. Female age was not found to influence Redhead brood success, the number of surviving ducklings, or brood movements among brood rearing habitats. I found that Redhead body mass, however, did exert an influence on such variation. Heavier females at hatch had higher brood survival and produced more ducklings compared to light females. Furthermore, I found that mass influenced the distance of the first brood movement from the nest site to a brood rearing wetland. Heavier females made greater overland brood movements, which were significantly and positively related to brood survival. I propose that females making greater overland movements potentially reached more preferred habitats resulting in greater survival rates.

Of the few studies conducted during the brood rearing phase that examined individual variation in success, female age and body mass were not found to influence variation in success (Arnold et al. 1995). In Redheads, age did not influence success. In contrast to others, I found that body mass at hatch was important in explaining variation in brood success. Females in better condition may incur advantages over females in poor condition. I propose that these advantages may include increased brood attendance, increased vigilant and defense behavior, and increased ability to move a brood greater distances to better quality habitats. During the brood rearing phase, females must balance the needs of the brood against her own self-maintenance and later pre-migratory fattening. Females in poor condition may neglect broods in order to ensure their own survival (Bustnes and Erikstad 1991), thus resulting in lower brood survival.

The environmental gradient of habitat types varied over the prairie landscape, but the proportion of various habitat types available to brood rearing females did not significantly differ. Although all females experienced similar availability, I found that habitat types were used differently among females. Redheads that successfully raised broods, across age groups, exhibited strong preferences for specific habitat types. Further, I found that older females exhibited strong preferences for specific habitat types. I propose that the observed preference of adults may reflect prior experience with the nesting area due to the philopatric nature of Redhead females. Choice of a particular habitat within a mosaic of available wetlands, however, does influence the success of a female.

Finally, I propose that behavioral decisions in the early part of the breeding season will result in behavioral differences during brood rearing, particularly in Redheads since differential energetic investment between nesters and dual strategists may result in variation in success. I earlier proposed that heavier females at the end of incubation were dual strategists, and hence found that heavier females had higher brood survival and produced more young. I propose that dual strategists parasitize and nest at the expense of body mass, but maintain lower constancy and thus end incubation with adequate reserves to increase brood survival as compared to their cohorts that nested only.

APPENDIX ONE: THE USE OF REDHEAD BODY MASS AS AN INDICATOR OF BODY CONDITION AND AS A COMPARATIVE MEASURE AMONG FEMALES.

Body mass and nutrient reserves are often used synonymously with body condition in birds. Fat is the most frequent limiting nutrient for waterfowl due to its importance in reproductive activities of egg synthesis and incubation, and as an energy source for migration and in times of food deprivation (Johnson et al. 1985). Further, lipid reserves are positively correlated with body mass in waterfowl (Bailey 1979, Krapu 1981, Chappell and Titman 1983, Johnson et al. 1985, Hohman and Taylor 1986). Previous investigators have used either body mass alone as an indicator of body condition (Hohman 1986, Gloutney and Clark 1991, Arnold et al. 1995, Zicus and Riggs 1996) or have developed condition indices that correct for variation in body mass due to structural size differences (Alisauskas and Ankney 1987, Meade 1996). A scaled body mass correction assumes that a single structural measurement or combinations of structural measurements explain a significant amount of variation in body mass.

In this study, structural measurements and body mass of 70 female Redheads ($n = 47$ wild, $n = 23$ captive) were obtained to determine whether body mass or a corrected body mass would be used as a measure for comparison between females. All females were weighed and measured at the end of incubation. Structural measurements included culmen, tarsus, right wing chord, and keel length.

In a multiple regression with mass as a dependent variable and the structural measurements as independent variables, only keel length significantly

predicted body mass (Table A1.1). Further, in a simple linear regression of body mass and keel length, keel length accounted for only 11% of the variation in body mass (Figure A1.1).

Johnson et al. (1985) determined that body mass alone was a fair index of fat, although scaling may improve the value. Bailey (1979) further determined that fat in Redheads was highly correlated with total body mass, uncorrected for structural size, so that mass explained 65% of the variation in carcass fat content. The best predictor from his study was body mass divided by total length, although this predictor only improved the estimate by 7% from 65% to 72% of carcass fat. Therefore, female body mass alone will be used as the most parsimonious and accurate comparative measure of body condition throughout this document.

Figure A1.1. Simple linear regression of hen body mass and keel length.

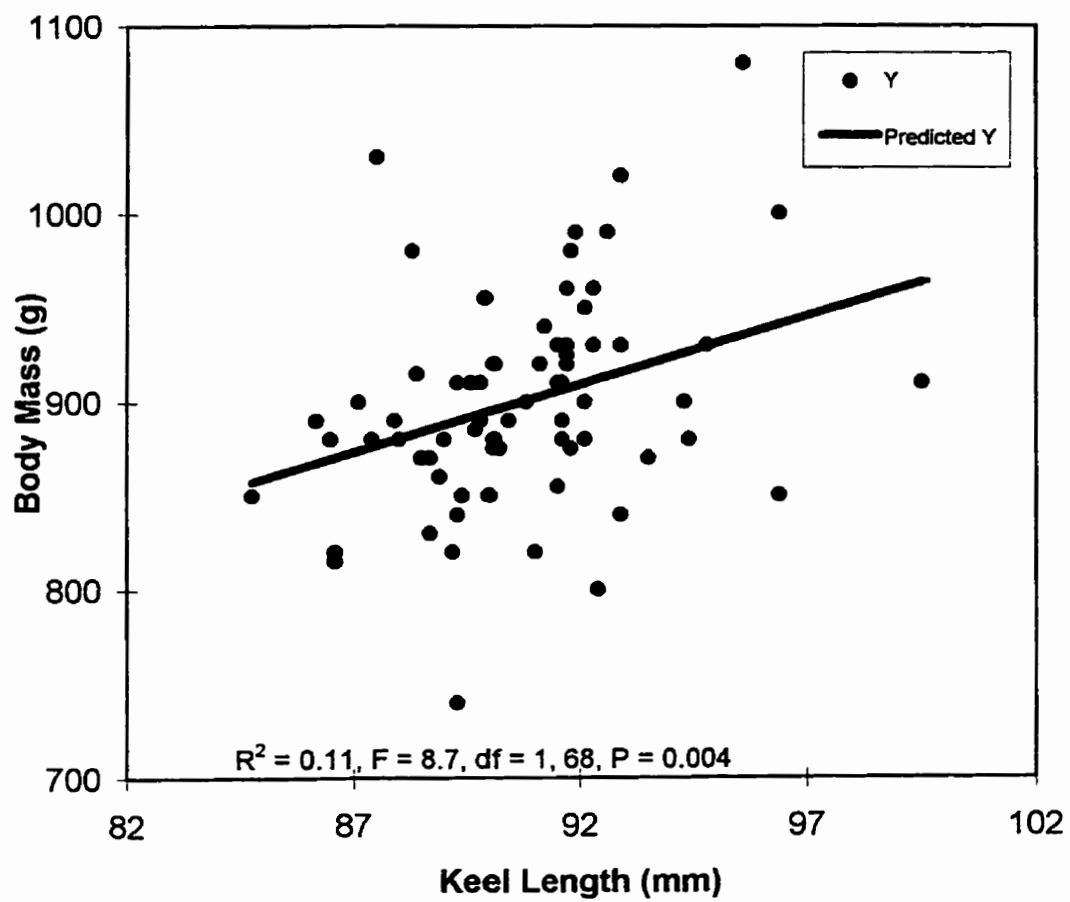


TABLE A1.1. Multiple regression of female Redhead body mass and structural measurements.

Model	R ² Value	df	F Value	P Value
Regression	0.16	4	3.07	0.02
Residual		65		
Total		69		

Model	t Value	P Value
Constant	-0.96	0.341
Culmen	0.73	0.47
Keel	2.77	0.01
Right wing	1.18	0.24
Tarsus	1.0	0.32

APPENDIX TWO: MASS LOSS PARAMETERS FOR REDHEAD REPRODUCTIVE STRATEGY CHOICE MODEL

Costs associated with various reproductive strategy options, measured as mass loss by the female, were determined from a captive study of female Redheads (for details see Chapter 4 Methods). Females were weighed every second day over the reproductive period from the beginning of the season in March to the end of incubation in July.

For all mass loss parameters, regression equations were used to determine mass at the beginning of a specific activity and mass at the end of that activity. For example, mass loss during parasitic events was determined by obtaining predicted mass values from the regression equation from the first parasitic egg laid to the last egg laid. Regression equations were used to estimate mass values since raw data points were highly variable from day to day.

Since clutch size of individual hens varied, mass loss per egg laid was calculated. An average mass loss per egg for parasitic females was used to determine the average mass loss that occurred during the laying of 10 parasitic eggs. The mass loss cost of laying nested eggs was determined in a similar manner using individual mass loss of hens that nested only.

Incubation costs were calculated from females that successfully completed at least 19 of the 24 days of incubation. Regressed mass loss values were obtained from the first day of incubation to the end at day 24. An average

mass loss value in grams was calculated for 11 hens and divided into three time periods as in the model.

The mass loss value determined for laying one parasitic clutch of 10 eggs was approximately 20 g (Table A2.1) as compared to mass loss of approximately 40 g for a nested clutch of 10 eggs (Table A2.2). Mass loss values were rounded to the nearest 10 g to reflect parameters outlined in the model. The average mass loss during incubation was 110.6 g (Table A2.3). Three incubation time periods are used in the model to represent a full incubation period, therefore the cost of incubating in each time period is approximately 40 g of body mass.

TABLE A2.1. Individual mass loss per parasitic egg laid and average mass loss for a parasitic clutch of 10 eggs.

Hen ID	Mass Loss Per Egg (g)	#Eggs	R ² Value	P Value
ARB	-3.1	11	0.25	0.21
BAR	-0.6	11	0.03	0.72
AYR	-2.7	13	0.24	0.15
AGG	-7.3	17	0.20	0.05
ARR	1.5	12	0.07	0.58
Average = - 2.4				
Mass Loss for 10 Egg Parasitic Clutch = - 24 g				

TABLE A2.2. Individual mass loss per nested egg and average mass loss for a 10 egg clutch.

Hen ID	Mass Loss Per Egg (g)	#Eggs	R ² Value	P Value
ABY	-7.0	10	0.79	0.04
GAG	4.7	8	0.73	0.15
ABB	-9.5	6	0.22	0.53
RAY	-5.9	11	0.30	0.26
AYY	1.2	8	0.004	0.92
AYB	-3.6	11	0.14	0.47
ARG	-3.2	8	0.14	0.63
AGY	-0.7	8	0.00	0.96
GAR	-12.9	7	0.77	0.12
BAB	-10.9	11	0.77	0.02
ARY	4.07	7	0.03	0.82
AGR	-10.0	8	0.24	0.40
Average = - 4.4				
Mass Loss per 10 Egg Nested Clutch = - 44 g				

TABLE A2.3. Individual mass loss during the incubation period.

Hen ID	Mass Lost (g)	R ² Value	P Value	n
ABR	-27.4	0.22	0.102	13
GAY	-133.5	0.77	<0.0000	13
ABG	-188.8	0.96	<0.0000	13
GAG	-125	0.71	0.0003	13
RAY	-53.1	0.54	0.004	13
GAB	-132.5	0.52	0.005	13
ARG	-127.3	0.40	0.02	13
AGY	-130.6	0.45	0.012	13
GAR	-172.4	0.51	0.006	13
ABB	-54.1	0.26	0.07	13
AYY	-71.8	0.38	0.026	13
Average =				
110.6				
Mass Loss per				
Period =				
36.9				

APPENDIX THREE: MASS LOSS TRENDS OVER THE REPRODUCTIVE PERIOD OF WILD FEMALE REDHEADS AND A COMPARISON BETWEEN WILD AND CAPTIVE FEMALE MASS LOSS.

Mass loss patterns over the reproductive period are often a reflection of the 'costs' of reproduction. Mass loss patterns observed in captive situations indicate that female Redheads lose a significant amount of mass over the reproductive period (Chapter 3). However, data obtained from captive females fed *ad libitum* may not reflect patterns of wild females due to the fact that captive females do not have to search for food, face limited food resources, or experience other differences.

Therefore, it was necessary to determine if female mass and general mass loss patterns observed over the reproductive period in captivity were different between captive and wild conspecifics. Thus, mass values from wild trapped females were obtained for a comparison. Due to nest abandonment rates of wild females, data on individual female mass loss was not obtained.

Masses of 100 females within 4 reproductive phases were obtained from a wild population in Minnedosa, Manitoba. The four reproductive phases were comprised of pre-laying, laying, early incubation, and late incubation females. Pre-laying hens were decoy trapped within two weeks of the spring arrival of Redheads to the study site. All other hens were trapped on the nest (Weller 1956). The categorization of pre-laying and laying hens was confirmed by inspection of reproductive tissue. Early and late incubating females were classified by the stage of eggs they were incubating. Early incubation females

were collected between 1 and 5 days of incubation while late females were collected during 20 to 24 days of incubation. Eggs were aged with field candling techniques (Weller 1956) and late incubation development was monitored by removing one egg from the nest and artificially incubating the egg. Female mass was obtained immediately after collection and measured to the nearest 5 g with a Pesola scale.

Within each reproductive period, masses from wild birds were compared with those observed in captivity. Captive female body mass was averaged for each individual within the designated reproductive period. Mass was significantly different between wild and captive females during pre-laying and early incubation, but was not significantly different between laying and late incubation (Table A3.1). Regressions of mass loss over time were significant for both wild hens ($R^2 = 0.47$, $P < 0.000$, $df = 99$)(Figure A3.1) and captive hens ($R^2 = 0.71$, $P < 0.000$, $df = 64$)(Figure A3.2).

Thus it was concluded that over the entire nesting cycle, mass loss patterns between captive and wild females are not drastically different. Although captive females begin reproductive activities heavier than wild counterparts and lost relatively and absolutely more mass (282.88 g vs. 170 g; 0.25 vs. 0.16, respectively), both groups finish incubation at a similar average mass. In general, captive females maintained higher incubation constancy (Chapter 3) than wild hens which may partially account for captive females losing more mass on average.

Figure A3.1. Mass loss for wild female Redheads from prelaying to late incubation.

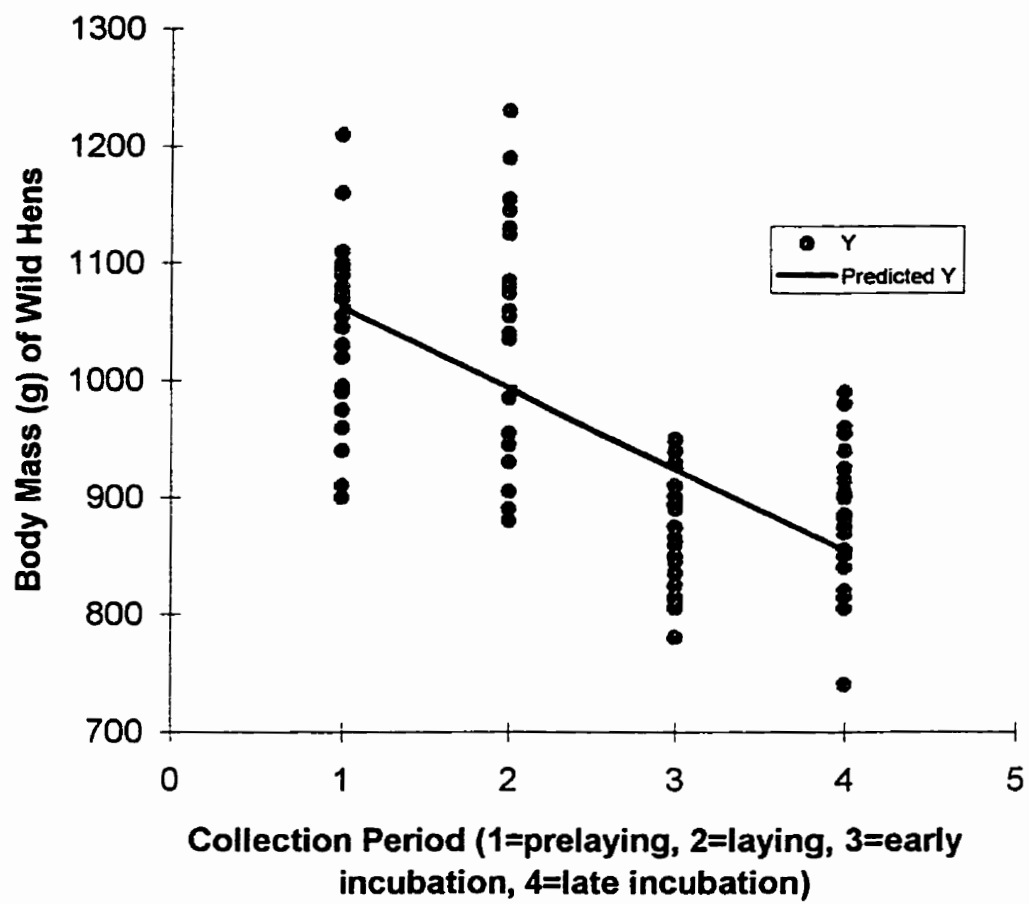


Figure A3.2. Mass loss for captive female Redheads from prelaying to incubation.

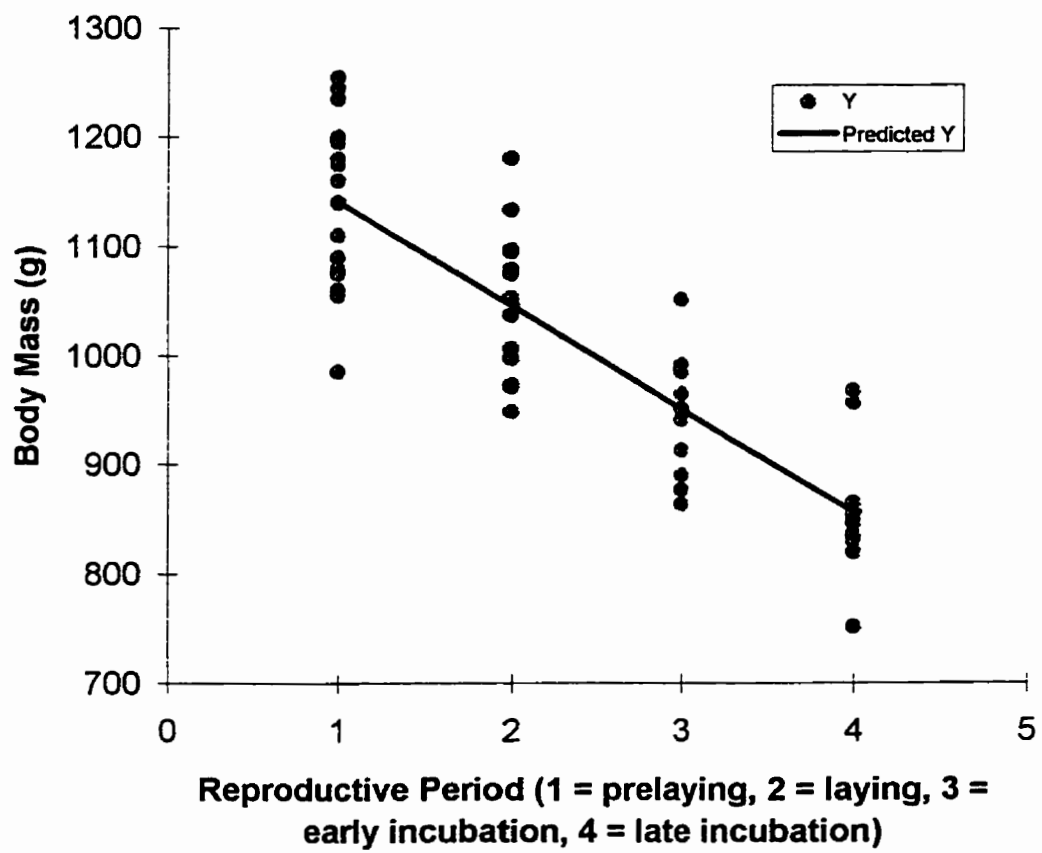


TABLE A3.1. Mass comparison between wild and captive female Redheads during different reproductive periods.

Reproductive Period	Average Mass (\pm SE) Wild Females	Average Mass (\pm SE) Captive Females	t Value	P Value	df
Prelaying	1051 \pm 15.6 n = 25	1138.6 \pm 17.5 n = 22	3.77	0.0005	45
Laying	1043 \pm 18.8 n = 25	1053.5 \pm 16.6 n = 22	0.38	0.70	38
Early Incubation	860.6 \pm 9.0 n = 25	947.1 \pm 17.3 n = 11	4.88	< 0.000	34
Late Incubation	881 \pm 11.7 n = 25	855.8 \pm 18.3 n = 11	-1.18	0.25	34

APPENDIX FOUR: SUMMARY OF PRAIRIE WETLAND HABITAT CLASSIFICATION

The classification system of Stewart and Kantrud (1971) was developed specifically to classify prairie wetland habitat. This system provides a more 'precise and realistic means of ecologically classifying wetlands in the glaciated prairie region' (Stewart and Kantrud 1971:2) where this study was conducted.

Seven major classes of wetlands are described on the basis of ecological differentiation. Four of these classes apply to the area in which this study was conducted. Each class is distinguished by vegetation zones occurring in the central or deeper part of wetlands and occupying 5% or more of the total wetland area. The four major habitat classes that apply to this study are summarized in Table A4.1. The remaining three classes (permanent ponds and lakes, alkali ponds and lakes, and fen ponds or alkali bogs) do not exist on the Minnedosa study site.

Classes of wetlands are further subdivided by cover type classifications. Cover types are related to average water depths. Generally, closed stands of emergent vegetation are found in shallow water, open stands in deep water, and variable stands of emergent vegetation are found in intermediate water depths. No emergent vegetation is generally found in very deep water. The four cover types are summarized in Table A4.2.

TABLE A4.1. Summary of Stewart and Kantrud's (1971) classification of major prairie pothole wetland classes.

Major Classes	Description
Class 1: Ephemeral Ponds	Central zone is represented by low-prairie vegetation. Due to the porous condition of the soil, surface water is maintained for only a brief period in early spring.
Class 2: Temporary Ponds	Central zone is represented by wet-meadow vegetation with a peripheral low-prairie zone present. Water loss from the basin is fairly rapid but is maintained for several weeks after spring snowmelt and occasionally after heavy rain in late spring, summer and fall.
Class 3: Seasonal Ponds and Lakes	The shallow marsh zone dominates the deepest part of the wetland with peripheral wet-meadow and low-prairie zones generally present. The central areas normally maintain water for an extended period in spring and summer but may be dry during late summer and early fall.

TABLE A4.1. Continued.

Major Classes	Description
Class 4: Semipermanent Ponds and Lakes	The deepest part of the wetland is dominated by the deep-marsh zone in addition to peripheral presence of shallow-marsh, wet-meadow and low-prairie zones. Surface water is maintained throughout the spring and summer and frequently into the fall.

TABLE A4.2. Summary of Stewart and Kantrud's (1971) classification of prairie pothole wetland cover types.

Cover Type	Description
Cover Type 1	Closed stands of emergent vegetation with open water or bare soil covering less than 5% of the wetland area.
Cover Type 2	Open water or bare soil covering 5 to 95% of the wetland area, with scattered closed or opened patches of emergent cover.
Cover Type 3	Open water or bare soil of greater than 5% of wetland area surrounded by peripheral bands of emergent cover averaging 6 feet or more in width.
Cover Type 4	Open water or bare soil covering greater than 95% of the wetland area. Marginal bands on emergent cover may be restricted to less than 6 feet in width.

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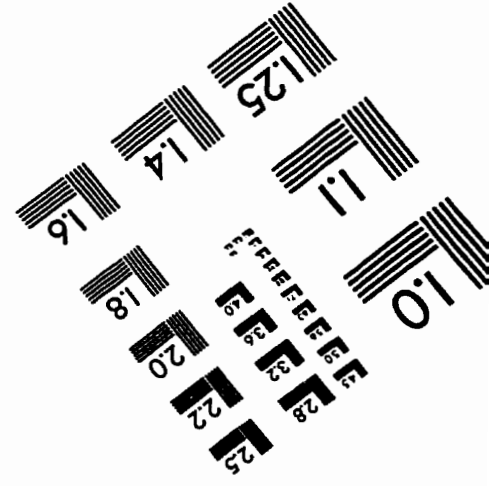
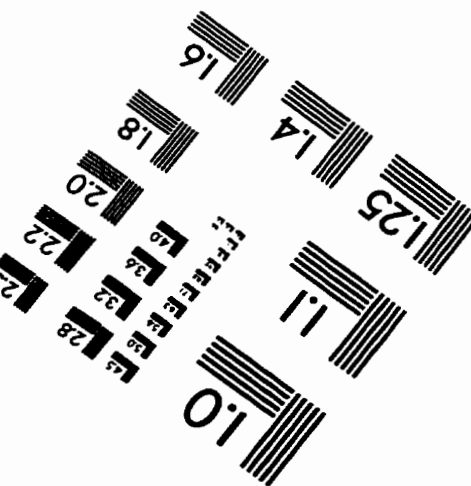
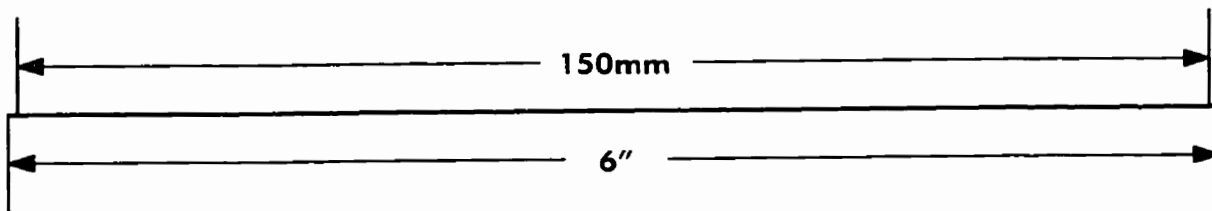
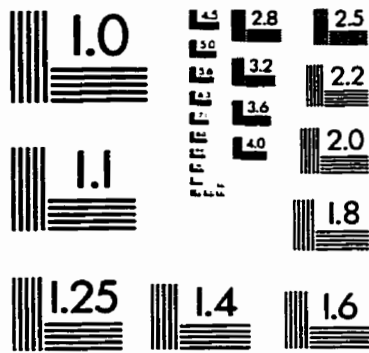
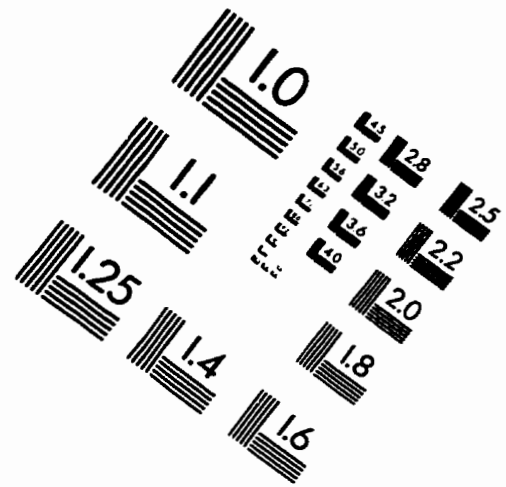
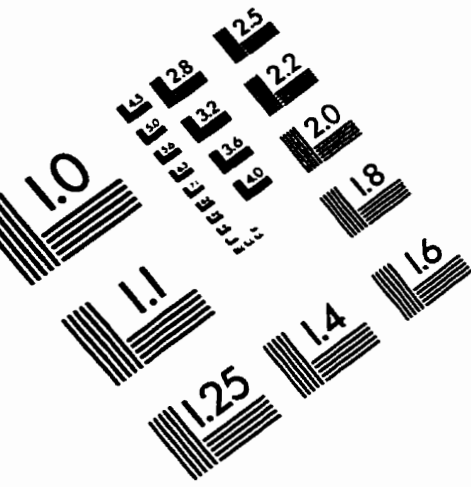
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IMAGE EVALUATION TEST TARGET (QA-3)



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