INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps. Each original is also photographed in one exposure and is included in reduced form at the back of the book.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

UMI

A Bell & Howell Information Company
300 North Zeeb Road, Ann Arbor MI 48106-1346 USA
313/761-4700 800/521-0600

Nest defence by female dabbling ducks:
life history and methodological considerations

by

Michelle A. Gunness

A thesis submitted to
the Faculty of Graduate Studies
in partial fulfillment of
the requirements for the degree of
Master of Science

Carleton University
Ottawa, Ontario

June 1998

© 1998, Michelle A. Gunness

National Library
of Canada

Acquisitions and
Bibliographic Services

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque nationale
du Canada

Acquisitions et
services bibliographiques

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence

Our file Notre référence

The author has granted a non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of this thesis in microform, paper or electronic formats.

The author retains ownership of the copyright in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

L'auteur a accordé une licence non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de cette thèse sous la forme de microfiche/film, de reproduction sur papier ou sur format électronique.

L'auteur conserve la propriété du droit d'auteur qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

0-612-36929-3

Nest defence by female dabbling ducks:
life history and methodological considerations

in partial fulfillment of the
requirements for the degree of
Master of Science.

P. J. Ventresca
Thesis Supervisor

ii

Abstract

Researchers are often unable to explain substantial variation in avian nest defence behaviour. In chapter 1, I explore this problem using female dabbling ducks, and show that unexplained variation arises for both methodological and biological reasons. Nest defence consists of several discrete behaviours, none of which covary strongly, and some of which are uncorrelated or negatively correlated. Thus, neither single variables nor composite variables will capture all of the variation in nest defence. Furthermore, both the number and frequency of human visits to duck nests affects the ducks' behaviour independent of other factors. Ducks also behaved differently depending on vegetation cover at their nests and on local predator densities.

In chapter 2, I tested the hypothesis that ducks should defend nests more intensely in wetter years because higher survival prospects in these years make ducklings more valuable. I found the opposite result, and suggest that lower costs of reproduction for parents in wetter years may increase their own survival prospects sufficient for them to favour future reproduction over current reproduction, and thus defend their nests less intensely.

Acknowledgments

I am indebted to a great many people without whom I could not have completed this project.

First and foremost, my thesis supervisor, Pat Weatherhead, has provided encouragement and been patient while I sometimes fumbled through various stages of this project. He has graciously come to my rescue more than once. Without his guidance and numerous suggestions, I would no doubt still be struggling with a project proposal.

The Natural Sciences and Engineering Research Council and Delta Waterfowl and Wetlands Research Station provided funding and logistic support. Special thanks to Dr. Frank Rohwer and Michael Hoff, without whose cooperation and assistance I would have been unable to undertake this project in its present scope. Thanks to Mike for sharing the wonder of ducks all summer, for helping me to realize that American beer isn't so bad, and for somehow finding a way to fix just about anything. Field assistants Josh Stafford, Jeb Linscome, Bill Sommerfeld, Stacey Fischer and particularly Peter Joyce and Meg Holt were always willing and helpful, while providing great company. Thanks to them all for keeping the grumbling and groaning about those tedious nest checks out of earshot. Scott Peterson and the rest of the staff of the Lonetree Wildlife Management Area provided generous support and advice on what roads were passable, among many other things. Thanks to the guys in the bunkhouse for sharing your space with all of us, and for trying to avoid running over our nests, and to Rick Severson for keeping us educated and entertained.

Bob Clark of the Canadian Wildlife Service kindly provided data and suggestions, and thanks are extended to those who collected and entered those data along the way. Drs David Currie and Mark Forbes provided helpful

criticisms and comments throughout the process, and their suggestions have encouraged me to think critically about my project. Special thanks also to Joanne Rust and Kerry Hecker for offering their time to provide editorial comments.

Gabriel Blouin-Demers, Kevin Dufour, Kelley Kissner, Chris Parent, Kent Prior and all of the folks across the hall have made the lab an enjoyable place to work and have taught me about the world outside of ducks, and about dos, don'ts, ups and downs of doing research. Special thanks to Brian Leung and Kevin Dufour for statistical conversations on my behalf, despite the fact that I wasn't always following the discussion. Kevin in particular was always willing to be interrupted for all manner of questions and advice.

I owe my remaining mental health to my husband, Calvin Martin, who always managed to have greater confidence in me than I had in myself. He has been a source of endless encouragement and patience, and has made me keep things in perspective and remember that there is life outside of school.

Table of Contents

	Page
Acceptance form.....	ii
Abstract.....	iii
Acknowledgments.....	iv
Table of Contents.....	vi
List of Tables.....	vii
List of Figures.....	ix
Chapter 1, sources of within year variation in nest defence	
Introduction.....	1
Methods.....	10
Results.....	16
Discussion.....	42
Chapter 2, sources of among year variation in nest defence	
Introduction.....	53
Methods.....	55
Results.....	57
Discussion.....	68
Literature cited.....	73

List of Tables

Table	Description	Page
1.1	Total number of nests and observations.....	17
1.2	Matrix of Spearman correlation coefficients for measures of defence behaviour at all second visits.....	19
1.3	Multiple regression analysis of the effects of incubation stage and number of previous visits on flushing distance.....	22
1.4	Simple linear regressions of the effects of incubation on flushing distance with visit number held constant and of the effects of visit number on flushing distance with incubation stage held constant.....	25
1.5	Ordinal logistic regression of the effects of incubation and visit on landing distance.....	28
1.6	Nominal logistic regression of incubation and visit effects on probability of distraction display.....	29
1.7	Nominal logistic regressions of the effects of incubation on the probability of distraction display with visit number held constant and of the effects of visit number on the probability of distraction display with incubation stage held constant.....	30
1.8	Sources of variation between females in flushing distance, determined by stepwise multiple regression.....	33
1.9	Sources of variation between blue-winged teal females in nearest landing distance.....	35
1.10	Stepwise logistic regression of sources of variation between females in distraction displays.....	37
1.11	Nominal logistic regression testing for relationship between nest defence and nesting success, by site treatment.....	39
1.12	General summary of results.....	41
2.1	Results of Analysis of Variance testing for differences in clutch initiation date, incubation stage, and number of eggs per clutch among years.....	63

2.2	Relationship between mean yearly flushing distance and number of July wetlands for early and mid-season nests vs. late season nests.	67
-----	---	----

List of Figures

Figure	Description	Page
1.1	Relationship between incubation stage and flushing distance for all third visits to blue-winged teal nests.....	24
1.2	Relationship between number of visits and flushing distance for observations at mallard nests on days 22 or 23 of incubation.....	26
1.3	Relationship between flushing distance and clutch initiation date for mallard and for gadwall.....	34
2.1	Number of wetlands on 1 May, 1 June, and 1 July at St. Denis National Wildlife Area, 1984-1997.....	58
2.2	Number of blue-winged teal, gadwall and mallard nests found at St. Denis National Wildlife Area, 1984-1992, 1994-1997.....	59
2.3	Mean yearly flushing distance in relation to number of wetlands on July 1, for blue-winged teal, gadwall and mallard.....	62
2.4	Mean yearly flushing distance of mallard in relation to mean yearly clutch initiation date.....	64

Chapter I: Sources of within year variation in nest defence

Introduction

Natural selection favours individuals that maximise the representation of their genes in the next generation. In order to maximise reproductive success over a lifetime, individuals face trade-offs between current and future reproduction. Successful future reproduction is contingent not only on the reproductive potential of the individual, but on the ability of that individual to survive the period between current and future reproductive attempts. These simple observations are the foundation for the study of parental care and parental investment. Trivers (1972) first coined the term “parental investment” to describe any physiological or behavioural investment that parents make in one offspring that increases the probability of survival of that offspring, but at a cost to the parent’s ability to invest in other offspring. Any parental behaviour that potentially increases the parent’s predation risk, or that may decrease its future reproductive success, has some cost to the parent. Nevertheless, the behaviour is only classified as investment if it increases the probability of survival of current offspring.

In birds, predation is the major cause of nest failure (Ricklefs 1969; Klett et al. 1988; Sargeant and Raveling 1992) so defending offspring from predators is one way that parents can improve the survival of their young. Nest defence is an ideal model for studying life history theory and trade-offs between future and current reproduction. The cost to the defending parent is the risk of being captured by the predator or drawing the attention of other predators, while defence presumably benefits the offspring by decreasing the probability of being discovered or captured by a potential predator. There is abundant evidence that nest defence by birds may improve the survival of dependent young (Andersson

et al. 1980; Greig-Smith 1980; Blancher and Robertson 1982; Breitwisch 1988; Weatherhead 1990; Sjöberg 1994; Wiklund 1990), although some studies have failed to find higher survival rates of more intensely defended nests (Bjerke et al. 1985; McLean et al 1986; Hobson et al. 1988; Martin and Horn 1993; Meilvang et al. 1997).

The central premise of nest defence theory is that as offspring become more valuable, or as the benefits of defence increasingly exceed the costs, the young should be defended with greater intensity. Offspring become more valuable as their survival probability increases, which generally occurs as the nesting attempt progresses (Montgomerie and Weatherhead 1988). Westmoreland (1989) summarised three major causes for a particular nesting attempt to become more valuable to the parents over time. As a given nesting attempt progresses: (1) there will be less potential for these offspring to be replaced in the same season if they die (Barash 1975); (2) the expected future benefits from this nesting attempt increase while the expected future costs decrease (Boucher 1977) and; (3) the difference between the survival probability of the parents and the young decreases, reducing the gap between reproductive potential of the offspring and reproductive potential of the parent (Andersson et al. 1980). These and other aspects of nest defence theory have been reviewed by Montgomerie and Weatherhead (1988) and Redondo (1989). Factors can influence nest defence either by affecting value of the offspring or by influencing the costs of defence. Some of the potential influences discussed by Montgomerie and Weatherhead (1988) include the age of the offspring, size of the clutch/brood, renesting potential within the current season, age and mortality rates of the parent, parental experience, and nest and predator characteristics.

The majority of studies of nest defence have produced support for the general principles of nest defence theory, but discrepancies remain between

results of different studies. For example, nest defence theory predicts that a greater number of young in the nest should lead to higher levels of nest defence. Consistent with this prediction, Robertson and Biermann (1979) found that incubating female red-winged blackbirds (*Agelaius phoeniceus*) defended experimentally reduced clutches with less intensity than experimentally enlarged clutches. Wiklund (1990) similarly found higher defence of enlarged broods than reduced broods by merlin (*Falco columbarius*) females. However, many studies incorporating naturally occurring variation in clutch size into nest defence analyses have failed to find the predicted correlations (e.g. Regelman and Curio 1983; Armstrong 1986; Redondo and Carranza 1989; Dufour and Weatherhead in press).

Nest defence theory also predicts that the amount of further investment that parents should be willing to provide for offspring, and hence the intensity with which they will defend them, should be related to the survival probability of those offspring. For many bird species, the probability of offspring surviving to fledge declines the later in the season that they are hatched (e.g. Orthmeyer and Ball 1990; Wiklund 1990; Rotella and Ratti 1992a; Tolonen and Korpimäki 1995; Dzus and Clark 1998; but see Dzubin and Gollop 1972, Savard et al. 1991). In accordance with the expectation that parents should defend offspring with greater value more intensely, several studies have found a decrease in defence of later initiated nests likely due to poorer probability of survival of those offspring (Wallin 1987; Weatherhead 1989; Wiklund 1990; Tolonen and Korpimäki 1995).

Despite extensive previous research on nest defence by birds and broad qualitative agreement between theory and observation, quantitatively the record is less positive. Most investigations of nest defence have been unable to explain much of the variation in defence behaviour. For example, Regelman and Curio (1983) investigated 16 independent variables to account for variation in great tit

(*Parus major* L.) nest defence and were still able to explain only 43 percent of the total variation in behaviour. As with many aspects of behaviour, there is substantial variation in nest defence both within the same individual at different times and between different individuals. Some degree of unpredictable variation in defence behaviour may be adaptive, as discussed by Montgomerie and Weatherhead (1988) and Winkler (1992). In addition to unexplained variation in nest defence in general, results have differed across studies of even closely related species (see below) making it still more difficult to understand the sources of this variation. My general goal in this study is to investigate several possible reasons why so much unexplained variation exists in nest defence behaviour. The difference in results between studies of avian nest defence and the large amount of unexplained variation in these studies could be due to important variables being excluded from these studies or due to variation in study methods and in the measurement of nest defence. My general objectives pertain to both of these issues. Specifically, I investigate biological factors influencing variation by assessing how a range of variables affect nest defence. Secondly, I address two methodological issues influencing the interpretation of nest defence studies. The first of these is how repeated visits to nests may cause changes in defence. The second methodological issue is to assess correlations between different measures of defence, and determine how measurement of defence may be an additional source of variation in nest defence studies.

Knight and Temple (1986a) were the first researchers to suggest that there were methodological problems with how nest defence had been studied. Many studies in the 1970's and early 1980's confirmed that nest defence increased as predicted with nesting stage, i.e. offspring age (Barash 1975; Curio 1975; Weatherhead 1979, 1982; Andersson et al. 1980; Greig-Smith 1980; Biermann and Robertson 1981; Blancher and Robertson 1982; Regelman and Curio 1983).

However, Knight and Temple (1986a) proposed that these results may be an artefact of how these studies and analyses had been conducted. They argued that most previous studies involved repeated testing of the same individuals, so that nests that were visited later in the nesting cycle had also been visited more often. The increase in response that was observed through the nesting cycle may simply have been because researchers always left nests unharmed. Thus, defending parents may have perceived their defence to have been successful, and therefore defended even more vigorously at the next encounter due to positive reinforcement. Most studies that have tested this positive reinforcement hypothesis have failed to confirm Knight and Temple's (1986a, b) results, and have found that, controlling for any effect of repeat visits, nest defence does increase with advancing nesting stage (e.g. Breitwisch 1988; Redondo and Carranza 1989; Weatherhead 1989, 1990; Westneat 1989; Westmoreland 1989; Rytkönen et al. 1990; Mallory and Weatherhead 1993; Sjöberg 1994).

Although many studies have now demonstrated that positive reinforcement is not responsible for the increase in nest defence through the nesting cycle, some of these studies have nevertheless shown that there are observer effects on nest defence. In a study of the cavity nesting common goldeneye (*Bucephala clangula*), Mallory and Weatherhead (1993) found an increase in some forms of defence with greater number of visits, but a decrease in other measures of defence. Forbes et al. (1994) found that where visit number influenced nest defence of some dabbling ducks, the direction of the relationship was opposite to that predicted by Knight and Temple (1986a). Contrary to both of these studies, Armstrong (1986) found no effect of previous visits on nest defence in female northern shovelers (*Anas clypeata*). These three studies have varied in the type of nesting habitat (nest boxes vs. ground nests) and in the variables used to score nest defence, and some have been limited by small

sample sizes (e.g. Armstrong 1986; Mallory and Weatherhead 1993). Nonetheless, it appears that, at least in waterfowl, repeatedly visiting nests can sometimes affect subsequent nest defence.

Contrary to Knight and Temple's positive reinforcement hypothesis, many other studies of the effects of revisitation on nest defence have found either no effect or a decrease in defence with more visits, as in Forbes et al. (1994). Coleman (1987) proposed an alternative explanation to Knight and Temple's (1986a) hypothesis to explain why repeated disturbance may alter nest defence. He suggested that, rather than "successful" defence leading birds to increase defence at subsequent encounters as the positive reinforcement hypothesis states, birds should only increase defence if they perceived previous defence to be unsuccessful. Since the predator returned to the nest, defence at the previous encounter was not sufficient to deter the predator from returning. Similarly, the predator may appear to be a greater threat if it returns to the nest regardless of whether eggs were left unharmed (Mallory and Weatherhead 1993). Otherwise, if the defender deemed defence at the first encounter to be "successful", they should only defend nests with the same or lower intensity on subsequent visits, to determine if lower costs can achieve the same benefit (Coleman 1987). Siderius (1993) suggested this latter hypothesis to explain why Eastern kingbirds (*Tyrannus tyrannus*) decreased nest defence with increasing visits. Birds should risk less when they face a situation that they know is not dangerous for the young. One of my specific goals is to investigate observer effects on nest defence in three different species of dabbling ducks. Repeat visits are more likely to lead to a decrease in defence in ducks rather than an increase. Experience from previous visits should indicate that the predator (observer) does not pose a significant danger to the offspring. Therefore, the benefits of defence presumably decrease but the costs do not change.

There is another potential problem with how nest defence is studied that may have general relevance to the unexplained variation in nest defence behaviour and differences in results across studies. Nest defence has generally been measured in one of two ways. Many studies have used a composite score of defence intensity, whereby the different components of nest defence are combined (e.g. Blancher and Robertson 1982; Hudson and Newborn 1990; Martin and Horn 1993; Tolonen and Korpimäki 1995; Meilvang et al. 1997). For example, a low intensity defence score might be given when the bird departs from its nest at the start of the approach by an observer, makes no alarm calls and does not attempt to draw the observer away from the nest using distraction displays. Conversely, a high score might be given when the bird flushes from its nest only when the observer has approached quite closely, and then vocalises and attempts to distract the observer. The assumption that underlies this approach to scoring nest defence is that all of the component parts covary positively. However, it is possible that some behaviours are used as alternative tactics: for example birds may vocalise or may attack the observer but they seldom do both simultaneously. If the various components of nest defence do not covary, then composite scores are likely to be ineffective at explaining much of the variation in nest defence. Other studies have used a single behaviour to quantify defence (Westneat 1989; Wiklund 1990; Forbes et al. 1994; Viñuela et al. 1995) even though nest defence usually involves several different behaviours. Again, the assumption that underlies this approach is that the different components of nest defence covary. Thus, by scoring one component of nest defence (e.g. frequency of alarm calls), it is assumed that one has essentially scored all components of nest defence.

Although the assumption of positive covariance between nest defence components underlies both approaches to quantifying nest defence, few studies

have evaluated correlations between these variables. Some indirect evidence suggests that the assumption may be correct. For example, Weatherhead (1979) showed that both alarm calls and approach distance by savannah sparrows (*Passerculus sandwichensis*) changed in a similar fashion with increasing brood age. However, other indirect evidence suggests that the assumption may be flawed. Mallory and Weatherhead (1993) found that the time it took female common goldeneyes to return to their nest after a disturbance followed a different pattern from other aspects of nest defence over the incubation period. Some studies have examined covariation between nest defence components directly. Regelman and Curio (1983) found that three of four measures of nest defence were significantly correlated in the great tit (*Parus major* L.), although these responses were still differentially sensitive to the influences of independent variables. Another specific goal of this study is to assess how different measures of nest defence are correlated, and whether the factors that influence nest defence affect all defence measures similarly.

Predation is responsible for the failure of a large proportion of dabbling duck nests (Sargeant and Raveling 1992), and is also a significant source of mortality of adult female ducks during the nesting season (Sargeant 1972; Greenwood et al. 1995). The latter is likely partially due to the fact that females provide all forms of care for young. These observations suggest that there must be strong selection pressure on female ducks to reduce nest predation while limiting risks to themselves. For these reasons, and to broaden the scope of nest defence study from its past emphasis on birds with altricial young, I study nest defence in three species of dabbling ducks: blue-winged teal (*Anas discors*), gadwall (*A. strepera*) and mallard (*A. platyrhynchos*).

Female ducks use several forms of behaviour that can be considered nest defence. I use the term “nest defence” to include any type of behaviour that may

be a risk to a female, while potentially improving the chances that her offspring will escape predation. Female ducks perform active defence behaviours, such as injury feigning displays, which are more generally termed distraction displays, that can draw a predator's attention away from the nest (e.g. Brunton 1990). Another form of nest defence by incubating ducks is to remain on the nest despite the approach of a predator. Thus, a useful measure of nest defence is to measure how close a potential predator can approach before the incubating bird first responds to the threat (usually by getting off of the nest). This is an appropriate measure of nest defence because it appears to satisfy the cost-benefit requirements of parental investment. The assumed benefit to the offspring is that as long as the cryptically coloured hen remains on the nest, the more likely it is that the nest will be undetected. However, there is a risk of the female being captured as the predator gets closer to the nest, and a greater risk of the exact nest site being revealed if the female flushes when the predator is close by. Therefore, as flushing distance decreases, the risk, and hence the defence intensity, increases.

If all measurements are equally representative of nest defence, I predict that all measurements of defence will be positively correlated (i.e. as a duck increases the risks it takes with one component of nest defence, it should also increase the risks associated with other components). Given this, those factors that are predicted to influence nest defence by ducks should influence all nest defence variables in the same manner. I predicted that nest defence would decrease with increasing visits to the nest, consistent with decreased benefits of defence. Nest defence should increase in intensity with advancing incubation stage, greater number of eggs, earlier nest initiation date and at nests poorly concealed by vegetation. The value of the offspring in the nest should be greater the older and more numerous they are, other things being equal. Ducklings from

later hatched nests have lower rates of survival (e.g. Orthmeyer and Ball 1990, Johnson et al. 1992, Dzus and Clark 1998), suggesting that late nests should be less valuable. Since increasing nest concealment presumably decreases the natural vulnerability of a nest to predation, females should defend less concealed nests with greater intensity, to compensate for their vulnerability to predation (Montgomerie and Weatherhead 1988). As well, if nest defence does function to increase survival probability of young, which is the assumed benefit, there should be a positive relationship between nest defence and hatching success of nests.

Study Area and Methods

This study was conducted in 1997 in Sheridan and Wells counties of central North Dakota, part of the most important nesting area for dabbling ducks in North America. Much of this study was done within Lonetree Wildlife Management Area, which is managed by the North Dakota Game and Fish Department. Other state-managed lands and private or federal lands that were within 20 miles of the main site and which included similar habitat were also used. The most common types of ground vegetation in this grassland habitat were alfalfa (*Medicago sativa*), sweetclover (*Melilotus* sp.), side oats gramma (*Bouteloua curtipendula*), tall and intermediate wheatgrass (*Agropyron elongatum* and *A. intermedium*) and little bluestem (*Andropogon scoparium*). Brome grass (*Bromus* sp.) was also present in some areas, with snowberry (*Symphoricarpos* sp.) being the most common woody vegetation. These areas were determined to be suitable nesting habitat for dabbling ducks, as wetlands and larger bodies of water were interspersed within grassland habitat.

This study was conducted in conjunction with a larger study investigating the effects of removing mammalian predators on duck nesting success. The main

site was a 36 square mile block of land from which mammalian predators were trapped and removed between February 1997 and June 1997. Control, or untrapped, sites were located at least 3 miles from the perimeter of the trapped lands and contained similar habitat, but predators were not managed in these areas. Common mammalian predators that were observed in this region were striped skunk (*Mephitis mephitis*), raccoon (*Procyon lotor*), red fox (*Vulpes vulpes*), coyote (*Canis latrans*), mink (*Mustela vison*) and badger (*Taxidea taxus*).

Sites were searched for nests between 0800 hours and 1400 hours beginning in early May and continuing until late June. Nests were found by driving two ATV's through fields with appropriate nesting habitat with a 30 m long chain suspended between. Ducks sitting at nests would flush as the chain went by, and nests were found by searching the immediate area from which the bird flushed. The date of nest discovery was considered the first nest encounter and was called visit number one, although no behavioural data were recorded on these visits. Nests were numbered and were each marked with a white stake approximately 10 m north of the nest, and a small orange rod 1 m south of the nest, to facilitate relocating nests at subsequent visits.

Nests of mallard, gadwall and blue-winged teal found on a given day were alternately assigned to one of two groups that would be visited either every fifth day or every tenth day, to vary the number and frequency of visits to nests. Because nest desertion is more likely when nests are disturbed during laying or early incubation (Gloutney et al. 1993), nests found during laying were not checked again until the predicted fifth day of incubation.

Although many studies of nest defence have used various live restrained or trained predators (Regelmann and Curio 1983; Curio et al. 1984; Hudson and Newborn 1990; Winkler 1991, 1992; Hakkarainen and Korpimäki 1994) or mounted model predators (Robertson and Biermann 1979; Rytkönen et al. 1990,

1995; Siderius 1993; Hatch 1997; Meilvang et al. 1997), many have simply taken advantage of the fact that birds respond to humans as potential predators (Weatherhead 1979; Andersson et al. 1980; Greig-Smith 1980; Breitwisch 1988; Brunton 1990; Mallory and Weatherhead 1993; Martin and Horn 1993; Forbes et al. 1994; Sandercock 1994; Sjöberg 1994). Several studies have found that birds that respond more strongly to humans approaching the nest have higher nest success (Andersson et al. 1980; Greig-Smith 1980; Weatherhead 1990), which suggests that the way that birds respond to humans is indicative of how they respond to other predators. Other studies have also confirmed that birds respond to humans similarly, or with even greater intensity than to model or live predators (e.g. Eckert and Weatherhead 1987; Brunton 1990; Martin and Horn 1993). Given these results, and the difficulty in placing model predators and observing responses undetected in open grassland habitats, I chose to observe the responses of ducks to human observers.

Upon each visit to a nest, an observer (either myself or an assistant) would approach the nest, slowly and on foot, from downwind. I chose to approach from downwind of the nest for several reasons. First, this procedure standardised approaches, while simultaneously avoiding the formation of trails to nests visited multiple times. Second, this approximated the direction of approach for a true mammalian predator, given that any scent from the nest would most likely be detected from downwind, leading predators to the nest. When incubating birds were on the nest, the observer measured the distance from the nest when the hen responded (hereafter called the flushing distance), and estimated the nearest landing distance after the female flushed from the nest (if she landed within sight of the observer). The observer also recorded the occurrence of distraction displays, and whether the bird vocalised, flew overhead, or was aggressive to the

observer. Where incubating females were not present, an observer returned to the nest later in the day or the next day to make behavioural observations.

At each nest visit, the number of eggs in the nest was counted and eggs were candled to estimate the current stage of incubation (Weller 1956). Date, time, estimates of temperature and wind speed and approximate distance to the nearest road were also recorded. At the first visit to a nest and on visits occurring not less than 10 days since the previous visit, vegetation characteristics at the immediate nest site were measured. To this end, a 1 m x 0.1 m board painted with a 0.05 m x 0.10 m grid of alternating red and white was staked upright at the nest (modified following Nudds 1977). The observer stood approximately 5 m away from the board, and recorded the number of squares on the board that were at least 50 percent covered by vegetation when viewed from 1 m above the ground. This was repeated at each of the four cardinal directions. The percent of the nest that was visible from above also was estimated by standing over the nest and looking straight down. Overhead cover was scored on a scale from 1 to 3 (1=76-100 % of nest visible, 2=26-75% visible, 3=0-25% visible).

Nest success was determined on the final visit to a nest. Nests that had been deserted were classed as either abandoned (eggs cold or very hot and no change in incubation stage since last visit), or depredated (usually all eggs destroyed). Nests that had hatched contained egg membranes and egg caps or, in some cases, still contained ducklings. Nest initiation date was determined by counting back from either hatching date, or from the last estimate of incubation stage if the nest had been depredated, using the average incubation stage for each species to calculate the appropriate number of days (see Afton and Paulus 1992 for average days of incubation).

Prior to data analysis, flushing distance was transformed to conform to assumptions of normality for parametric statistics ($\ln [\text{flushing distance} + 1]$; Zar

1984). Females that immediately flew out of sight of the observer after flushing from the nest were given an arbitrarily large landing distance of >150 m, since beyond this distance it was assumed that females would be at too great a distance to affect activities at the nest. Due to a highly skewed distribution (many >150 m observations), I converted nearest landing distance to an ordinal variable (1= landed <25 m from observer, 2= landed 26-75 m from observer, 3= 76-150 m from observer, 4= >150 m or out of sight of observer). Distraction displays and other responses were treated as nominal binary variables, that is, the behaviour was either observed (1) or not observed (0).

Statistical methods

All statistical analyses were performed using the statistical software JMP (SAS Institute 1994). Statistical significance was accepted at $\alpha \leq 0.05$. Unless otherwise stated, each analysis was performed for each of the three species. Where repeated analyses were performed on the same species to address the same hypothesis, sequential Bonferroni procedures were used to correct significance values (Rice 1989).

For all analyses of factors influencing flushing distance, a general linear models approach was used. Logistic regression was used in analyses of the other response variables, distraction displays and landing distance. In those cases where I suspected that several independent variables may influence the response, but few appeared to have any influence when analysed together in a multiple model, stepwise regression was used. Analysis of factors influencing defence behaviour was done in two parts; 1) testing the factors that may influence the response of a given female between different visits (within-female effects); and 2) factors that may influence differences in response between different individuals (among-female effects).

There is evidence that factors such as stage of incubation, previous encounters with the predator, nest initiation date and clutch size influence nest defence as discussed above. Although there is some evidence that natural variation in clutch size does not influence defence, other studies have confirmed that experimentally manipulated clutch or brood size influences defence and, in some cases, natural variation in clutch size influences defence (e.g. Forbes et al. 1994). Given equivocal results on this matter, I included clutch size as a predictor as well.

Since birds may alter their behaviour due to repeated disturbance, I included other factors that may cause variation in disturbance between nests. The average number of days between visits to a nest (visit frequency), and whether the nest was located near a road, were included as additional predictors. Because few nests were located close to roads, I made this a nominal variable, choosing an arbitrary distance of 150 m from roads, to differentiate nests that were presumably far enough from road traffic so that incubating females would be undisturbed by the traffic. Similarly, encounters with natural predators may influence the response of females. For this reason, I included the site treatment (mammalian predators trapped vs. control sites with no predator control) as an additional variable to account for potential differences in female behaviour due to predator density. I included vegetation characteristics at the nest site because this could influence the ability of an incubating female to detect or escape from an approaching predator. Vegetation characteristics also affect the natural susceptibility of the nest to discovery by a predator, and hence, the relative costs and benefits of defending the nest.

Prior to some analyses, responses were screened for variation due to potential confounding variables. I investigated the effects of time of day, wind and temperature prior to investigating the effects of the primary independent

variables on a female's nest defence response. I expected that these factors could potentially affect the ability of the female to detect an approaching observer, the vulnerability of the nest to exposure during her absence, or the hen's propensity to leave the nest, relative to regular incubation recesses. Other studies have found evidence that parental behaviour or defence of young can be influenced by weather and temperature (e.g. Gramza 1967; Regelmann and Curio 1983; Bures and Pavel 1997).

When investigating the relationship between nest defence and nesting success, I first tested for the potential effects of other factors that may affect the vulnerability of duck nests to predation. I included: (1) clutch initiation date since predation pressure changes through the season (Greenwood et al. 1995); (2) vegetation; (3) location near roads since habitat edges appear to be natural travelways for predators (e.g. Pasitschniak-Arts and Messier 1995); and (4) frequency of visits since the chances of changing natural vegetation characteristics or leaving human scent near the nest would be greater at nests visited more frequently.

Results

In total, 97 mallard nests, 82 gadwall nests and 174 blue-winged teal nests were found, with the number of observations at each nest varying between one and six (Table 1.1). Of these three species, only blue-winged teal ever showed aggression to an observer, and was also the most likely of any of these species to perform distraction displays (46% of blue-winged teal observations). Conversely, distraction displays were observed on only 8 of 138 visits to gadwall nests. Similarly, overhead flights and vocalisations were rarely observed in incubating gadwall females, and were only slightly more common in mallard and blue-winged teal. From this, it appears that the most important form of active defence

Table 1.1 Total number of nests and observations

	Blue-winged Teal	Gadwall	Mallard
Total number of nests	174	82	97
Nests with one observation	72	46	34
Nests with two observations	58	21	26
Nests with three observations	24	11	23
Nests with four observations	13	3	10
Nests with five observations	6	1	3
Nests with six observations	1	0	1
Total number of observations	348	138	216

by dabbling ducks is the distraction display. Many of the other potential forms of active defence that were observed were usually performed in conjunction with distraction displays (e.g. vocalisations or aggression were usually performed by birds that also gave displays). Vocalisations were given by most females that showed aggression to the observer, but were uncommon in other cases.

Correlations between the measures of defence were tested using Spearman rank correlation. Because there was more than one observation per female, and correlations are likely to be higher between observations of the same female than between observations of different females, I repeated the correlation analysis using only observations at second visits to nests, to ensure only one observation per female. The results of the analyses using second visits were qualitatively similar to the analyses using all observations, so these are presented in Table 1.2. Relationships between pairs of variables were confirmed using parametric pairwise tests appropriate to the type of variable.

With few exceptions, correlations between measures of defence were generally low (Table 1.2). Since all other types of behaviour were very uncommon in gadwall (i.e. ≤ 8 of 138 observations), I only calculated the correlation between flushing distance and landing distance (at second visits $n=82$, Spearman $\rho=0.28$, $P=0.01$). Some of the significant correlations presented are for variables with few positive observations, as discussed above. For example, in mallard, only 10 percent of observations included overhead flights, and 8 percent of observations included vocalisations. All of the correlations that were statistically significant were in the predicted direction, that is, these measures of risk-taking were positively associated. Correlations in the direction opposite to that predicted between components of nest defence were found only for overhead flights (i.e. flights were less likely to occur as some measures of defence increased in intensity), although none of the correlations was significant.

Table 1.2 Matrix of Spearman correlation coefficients for measures of defence behaviour at all second visits (Blue-winged teal n=170, Mallard n=96).

a. Blue-winged teal					
	DD ^a	LD	FD	OvrFlt	Vocal
Landing Distance (LD)	-0.17* ^b				
Flushing Distance (FD)	-0.06	0.09			
Overhead Flight (Ovrflt)	0.06	0.15	-0.001		
Vocalizations (Vocal)	0.21**	-0.20* ^b	-0.14	0.10	
Agression	0.21** ^b	-0.20* ^b	-0.21** ^b	-0.03	0.48** ^b

b. Mallard				
	DD ^a	LD	FD	OvrFlt
Landing Distance (LD)	-0.40** ^b			
Flushing Distance (FD)	-0.002	-0.03		
Overhead Flight (OvrFlt)	-0.15	0.01	-0.13	
Vocalizations	0.07	-0.23* ^b	-0.03	0.05

** P<0.01

* P<0.05

^a DD = distraction display

^b Confirmed significance at P<0.05 by sequential Bonferroni method (Rice 1989).

The only consistently significant relationships were negative correlations between landing distance and both distraction displays and vocalisations, such that birds that landed nearer the observer tended to be those that displayed and vocalised. In blue-winged teal, birds that were aggressive toward the observer were more likely to flush from closer and land nearer, and they were more likely to perform distraction displays. Aggression was the only variable that was significantly correlated with flushing distance ($P < 0.05$). This correlation occurred because aggression was only observed when birds that remained on the nest pecked at the observer's hand. Because landing distance, the occurrence of distraction displays, and flushing distance are only weakly correlated with each other, I consider each separately in subsequent analyses of nest defence. While I may have excluded some information regarding defence from further analyses by considering only three defence measures, small sample sizes of infrequent behaviours would make statistical analyses of these other variables inappropriate. Due to the nature of the three defence variables, flushing distance (transformed), nearest landing distance, and occurrence of distraction displays, (continuous, ordinal and nominal, respectively), I was unable to include them in a single multivariate analysis. Analyses for each of these response variables were therefore performed individually. While it may have been preferable to use multivariate analysis so that all of these variables could be included in one model (e.g. Stevens 1996), given that the correlations between these variables are generally weak, I expect that there will not be a great deal of information lost in analysis due to treating these variables individually.

Variation in behaviour between visits

Incubation stage and the number of previous visits were the two primary potential influences on behaviour of females visited multiple times which I

investigated. Preliminary investigation of the potential influences of wind, temperature and time of day on the nest defence responses observed (multiple regression analyses, multiple logistic regression of landing distance and distraction displays) suggested that these factors did not significantly influence flushing distance, landing distance or occurrence of distraction displays ($P > 0.05$ in all cases).

To test the effects of incubation stage and number of previous visits on nest defence behaviour, I included both variables in multiple regression models where the response variable was flushing distance, and in multiple logistic regression models for the response variables landing distance and distraction displays. However, using this method, the data violate the assumption of independent observations because there were several observations for some females. To confirm the direction and influence of each factor without the potential problem of pseudoreplication, a subset of data was extracted from the data set, such that one variable was constant within that subset of observations. For example, all second visits were extracted so that there was only one observation per female and thus no variation in visits. A simple linear regression was then used to examine the relationship between incubation and flushing distance, with independent observations and the number of visits held constant. This approach was repeated with three unique subsets of data containing observations with number of visits held constant and three unique subsets of data with incubation stage held constant.

Multiple regression analyses including all observations indicated a significant increase in flushing distance with greater number of visits in all three species (partial coefficient $P < 0.0001$ in blue-winged teal and gadwall and $P = 0.0008$ in mallard), but variation among species in the effect of incubation stage (Table 1.3). Flushing distance decreased with incubation stage in blue-

Table 1.3 Multiple regression analysis of the effects of incubation stage and number of previous visits on flushing distance.

Species	n	R ²	Model P	Source	Coefficient	F	P
Blue-winged Teal	347	0.17	<0.0001	Incubation	-0.02	19.53	<0.001
				Visits	0.26	68.98	<0.001
Gadwall	137	0.13	0.0001	Incubation	-0.01	3.50	0.06
				Visits	0.28	19.60	0.000
Mallard	216	0.07	0.0003	Incubation	-0.001	0.07	0.78
				Visits	0.15	11.67	0.001

winged teal ($P < 0.0001$), and also in gadwall, although for gadwall the relationship was only marginally significant ($P = 0.064$). Flushing distance was unrelated to incubation stage in mallard. Simple linear regression analyses (number of visits controlled) confirmed a decrease in flushing distance with advancing incubation in blue-winged teal (two of three tests; Figure 1.1), but failed to show an effect of incubation on flushing distance for gadwall or mallard (Table 1.4). Analyses testing for the effects of visit (incubation stage controlled) confirmed an increase in flushing distance with increasing number of visits to blue-winged teal nests, although results were less clear for gadwall or mallard (Table 1.4). Two of three tests indicate that flushing distance of mallards was greater with increasing number of visits (Table 1.4; Figure 1.2), but only one of three tests confirmed this effect in gadwall.

To determine which factor had the greater influence on changes in flushing distance of individual females, I used a binomial test to compare the number of birds whose response increased over time with the number of birds whose response decreased over time. Given the directions of the coefficients from the multiple regression models (an increase in flushing distance with visits, a decrease in flushing distance with incubation stage; Table 1.3), I predicted that if incubation stage had the greater effect, more birds would show a decrease in flushing distance. If the number of visits had the greater effect, more birds would show an increase in flushing distance. These binomial tests indicated that significantly more females of each of the three species increased flushing distance over time than decreased flushing distance over time (blue-winged teal, 58 of 94 birds, $P = 0.01$; gadwall, 24 of 34, $P = 0.01$; mallard, 44 of 62, $P = 0.001$). This suggests that visit number did have an effect on all three species. The fact that significantly more birds increased flushing distance, consistent with increased

Figure 1.1 Relationship between incubation stage and flushing distance ($\ln[fd+1]$ transformed) for all third visits to blue-winged teal nests ($n=105$, $r\text{-sq}=0.120$, $F=14.07$, $P=0.0003$).

Table 1.4 Simple linear regressions of the effects of incubation on flushing distance with visit number held constant and of the effects of visit number on flushing distance with incubation stage held constant. Only one observation per nest is included in each of these analyses.

Species	Test	Constant	n	r	F	P	Pa
Blue-winged teal	Inc. ^b	Second visits	169	-0.12	2.45	0.12	0.12
		Third visits	105	-0.35	14.07	0.0003	0.001
		Fourth visits	45	-0.46	11.43	0.002	0.003
	Visit ^c	7-9 days inc.	56	0.51	18.53	0.000	0.000
		14-16 days inc.	53	0.67	40.46	0.000	0.000
		18-21 days inc.	70	0.54	27.90	0.000	0.000
Gadwall	Inc.	Second visits	81	-0.22	4.07	0.05	0.14
		Third visits	34	-0.07	0.15	0.70	0.70
		Fourth visits	15	-0.327	1.53	0.24	0.48
	Visit	7-10 days inc.	19	0.317	1.84	0.19	0.19
		16-19 days inc.	16	0.43	3.14	0.10	0.20
		20-22 days inc.	20	0.55	8.03	0.01	0.03
Mallard	Inc.	Second visits	96	0.03	0.10	0.75	0.75
		Third visits	62	-0.09	0.46	0.50	1.0
		Fourth visits	37	-0.18	1.16	0.29	0.87
	Visit	12-14 days inc.	31	0.44	6.79	0.01	0.03
		18-19 days inc.	23	0.27	1.61	0.22	0.22
		22-23 days inc.	34	0.42	6.88	0.01	0.04

^a Bonferroni adjusted P values (Rice 1989). Three repeated analyses of the same test were performed for each species, so a k value of 3 was used for the Bonferroni adjustment.

^b Visit number held constant.

^c Incubation stage held constant.

Figure 1.2 Relationship between number of visits and flushing distance ($\ln(\text{flush distance} + 1)$ transformed) for observations at mallard nests on days 22 or 23 of incubation ($n=34$, $r\text{-sq}=0.17$, $F=6.88$, $P=0.0132$).

number of visits, also suggests that where incubation stage did affect flushing distance, its influence was outweighed by the influence of visit number.

Tests of the effects of both incubation stage and number of visits in an ordinal logistic regression suggest no relationship between either of these factors and landing distance for any species except mallard (partial $P=0.03$; Table 1.5). However, the potential influence of incubation stage on landing distance in mallard was not confirmed by analyses where visit number was controlled (partial $P>0.16$ for all analyses). Similarly, the simple logistic regression analyses controlling incubation stage and visit number individually for gadwall and blue-winged teal suggest no effect of either variable on landing distance (partial $P>0.16$ for all analyses except test for effect of visits in gadwall at 11-14 days of incubation, $n=21$, coefficient =2.94, $P_{\text{Bonferroni}}=0.003$; however, all other analyses not significant and multiple regression model not significant). Neither incubation stage nor number of previous visits appeared to influence landing distance in these three species of ducks.

Multiple logistic regression models suggested that blue-winged teal and mallard hens were more likely to perform distraction displays later in incubation (nominal logistic regression; partial $P=0.03$ and 0.0002 respectively; Table 1.6), and, blue-winged teal were also more likely to perform distraction displays when they had been exposed to a greater number of previous visits (partial $P=0.02$; Table 1.6). However, these relationships were not confirmed in blue-winged teal when incubation stage and visit number were controlled for and the potential influences of pseudoreplication were removed (most analyses $P>0.1$, exceptions occur only once per variable; Table 1.7). Repeated analyses of the effects of incubation in mallard, with visit number controlled and only one observation per female, suggest that there was an increased probability of distraction displays

Table 1.5 Ordinal logistic regression of the effects of incubation and visit on landing distance.

Species	n	R ²	Model P	Source	Coefficient	Wald χ^2	P
Blue-winged teal	333	0.004	0.16	Incubation	0.01	0.38	0.54
				Visits	0.14	1.43	0.23
Gadwall	135	0.002	0.70	Incubation	0.01	0.04	0.83
				Visits	0.12	0.34	0.56
Mallard	208	0.02	0.01	Incubation	0.06	4.65	0.03
				Visits	0.04	0.08	0.78

Table 1.6 Nominal logistic regression of incubation and visit effects on probability of distraction display. Test is for probability of no display (class 0).

Species	n	R ²	Model P	Source	Parameter	Wald χ^2	P
Blue-winged Teal	348	0.04	0.000	Incubation	-0.05	4.98	0.03
				Visits	-0.29	5.10	0.02
Mallard	216	0.08	0.000	Incubation	-0.14	13.10	0.0002
				Visits	0.25	1.70	0.19

Table 1.7 Nominal logistic regressions of the effects of incubation on probability of distraction display with visit number held constant and of the effects of visit number on probability of distraction display with incubation stage held constant. Only one observation per nest is included in each of these analyses.

Species	Test	Constant	n	R ²	Parameter	χ^2	P	P ^a
Blue-winged teal	Inc. ^b	Second visits	170	0.001	-0.01	0.12	0.73	0.73
		Third visits	105	0.05	-0.10	6.71	0.01	0.04
		Fourth visits	44	0.03	-0.10	2.02	0.16	0.33
	Visit ^c	7-9 days inc.	56	0.02	0.95	1.47	0.26	0.51
Mallard		14-16 days inc.	53	0.001	-0.08	0.05	0.82	0.82
		18-21 days inc.	68	0.07	-0.55	6.27	0.02	0.05
		Second visits	96	0.07	-0.11	6.38	0.01	0.04
	Inc.	Third visits	62	0.09	-0.18	4.82	0.04	0.09
		Fourth visits	37	0.10	-0.23	4.29	0.07	0.07
		12-14 days inc.	31	0.18	11.38	3.49	0.95	0.95
Visit		18-19 days inc.	23	0.06	-0.99	0.86	0.39	0.78
		22-23 days inc.	34	0.08	0.71	3.15	0.10	0.30

^a Bonferroni adjusted P values (Rice 1989). Three repeated analyses of the same test were performed for each species, so a k value of 3 was used for the Bonferroni adjustment.

^b Visit number held constant.

^c Incubation stage held constant.

later in incubation ($P=0.05$ at second visits, $P<0.1$ and in the same direction with smaller sample size at third and fourth visits; Table 1.7).

Factors influencing differences in behaviour among individuals

To test the factors responsible for differences in behaviour between individual birds, it was necessary to create a single score for each response variable per female. To determine a score that describes the variation in the flushing distance of each female, accounting for effects of number of visits and incubation stage, the residuals of the regression analyses of visit number and incubation stage on flushing distance for all visits to all nests were used from the analyses described above. Where both variables had a significant effect on flushing distance, the residuals from the multiple regression were used (i.e. blue-winged teal). Where only one of these variables influenced flushing distance, the residuals of the simple linear regression of that variable were used. I calculated the mean of these residuals for a given female to find a single score for that female. This score gives a measure of her average deviation in flushing distance relative to the population. For the categorical variable landing distance, I calculated the median score for each female. For the nominal variable, distraction displays, I assigned females who gave distraction displays on at least one occasion a score of 1, and females who never gave distraction displays a score of 0.

Some of the variables considered in these analyses may have little influence on behaviour. However, by including variables that do not influence the response in a multiple regression model, not only are the degrees of freedom affected, but the test statistic for the estimates of the other variables are reduced, making it more difficult to detect a significant result (Berry and Feldman 1985). Because of this reduced power with extraneous variables included in the model, I

used a stepwise regression to determine those potential predictor variables that were responsible for the differences in nest defence behaviour between individual ducks (Zar 1984). The initial predictors used were site (predator removal sites or control areas), clutch size, clutch initiation date, frequency of visits to the nest, mean vegetation density at the nest, median overhead visibility of the nest and whether the nest was located within 150 metres of a road. The responses landing distance and distraction displays were analysed using stepwise multiple logistic regression.

Five of the seven variables investigated contributed significantly to variation in flushing distance of blue-winged teal individuals (Table 1.8). Flushing distance decreased (defence increased) with increasing clutch size, overhead vegetation cover, horizontal vegetation density, and frequency of visits, and was significantly lower for females nesting on control sites versus those nesting in the area where predator removal had taken place (Table 1.8). Neither site nor clutch size affected flushing distance of gadwall or mallard. Flushing distance did decrease with increasing clutch initiation date for mallards, although the reverse was the case in gadwall (Table 1.8; Figure 1.3). Flushing distance decreased with an increase in horizontal vegetation density in gadwall, similar to blue-winged teal, but vegetation did not affect flushing distance of mallard (Table 1.8). Frequency of visits also affected gadwall similarly to blue-winged teal in that birds flushed from farther away with more frequent visits.

There was little effect of any of the predictor variables on the nearest landing distance of ducks. Blue-winged teal nesting on the control sites were more likely to land near the nest after flushing than those on the predator removal sites (partial coefficient $P=0.04$; Table 1.9), and also were more likely to land nearer when visits were less frequent (partial coefficient $P=0.06$; Table 1.9). There was no evidence of any of the selected predictor variables influencing

Table 1.8 Sources of variation between females in flushing distance, determined by stepwise multiple regression. Site differentiates nests in areas where there was no predator removal (c) vs. nests in areas with mammalian predators removed (t). Overhead vegetation contained three classes of increasing vegetation cover over the nest. Continuous variables were clutch initiation date (CID), clutch size (CS), average days between visits (DBV) and horizontal vegetation density (Vegdens).

Species	n	R ²	Model P	Source	df	Coeff.	t ratio	P
Blue-winged teal	170	0.24	0.000	Site(c-t) ^a	1	-0.13	-3.88	0.0002
				CS	1	-0.06	-2.01	0.05
				DBV	1	-0.03	-3.56	0.001
				Vegdens	1	-0.04	-2.38	0.02
				Ovrhd(2) ^b	1	-0.16	-2.00	0.05
Gadwall	79	0.15	0.01	Ovrhd(3)	1	-0.13	-1.72	0.09
				CID	1	0.02	2.98	0.004
				DBV	1	-0.04	-2.02	0.05
				Vegdens	1	-0.04	-2.10	0.04
				CID	1	-0.01	-3.18	0.002
Mallard	97	0.10	0.02	CID	1	-0.01	-3.18	0.002

^a Negative parameter indicates subtract from mean if site=c, add to mean if site=t.

^b Overhead(2) tests the effect of increasing from level 1 to level 2 of overhead cover. Overhead(3) tests for the effect of increasing from level 2 to level 3 of overhead cover.

Figure 1.3 Relationship between flushing distance ($\ln[\text{flush distance} + 1]$ transformed) and clutch initiation date for mallard ($n=97$, $r\text{-sq}=0.096$, $F=10.10$, $P=0.002$) and for gadwall ($n=82$, $r\text{-sq}=0.073$, $F=6.32$, $P=0.014$). Mallard initiation dates range from 111-167 (Julian date), and gadwall range from 135-171. For comparison, blue-winged teal clutch initiation dates range between 125 and 168.

Table 1.9 Sources of variation between blue-winged teal females in nearest landing distance. Stepwise regression did not indicate that any of the predictor variables had a significant effect on landing distance of gadwall or mallard (all partial coeff $P > 0.05$).

n	R ²	Model P	Source	df	Coefficient	χ^2	P
174	0.02	0.04	Site(c-t) ^a	1	0.30	4.10	0.04
			Cid	1	-0.03	2.87	0.09
			DBV	1	0.07	3.65	0.06

^a Since coefficient is positive, add if site = 'c', subtract if site = 't', i.e. there is a higher probability of near landing distance if site = 'c', lower if site = 't'.

landing distance of gadwall or mallard (all partial coefficients $P > 0.10$, no variables in stepwise model).

Distraction displays were more common in both mallard and teal on predator removal sites than on control sites (partial coefficient $P = 0.02$ and 0.04 respectively, Table 1.10). Blue-winged teal showed a trend suggesting that birds that had higher vegetation density at the nest were more likely to perform distraction displays ($P = 0.08$, Table 1.10). As well, mallards that had been visited at shorter intervals were more likely to perform distraction displays. This last result is counter to the prediction and to all other visit effects, where defence decreased with greater number of visits, or more frequent visits. Because of this, I investigated this effect further since another factor that influenced the probability of distraction displays in mallard was the stage of incubation (Tables 1.6, 1.7). Although incubation stage influenced the probability of distraction displays in mallard, I was unable to factor this relationship into the variable representing distraction displays when calculating a single score per female. I simply classified females into those that displayed at least once and those that did not display at all, without including differences in incubation stage. However, simple linear regression between visit frequency and mean incubation stage indicated that nests that were visited at shorter intervals also tended to be those late in incubation, when distraction displays were more probable ($n = 97$, $r^2 = 0.051$, $F = 5.11$, $P = 0.026$). Because of this pattern, I repeated the stepwise logistic regression presented in Table 1.10, including mean incubation stage per nest as an additional variable. The results were similar, except that mean incubation stage replaced visit interval in the final model (partial coefficient of mean incubation $\chi^2 = 9.63$, $P = 0.002$). This suggests that the increased probability of distraction display at nests with more frequent visits may have been due to the fact that these nests tended to have a later mean incubation stage.

Table 1.10 Stepwise logistic regression of sources of variation between females in distraction displays. Test is for probability of no display vs. display.

Species	n	R ²	Model P	Source	df	Coeff.	χ^2	P
Blue-winged teal	170	0.03	0.03	Site(c-t) ^a	1	0.32	4.19	0.04
				Vegdens	1	0.13	3.14	0.08
Mallard	97	0.10	0.003	Site(c-t) ^a	1	0.80	5.62	0.02
				DBV	1	0.20	4.02	0.05

^a Since coefficient is positive, probability of *no display* is higher for control sites than for site where predators had been removed, or conversely, the probability of display was higher on the site with predator removal than on the control sites.

Nest defence and nesting success

Nest success was a binary variable, where nests that hatched successfully were given a score of 1, and nests that had been depredated or abandoned were given a score of 0. Given that very few nests were abandoned in this study (10 of 353 nests), it was not possible to include abandoned nests as a separate group. Since the probability of nest success was largely related to treatment within the predator removal experiment (43% Mayfield nest success on predator removal sites versus 9% on control sites; Mayfield calculations following Johnson (1979)), these analyses were done separately by site. I used multiple logistic regression for all of these analyses, but first tested for the effects of other variables that I believed could influence nesting success. These included clutch initiation date, frequency of visits, vegetation at the nest, and whether the nest was located near a road. Any of these variables that showed a significant effect on nesting success were included in the multiple regression model, with the nest defence variables as the independent variables and nest success as the dependent variable.

The only potentially confounding variables that influenced nesting success in this study were clutch initiation date of gadwall on predator trapped sites ($n=36$, full model $P=0.26$, partial coefficient $=0.12$, $P_{\text{coeff.}}=0.047$), and frequency of visits to mallard nests on control sites ($n=23$, full model $P=0.005$, partial coefficient $=1.36$, $P_{\text{coeff.}}=0.044$). Each of these variables were included as additional predictors in the appropriate analyses testing the relationship between nest defence and nesting success.

The only defence variable that had any significant relationship with success of blue-winged teal nests was landing distance (Table 1.11). There was a statistically significant difference suggesting that blue-winged teal nesting on control (no predator removal) areas that landed in category 2 (25-75 m from observer) were less likely to have successful nests than those that landed in

Table 1.11 Nominal logistic regression testing for relationship between nest defence and nesting success, by site treatment. Tests probability of a nest being unsuccessful (unsuccessful=0 vs. successful=1). Nest defence measures included are flushing distance, nearest landing distance (ordinal, 4 classes) and occurrence of distraction displays (nominal, 2 classes).

a. Blue-winged teal								
Model	n	R ²	Model P	Source	df	Coeff	χ ²	P
Trapped	93	0.07	0.32	Flush	1	0.44	0.39	0.53
				Land(2) ^a	1	-1.40	3.31	0.07
				Land(3)	1	-0.29	0.06	0.81
				Land(4)	1	1.23	1.00	0.32
				Display	1	0.34	1.23	0.27
Control	80	0.05	0.40	Flush	1	0.25	0.22	0.64
				Land(2) ^a	1	1.16	4.17	0.04
				Land(3)	1	-0.50	0.52	0.47
				Land(4)	1	-0.36	0.15	0.69
				Display	1	0.03	0.01	0.91

b. Gadwall								
Model	n	R ²	Model P	Source	df	Coeff	χ ²	P
Trapped	38	0.12	0.43	Flush	1	1.81	2.61	0.11
				Land(2) ^a	1	-0.86	0.19	0.66
				Land(3)	1	-0.35	0.04	0.84
				Land(4)	1	0.49	0.23	0.63
				CID ^b	1	0.03	0.42	0.52
Control	43	0.15	0.12	Flush	1	-2.45	5.35	0.02
				Land(2) ^a	1	-0.05	0.00	0.97
				Land(3)	1	0.77	0.41	0.52
				Land(4)	1	0.73	0.59	0.44

c. Mallard

Model	n	R ²	Model P	Source	df	Coeff	χ^2	P
Trapped	74	0.09	0.19	Flush	1	1.52	4.27	0.04
				Land(2) ^a	1	-0.99	0.60	0.44
				Land(3)	1	0.30	0.11	0.74
				Land(4)	1	-0.05	0.00	0.95
				Display	1	0.37	1.06	0.30
Control	22	0.51	0.02	Flush	1	0.25	0.03	0.87
				Land(2) ^a	1	10.21	0.00	0.98
				Land(3)	1	-13.07	0.00	0.96
				Land(4)	1	14.35	0.00	0.96
				Display	1	5.65	0.00	0.96
				DBV ^b	1	0.70	3.04	0.08

^a Landing distance effects are measured as effect of a change in levels. Therefore 'Land(2)' measures the effect of a change in landing distance from level 1 to level 2, 'Land(3)' measures the effect of a change in landing distance from level 2 to level 3 and 'Land(4)' measures the effect of a change in landing distance from level 3 to level 4.

^b Variables that were statistically significant in the preliminary analysis of factors influencing nesting success are included as additional variables in this analysis to account for variation in nesting success due to these factors. CID represents clutch initiation date and DBV represents average days between visits, both continuous variables.

Table 1.12 General summary of results

Methodological issues

- nest defence decreased with increasing number and frequency of visits to nests
- aspects of defence were weakly correlated if at all
- aspects of defence did not vary simultaneously, in some cases the same factor lead to an apparent increase in one form of defence, while leading to a decrease in another form of defence

Life history issues

- ducks defended offspring of higher value with greater intensity
- vegetation density influenced nest defence of female ducks such that flushing distance was closer in more dense vegetation, and probability of distraction displays was higher at nests in less dense vegetation
- relative density of mammalian predators influenced nest defence such that the frequency of distraction displays was higher on the site where mammalian predators were trapped than on the sites with unmanipulated predator populations, and birds flushed from farther on the trapped site than on the control site

category 1 (<25 m from the observer) (partial $P=0.04$; Table 1.11). However, there was a non-significant trend in the opposite direction for birds nesting on the predator removal sites (partial $P=0.07$; Table 1.11). The only significant relationship between nest defence and nesting success in gadwall was on the control sites, where nests that were successful tended to have greater flushing distances (partial $P=0.02$; Table 1.11). For mallard nests, there was also a relationship between flushing distance and nesting success, but in this case it was on the predator removal sites and in the opposite direction, such that females with nests that hatched successfully tended to have flushed at shorter distances (partial $P=0.04$; Table 1.11).

The general results presented above are summarised in Table 1.12.

Discussion

Biological factors affecting nest defence

In general, my results suggest that female dabbling ducks respond to observers approaching the nest as predicted by nest defence theory. As measures of offspring value increased, such as clutch size and incubation stage, so did the intensity of nest defence. Birds at nests that were better concealed by vegetation, and hence, presumably less vulnerable to predation, were less likely to perform distraction displays than birds at nests that were in more open vegetation. Also, nests that were initiated later in the season were defended less than earlier nests. However, neither the direction of the relationships nor the amount of influence each variable had were the same for all measures of defence, nor for all species.

One of the most unexpected influences on nest defence is that ducks on the predator removal sites responded differently from ducks on the unmanipulated sites. The removal of mammalian predators began only a few months prior to the 1997 nesting season, and therefore the fact that responses

differed between sites suggests that female ducks somehow assess the predator population in the nesting area and adjust their behaviour accordingly. Other studies have suggested that birds use different defence tactics depending upon the type of predator (e.g. Brunton 1990, Winkler 1992, Dale et al. 1996), but only Hudson and Newborn (1990) have included any consideration of how predation pressure may influence defence. The fact that close to 200 mammalian predators were removed from the 36 square mile trapping area (M. Hoff, unpublished data), and that nesting success was much higher, suggests that mammalian predator densities were significantly lower in this area than in nearby areas that were not trapped. The predator community was altered, such that avian predation may have been a more important source of predation on the trapped areas than on the other sites.

Both mallard and blue-winged teal were more likely to perform distraction displays on the trapped sites than on the unmanipulated sites. Sonerud (1988) suggested that the effectiveness of nest defence behaviour, particularly distraction displays, may be related to predator experience. Predators who have encountered displaying birds before and have found the offspring being defended may in future encounters use defence behaviour as a cue to perform an area concentrated search for young, ignoring the adult entirely. Distraction displays could then be less effective in an area of higher predator density than in an area of lower predator density. Regardless of the cause for the difference between sites, the result implies that the predator community, and predator densities, may have a significant influence on nest defence behaviour in birds.

Observer effects on nest defence

Female dabbling ducks altered their nest defence behaviour in response to repeated visits to the nest. However, this change in response was not due to “positive reinforcement” of apparently effective behaviour, as suggested by Knight and Temple (1986a). Rather, for all three species, nest defence (measured by flushing distance) decreased not only as nests were visited more often, but also at nests visited at shorter intervals. In another study, Forbes et al. (1994) found similar trends for number of visits in female ducks, but it is interesting to note the additional effect of frequency of visits. Several studies have investigated how the number of visits to a nest influences defence, but my results suggest that there are additional influences of observer visits on nest defence.

The fact that defence decreased, rather than increased, with greater and more frequent visits agrees with Coleman’s (1987) suggestion that if nest contents are left unharmed, parents may be inclined to defend less intensely on subsequent visits. However, most research investigating visit effects in passerines suggests either no effect of visits or an increase in defence (Curio et al. 1984; Knight and Temple 1986b; Breitwisch 1988; Redondo and Carranza 1989; Westmoreland 1989; Rytönen et al. 1990; but see Siderius 1993, Rytönen and Soppela 1995). Evidence in other precocial birds similarly has found no effect of repeated visits, counter to this trend in ducks (Martin and Horn 1993; Sjöberg 1994). One major difference between ducks and many of these other taxa is that offspring are defended only by the female in ducks. As well, many altricial birds use aerial displays such as mobbing or diving and striking at predators in defence of their nests. More aggressive behaviour involving close contact with the predator may better inform the defending birds of the risk to themselves, in addition to the risk to the nest. If the predator appears to pose little threat to the defending parents, such that they remain unharmed, they may be more likely to

increase defence. However, through repeated visits to nests, ducks have learned that the predator is less of a threat to the nest, but they have not learned of the risk to themselves. Rytkönen and Soppela (1995) found that willow tits (*Parus montanus*) that were more familiar with a raptor near the nest defended less than birds that were not. They suggested that this was because this predator did not harm the nest, but still had the potential to harm the parent. Similarly, when an incubating hen faces a situation that is apparently not dangerous for the young, the benefits of defence are decreased, yet the potential costs may still be high, resulting in females risking less with repeated encounters.

Flushing distance was the only defence variable that was significantly influenced by visit effects. Blue-winged teal that were visited at shorter intervals also tended to land farther from the observer, but landing distance was not influenced by visits in either gadwall or mallard. This suggests that only some types of behaviour are altered by repeated exposure to predators. Again, this may provide some explanation for disagreement on the issue of the effects of repeated visits on nest defence (e.g. Knight and Temple 1986a, b, versus Westmoreland 1989, Rytkönen et al. 1990, versus Siderius 1993, Forbes et al. 1994). In ducks, active defence, that which is presumed to be more risky, is unrelated to the number of visits, but a more passive form of defence, flushing distance, is reduced in intensity influenced by visits. Factors relating to offspring value may outweigh any change in behaviour due to familiarity with the predator for riskier types of behaviour.

Practical implications for quantifying nest defence

Overall, the measures of defence behaviour observed in this study appear to describe unique aspects of defence. Most of the variables that were highly correlated with others were those that were uncommon and were probably

riskier behaviours, or were associated with risky behaviours. Even where correlations were statistically significant, the correlation coefficients were not high, the largest being that between aggression and vocalisations in blue-winged teal ($r=0.48$, Table 1.2). Low correlations between measures of defence may mean that these variables describe independent aspects of defence. However, when the incidence of the responses are also very low, this may indicate that these measures are only representative of the extremes within the population, or are simply unreliable measures of defence. For example, birds that showed aggression to the observer almost always vocalised, but otherwise the frequency of vocalisations was quite low and may serve some other purpose, such as to alert mates. On some occasions females were joined by males while in flight or on nearby wetlands after calling (pers. obs.). Since most incubating females would have been deserted by their mates at the time that the observations were made, the relative rarity of this behaviour could be explained if its purpose is simply to call mates. The low variation in the types of behaviour observed may be a reflection of low risk taking in this group of birds in general, in that most birds perform very few types of defence behaviour. In the case of dabbling ducks, I believe that these behaviours that were rarely observed do not constitute good measures of defence.

Apart from the defence variables with few observations, the most consistent correlation between measures of defence was that birds that performed distraction displays tended to land nearer to the observer ($r=-0.17$ in blue-winged teal, $r=-0.40$ in mallard; Table 1.2). One simple explanation is that if the function of distraction displays is to try to lead predators away from the nest, birds that display may be more likely to land nearer to the nest simply to encourage the predator to follow. Otherwise, birds that are willing to perform distraction displays may be those that are willing to take greater risks, and

therefore, were more likely to land closer. However, flushing distance would presumably also be correlated with distraction displays, if this were the sole explanation. Landing near to a predator involves a measure of risk in terms of remaining more vulnerable to a predator, as well as potentially indicating a willingness to defend or distract the predator further. Yet, relative to the risk of performing distraction displays, there may not be additional risk associated with landing near. Landing distance may be a more meaningful estimate of risk taking for birds that did not display than for those that did. However, landing distance was influenced by few variables that were used to indicate offspring value, hence it is likely a poor measure of risk-taking in dabbling ducks. In other birds, it has been used among other variables to measure nest defence (e.g. Winkler 1991, Mallory et al. 1993, Mallory et al. in press, Rytkönen et al. 1995). In this study, it is possible that I simply used too coarse of a scale by which to measure landing distance. Regardless, landing distance does not appear to be an important component of nest defence in dabbling ducks. Including variables that are not strongly representative of defence introduces additional variation into the measurement of defence intensity, yet apparently not all types of behaviour that satisfy the cost-benefit requirements of nest defence are adequate measures of defence.

Since correlations among nest defence measurements were low, these measures of defence may be indicative of alternative tactics used by ducks or, more likely, the importance of each type of risk-taking may vary relative to other behaviours. Although different variables may measure risk-taking, they are not necessarily correlated. A bird that will display may flush sooner and then concentrate on distracting the predator away from the nest. Measures of risk-taking do not necessarily vary in the same direction, nor are all measures influenced equally by the same factors. For example, repeat visits to a nest

influenced flushing distance, but not distraction displays. Distraction displays are probably the most costly of the three variables considered in these analyses, in terms of requiring active postures, and hence, some degree of energy expenditure, as well as potentially exposing the female to predation. Therefore, it may be expected that only those independent variables that have the largest influence on offspring value would influence this type of behaviour, whereas, less critical factors may influence less costly behaviour. Distraction displays were measured as a binary variable, distraction display or no display. Conversely, the types of defence behaviour that can be described by a continuous response can be altered gradually, rather than requiring a response that is only present or absent. Accordingly, continuous variables that are subject to greater variation, such as flushing distance, may be expected to be influenced by a larger range of independent variables.

In some cases different aspects of defence were influenced by the same factor, but in opposite directions, one measure of defence increasing, with another decreasing. Where this was the case, the variables were not negatively correlated, suggesting that these differences were related to the particular situation or predictor, and were not due to consistent relationships between variables. For example, when measured by distraction displays, defence was greater on trapped sites, but when measured by flushing distance, defence was lower on trapped sites, since birds flushed from farther away. Similarly, when measured by distraction displays, defence was greater at poorly concealed nests; however, when defence was measured by flushing distance, it was lower at poorly concealed nests. These apparently opposing responses may be reconciled by considering the way that different aspects of defence function to protect the nest. As measures of risk taking, it would appear that they should vary together. However, considering that flushing distance acts to increase crypticity of the

nest, but distraction displays act to distract a predator once it is near the nest, there may be situations where the nest may not be very cryptic in any case. Accordingly, remaining on the nest beyond some critical distance is not beneficial. The female may then flush sooner but perform distraction displays. Interactions between variables, or the effectiveness of different aspects of defence in a given situation, may cause opposing responses to the same predictor.

Thus far, I have only discussed *sources* of variation in nest defence, and have not attempted to determine what proportion of variation in nest defence I can explain using the factors that I examined. In this study, it is difficult to approach the problem of describing variation in defence, for the same reason that I suggest that it may have been problematic in past studies. Nest defence is a complex suite of behaviours. In addition, some variables that seem to satisfy the cost-benefit requirements of nest defence may not actually describe defence well, as was the case for landing distance in this study. Landing distance has the necessary trade-offs of nest defence behaviour, yet it was not influenced by most factors that contributed to other aspects of defence. To explain variation, defence variables must necessarily be combined in some way. Because my nest defence measures were on different scales (continuous and nominal) they could not be combined in a multivariate analysis appropriately. However, combining these variables somehow into a composite score would necessarily leave variation unexplained by excluding information about each variable. Particularly considering that some predictor variables influenced different aspects of defence in different directions, it is possible that these relationships would be undetectable, or only partially explained, by forming a composite measure of defence. In some cases, a composite defence score may increase variation in defence.

Implications for unexplained variation in nest defence research

It appears that the way in which defence is measured may lead to increased variation in defence. Correlations among components of defence may be weak, as in this study. When variables with low correlations are used to create a composite score, or when a single variable is chosen to represent variation in nest defence, this score may not be an accurate representation of defence intensity. Regelman and Curio (1983) found that even highly correlated measures of defence were not similarly influenced by independent variables. Choosing a single measure of nest defence or combining measurements into a composite score necessitates the loss of some information about defence. However, when correlations between those variables are also weak, and they are not all influenced in similar ways by independent variables, there will be a great deal more variation in the measure of defence which may make it more difficult to detect relationships. Furthermore, additional noise is introduced into the measurement of defence when aspects of behaviour that are assumed to be representative of defence, but are not actually influenced by the same factors, are included in the measurement. Nest defence is inherently difficult to measure and has a great deal of unpredictable variation, conditions which probably account for a large amount of unexplained variation in nest defence studies. Rather than creating a composite score, multivariate analysis which allows variables to be analysed together should be a more accurate way to account for correlations among variables, provided that aspects of defence are measured in such a way as to utilise this type of analysis. The fact that each study, and those involving different organisms, often have different methods for quantifying defence could create a great deal of variation in results among studies, and may be responsible for some apparently inconsistent results across studies.

As well as large variation in nest defence results due to types of measurement, there are other additional components of variation that have been documented in this study. Although observer effects have been investigated in several studies, the number of visits has been the only type of observer effect that has been evaluated. Here I found that the frequency with which a nest was visited also contributed to differences in behaviour between nests. In addition, not all aspects of defence in this study were influenced by observer effects. The differences in the relationships between visits to nests and changes in response may be due in part to measurement differences, as well as to nest site, predator characteristics and other aspects of parental investment.

In ducks, the change in response due to repeated visits may have more wide ranging implications than interpreting nest defence studies, since waterfowl are studied intensively by humans, and often in relation to nesting success. If the change in response to humans influences a duck's response to other predators, the effectiveness of natural nest defence responses and hence predation rates, could then be affected in specific study areas. It is not possible to assess this effect using these data, particularly given the many potential influences of other habitat and location variables on nest success, but further study may be valuable.

The fact that female ducks responded differently on trapped sites than on sites without predator removal suggests that some degree of variation in behaviour may be related to the local predator populations or predator densities. This would have particular implications in comparing between studies, or within studies that span more than one season, where predator populations may change. Other researchers have found that birds use different types of defence, and that different aspects of defence have different effectiveness against different types of predators (Brunton 1990; Winkler 1992; Dale et al. 1996). If birds are able

to assess the composition of the predator community, and the common types of threats, their general patterns of defence behaviour may be altered as well.

Where predator densities are higher, a larger amount of the predator population may be experienced, and hence more effective at finding nests that are being defended (Sonerud 1988). This may also lead to different defence tactics relative to predation pressure. Accordingly, the predator community, or predator densities, may also be responsible for variation in nest defence within and across studies.

To summarise, ducks generally defended their nests in patterns consistent with nest defence theory. However, additional variation may exist due to various observer effects on defence and in relation to the predator community in the areas of study. These factors may be partially responsible for inconsistent results between other studies of nest defence behaviour. In addition, studies of nest defence have used various ways of measuring defence, without always evaluating the correlations and interactions between predictors and different aspects of defence. Problems associated with using composite defence scores include introducing additional variation into the measurement by incorporating inaccurate measures of defence, excluding aspects of variation in defence by gaining only partial information about each aspect of defence, and the potential that relationships may be undetected due to different effects of predictors on various aspects of defence. However, using other methods to measure defence, or a combination of variables to determine which influence defence, prevents the researcher from determining specifically how much variation is accounted for by the factors that they study.

Chapter II: Sources of among year variation in nest defence

Introduction

Nest defence is one way that female ducks invest in their offspring. The cost of defence is an increased risk of predation on the female (e.g. Brunton 1986), but there is also the benefit of increased survival probability of the offspring (e.g. Weatherhead 1990; Wiklund 1990; Sjöberg 1994). The major premise of nest defence theory is that parents should balance the costs and benefits of defending their offspring, so that the parents only accept more risk to themselves when defending offspring that are more valuable (Montgomerie and Weatherhead 1988). Therefore, anything that can be perceived by a female duck as increasing the probability of survival of her young (i.e. increasing the value of those offspring) should prompt her to defend more intensely. The survival probability of ducklings in the prairies is related to wetland conditions, with survival being higher in wetter years (Leitch and Kaminski 1985; Johnson et al. 1992; Rotella and Ratti 1992a; Mauser et al. 1994). If female ducks use wetland conditions as a cue to offspring value, nest defence should vary among years accordingly. My goal in this chapter is to assess annual variation in nest defence behaviour of several species of prairie nesting ducks in relation to annual variation in wetland abundance.

Wetland abundance affects duckling survival in several ways, beginning before the eggs hatch and continuing until well after fledging. Nesting success tends to be higher in wetter years and in areas with more wetlands (references in Johnson et al. 1992). After broods are hatched, they must move overland to wetlands with appropriate feeding areas. During these overland movements, ducklings are more vulnerable to predation, and have lower rates of survival the farther they move (Ball et al. 1975; Rotella and Ratti 1992b; Sedingner 1992;

Leonard et al. 1996; but see Dzus and Clark 1997, Talent et al. 1983). When wetland density is lower, broods must move greater distances (Rotella and Ratti 1992b). With less available feeding habitat, the density of broods and competition for food will be higher on wetlands that are available. Patterns of decreased habitat availability and concentration of prey likely lead to concentration of nest and brood predators as well (e.g. Johnson and Sargeant 1977), thereby exacerbating predation effects. In accordance with these potential detrimental effects of brood density, there is evidence that duckling survival is lower when brood density is higher (Savard et al. 1991; Johnson et al. 1992). Higher densities of suitable habitats would reduce the necessity for long overland movements, potentially lowering exposure to predation, and would lead to greater dispersion of broods and possibly predators.

Wetland conditions may also influence post-fledging survival of ducklings. Developing ducklings require substantial protein intake, in the form of aquatic invertebrates, to maintain the high growth rates required for rapid maturation (Sedinger 1992; Baldassarre and Bolen 1994). Younger birds are known to have lower survival rates through migration (Johnson et al. 1992), and further, birds with poor body condition in the fall experience higher probability of hunting mortality (Greenwood et al. 1986; Dufour et al. 1993). If food availability limits duckling growth rates, young of the year are more likely to be in poorer condition at the onset of fall migration, and may be even further susceptible to mortality due to hunting or during migration.

Females are known to move to other regions or to forego nesting altogether in response to drought and reduced wetland density in breeding areas (e.g. Smith 1969; Smith 1970; Stewart and Kantrud 1973; Krapu et al. 1983; Krapu and Reinecke 1992). Given that females use environmental cues during preparation for nesting, presumably they are able to perceive differences in

conditions that will affect potential nesting and brood rearing success as well. If so, females should adjust their parental care, or investment, accordingly. Here I test the prediction that breeding female dabbling ducks vary their nest defence behaviour according to annual variation in wetland conditions, with defence being more intense in wetter years. Because many of the deleterious effects of reduced wetland abundance occur during the brood rearing period (i.e., after the young have left the nest), the prediction of higher nest defence in wetter years rests on the assumption that conditions early in the season are indicative of conditions later during the brood rearing period. I also assess the validity of this assumption.

Methods

This study was performed at the St. Denis National Wildlife area, located approximately 35 km east of Saskatoon, Saskatchewan, Canada. Habitat in this area has been described in Clark et al. (1991). The data used herein were collected as part of a long term study of waterfowl nesting success in this area and span the years 1984-1992 and 1994-1997. During this period, there was substantial variation in wetland numbers on the study area. Data collected at nests of mallard (*Anas platyrhynchos*), blue-winged teal (*A. discors*) and gadwall (*A. strepera*) were analysed separately for the relationship between annual flushing distance and wetland abundance.

Nesting habitat was searched either by pulling a cable through the vegetation between two ATV's, or by searchers beating vegetation with a cane while on foot. Nests were located when laying or incubating birds were flushed by the cable or the searcher. Flushing distance of the female was recorded on each subsequent visit to the nest where the female was present, and eggs were

counted and candled to determine incubation stage (Weller 1956). Flushing distance was the only nest defence measurement recorded at this study site.

Each year on the same dates, a fixed number of wetland basins within the St. Denis National Wildlife Area was surveyed. The area contained a maximum of approximately 100 wetlands. The number of wetland basins containing water on the first day of May, June and July were used in this study as an index of wetland habitat abundance during each year. These dates cover much of the duration of the nesting season and the early brood rearing period for the three species studied.

Statistical methods

All statistical analyses were performed using the statistical software JMP (SAS Institute 1994). Statistical significance was accepted at an $\alpha \leq 0.05$. The analyses of behaviour were performed for each of the three species, blue-winged teal (*Anas discors*), gadwall (*A. strepera*) and mallard (*A. platyrhynchos*). Unless described otherwise, a general linear models approach was used for data analysis. Because flushing distance was not normally distributed, I transformed this variable to $\ln([\text{flushing distance}] + 1)$ to satisfy the assumptions of parametric tests (Zar 1984). Because the number of previous visits to a nest influences the flushing distance of these three species of ducks (see previous chapter), only the first visit after nest discovery (second visit) was used for each nest. This allowed visit effects to be controlled, while still maintaining as many nests in the analysis as possible.

Results

The number of wetlands containing water on the St. Denis study area ranged from a low of 10 on 1-July 1989, to a high of 96 on 1-May 1997 (Figure 2.1). Correlation analysis indicated that wetland conditions early in the nesting season were indicative of wetland conditions later in the season. The correlation between 1-May and 1-June wetlands was 0.97, between 1-May and 1-July wetlands was 0.81, and between 1-June and 1-July was 0.90 (all P values <0.001). I used July wetlands as my measurement of wetland abundance because this was the period during which the largest proportion of nests was active.

The number of nests found also varied greatly among years (Figure 2.2). The number of nests found was correlated with the number of July wetlands in this study area for all species (blue-winged teal $n=13$, $r=0.74$, $P=0.004$; gadwall $n=11$, $r=0.66$, $P=0.026$; mallard $n=13$ $r=0.57$, $P=0.041$), as would be expected if longer nesting periods are related to wetland number and persistence.

To ensure that the influence of clutch initiation date and incubation stage on flushing distance was not different among years, I developed models with these effects, as well as a term describing their interactions with year. For blue-winged teal, there was no interaction between either incubation stage or initiation date and year in their effects on flushing distance (partial regression coefficients $P=0.56$ and $P=0.41$ respectively). For gadwall, however, there was a significant interaction between incubation stage and year, indicating that the effects of incubation stage on flushing distance were not the same in all years of the study ($F_{\text{coefficient}}=2.36$, $P_{\text{coefficient}}=0.009$). To determine the source of the interaction between year and incubation stage, I calculated the relationship between flushing distance and incubation stage for gadwall within each year. There was a significant decrease in flushing distance with advancing incubation stage in four years of the study ($P<0.05$), and, in most other years the trend was

Figure 2.1 Number of wetlands on 1 May, 1 June, and 1 July at St. Denis National Wildlife Area, 1984-1997.

Figure 2.2 Number of blue-winged teal (BWT), gadwall (GAD), and mallard (MALL) nests found at St. Denis National Wildlife Area, 1984-92, 1994-97.

in this direction. The major exception was 1988 where there was a significant increase in flushing distance with advancing incubation stage ($n=16$, $F=6.27$, $P=0.0252$). Closer inspection of the 1988 data indicated that most nests were tested early in incubation (14 nests <10 days incubation) where there was large variation in flushing distance, but only two nests were tested late in incubation (>20 days), both of which had large flushing distances. By excluding these two nests (of the 233 total nests), the interaction between incubation and year was no longer significant ($n=231$, $F_{\text{coefficient}}=1.5$, $P_{\text{coefficient}}=0.14$), and the interaction between initiation date and year remained non-significant ($n=231$, $F_{\text{coefficient}}=0.71$, $P_{\text{coefficient}}=0.71$). These two nests were excluded from all subsequent analyses.

There was a significant interaction between clutch initiation date and year in mallard suggesting that there was an effect of clutch initiation date on flushing distance of mallard that was not the same each year (partial regression coefficient for $\text{Yr} \times \text{CID}$, $F=1.88$, $P=0.036$). Simple linear regressions of clutch initiation date and flushing distance indicated that flushing distance decreased significantly with initiation date ($P<0.05$) only in 1990 and 1991. Because 1991 contained the fewest nests (13 nests), and unlike other years, wetland numbers increased rather than decreased from May to July, I removed 1991 from the analysis and repeated the test for interactions. The interaction term for clutch initiation date and year was no longer significant ($n=343$, $F_{\text{coefficient}}=1.65$, $P_{\text{coefficient}}=0.09$), and the interaction between incubation and year also remained non-significant ($n=343$, $F_{\text{coefficient}}=1.58$, $P_{\text{coefficient}}=0.10$). To avoid possible confounding relationships, I excluded 1991 from all other analyses of mallard nest defence behaviour, except where otherwise noted. Excluding these data from subsequent analyses of mallard or gadwall did not qualitatively alter the results of those analyses.

Contrary to my central prediction, simple linear regression indicated that all three species increased rather than decreased flushing distance in years with

more wetlands ($P=0.026$ for blue-winged teal, $P=0.024$ for gadwall, and $P=0.016$ for mallard; Figure 2.3). However, one-way ANOVAs revealed that there were also differences among years in clutch initiation dates, incubation stage and egg number (Table 2.1). To determine if annual variation in flushing distance was due to wetland numbers or to differences in other factors among years, I performed simple linear regression analyses of mean yearly flushing distance versus mean yearly incubation stage, clutch initiation date, and egg number. For blue-winged teal, none of these analyses indicated a significant relationship (all $P>0.1$). Similarly, there were no significant relationships between any of these factors and flushing distance of gadwall (all $P>0.3$). However, in mallard there was a highly significant positive relationship between mean annual clutch initiation date and mean annual flushing distance ($P=0.011$; Figure 2.4). There was a marginally significant positive relationship between clutch initiation date and July wetlands ($n=12$, $r^2=0.31$, $F=4.53$, $P=0.059$) suggesting that mallards delay nest initiation in wetter years. In wet years it may be more difficult to find dry upland sites for nest location early in the season. Although the power to detect significant effects of predictors would be low (Berry and Feldman 1985; Stevens 1996), to determine the relative influence of clutch initiation date and July wetlands on flushing distance of mallards, I included these two factors in a multiple regression model. Although the effects of neither variable were statistically significant, mean clutch initiation date had a stronger effect than did the number of July wetlands on yearly flushing distance ($n=12$, model $F=6.9$, model $P=0.015$, model $R^2=0.61$, $P_{\text{cd}}=0.095$, $P_{\text{wetlands}}=0.14$). Within a year, clutch initiation date has a significant effect on flushing distance of mallard (chapter 1), and among years, it appears that initiation date may have had a stronger influence on the yearly differences in flushing distance than did the number of wetlands.

Figure 2.3 Mean yearly flushing distance in relation to number of wetlands on July 1, for blue-winged teal ($n=13$, $r\text{-sq}=0.38$, $F=6.62$, $P=0.03$), gadwall ($n=11$, $r\text{-sq}=0.45$, $F=7.38$, $P=0.02$) and mallard ($n=12$, $r\text{-sq}=0.45$, $F=8.28$, $P=0.02$).

Table 2.1 Results of Analysis of Variance testing for differences in clutch initiation date (CID), incubation stage and number of eggs per clutch among years.

Species	N Years	Response	n	r ²	F	P
Blue-winged teal	13	CID	189	0.18	3.30	0.000
		Incubation	189	0.30	6.38	0.000
		Eggs	211	0.17	3.30	0.000
Gadwall	11	CID	234	0.22	6.21	0.000
		Incubation	235	0.36	12.35	0.000
		Eggs	237	0.02	0.43	0.93
Mallard	13	CID	356	0.07	1.97	0.03
		Incubation	356	0.31	12.58	0.000
		Eggs	386	0.06	2.0	0.02

Figure 2.4 Mean yearly flushing distance of mallard in relation to mean yearly clutch initiation date ($n=12$, $r\text{-sq}=0.49$, $F=9.59$, $P=0.01$).

To determine if wetland density influences flushing distance of mallard when among year differences in clutch initiation date are controlled, I used a subset of data for which clutch initiation dates were similar across years. I chose nests from all years within a range of initiation dates between the date of the first nest in the year that nest initiation began the latest, and the date of the last nest in the year that nest initiation was completed the earliest. This subset of data included only nests initiated between days 129-157 (Julian date). In 1984, nest initiation ended unusually early (day 129) and few nests were found in this year ($n=12$, several with initiation date unknown). Because of this, I excluded 1984 from this set of analyses. I again investigated interactions between year and initiation date and year and incubation stage, to ensure that effects of these variables were similar across all years. The interactions were not statistically significant ($P>0.15$) so for this set of analyses 1984 was excluded, but 1991 and all other years were included. Simple linear regressions indicated that flushing distance was not significantly correlated with mean clutch initiation date, mean incubation stage or mean clutch size ($P>0.13$). However, flushing distance was marginally significantly correlated with July wetlands ($n=12$, $r^2=0.28$, coefficient=0.01, $F=3.93$, $P=0.07$). This suggests that, controlling for differences in clutch initiation dates among years, the number of wetlands did influence flushing distance of mallards. As with the other two species, this relationship was opposite to that predicted, in that mallards also flushed at greater distances in wetter years.

Because the relationship between yearly wetland numbers and nest defence was opposite to that predicted, and remained unexplained by among year differences in other variables, I investigated other factors that could have produced this pattern. One noticeable difference in nesting patterns, in wet as compared to dry years, is that the nest initiation period was generally longer in

wet years (correlation analysis between July wetlands and duration of nest initiation period: blue-winged teal, $n=13$, $r=0.60$, $P=0.03$; mallard $n=13$, $r=0.64$, $P=0.005$; but not significant in gadwall, $n=11$, $r=0.52$, $P=0.10$). This is largely a consequence of more females replacing clutches lost to predation in wetter years (Krapu et al. 1983; Johnson et al. 1992; Krapu and Reinecke 1992; Greenwood et al. 1995). Nests that can be replaced are less valuable than nests that cannot be replaced (Montgomerie and Weatherhead 1988). Thus, in dry years when it may be more difficult to replace nests, all nests may have been defended vigorously, while in wet years, only late nests may have been defended vigorously. To determine whether differences in renesting opportunities associated with differences in wetland abundance produced the unexpected pattern in flushing distances, I divided the nests from each year into two groups; early to mid-season nests and late season nests, and calculated mean yearly flushing distance for each group. Late season nests were those initiated in the fourth quartile of nest initiation dates for each year. Although the relationships were not statistically significant, simple linear regression analyses indicated that flushing distance for early to mid-season nests and for late nests both increased with wetland abundance (Table 2.2). The fact that females on late nests, where renesting opportunities were uniformly low regardless of wetland abundance, flushed at greater distances in wetter years, indicates that the overall pattern of flushing distance relative to wetland abundance was not a consequence of annual differences in renesting opportunities.

The original prediction that nest defence would be higher in wet years and lower in dry years was based on there being a positive relationship between brood survival and wetland availability. However, there may be other factors occurring prior to hatch that have a different influence on nest success. In general, there is evidence that hatching success is greater in wetter years

Table 2.2 Relationship between mean yearly flushing distance and number of July wetlands for early and mid-season nests vs. late season nests. Note that, while none of the analyses are statistically significant, all coefficient estimates are positive, suggesting that flushing distance tended to increase with increasing wetland numbers for both early-mid and late season nests.

Species	Nesting period	n	Coeff.	r ²	F	P
Blue-winged teal	early-mid	12	0.005	0.2	2.52	0.14
	late	13	0.004	0.05	0.60	0.45
Gadwall	early-mid	11	0.01	0.27	3.38	0.10
	late	10	0.01	0.10	0.91	0.37
Mallard	early-mid	13	0.01	0.27	4.14	0.07
	late	13	0.01	0.14	1.82	0.20

(Johnson et al. 1992), but this evidence is somewhat limited. Patterns may differ in different study areas. For example, at this management area, nest predators may be more abundant in wet years and hatching success may therefore have been lower. Factors that influence nest survival in this way may lead to decreased defence during the nesting stage, despite the fact that once a nest does hatch, brood survival may be greater. To determine if wetland abundance influenced nest success, I used non-parametric correlation to determine the relationship between the proportion of nests hatching successfully in a given year and the number of July wetlands in that year. There was no suggestion of a relationship between the proportion of nests hatched and the number of July wetlands (blue-winged teal $P=0.25$, gadwall $P=0.8$, mallard $P=0.15$).

Discussion

I predicted that incubating ducks should risk more in defence of nests for which the survival prospects of their ducklings was higher. Because ducklings survive better in wetter years, females should have allowed observers to approach nests more closely before flushing in years when wetlands were more abundant. Contrary to this prediction, however, mean flushing distances of blue-winged teal, gadwall and mallard were greater in years with more wetlands. This result was not a consequence of the ducks being unable to predict wetland abundance during brood rearing based on conditions during incubation because wetland abundance at different times of the breeding season were highly correlated. Furthermore, among year differences in reneesting potential and nesting success did not explain the observed pattern. Another possibility is that wet years coincided with years of better vegetation growth. Nests that were better concealed by vegetation may have been defended less because they were less vulnerable to predation (Montgomerie and Weatherhead 1988). Two lines of

evidence argue against this possibility. First, as mentioned above, nest success did not vary with wetland density. Second, in the previous chapter, I showed that ducks actually flushed closer to the observer when vegetation density was higher. Thus, none of the obvious potential confounding factors that I measured can explain the relationship between wetlands and flushing distance.

Given that the behaviour of the ducks cannot be accounted for by the various other factors that I have considered, it is appropriate to re-examine the theoretical underpinnings of the hypothesis that I tested to find an explanation for my results. Nest defence theory attempts to predict how a parent should optimise the tradeoffs between costs and benefits when defending its young (Montgomerie and Weatherhead 1988). In predicting more intense defence in wetter years I only considered the benefits side of this relationship. However, if variation in wetland abundance also affects the costs of nest defence, then it might be possible to account for nest defence decreasing in intensity in wetter years. The major cost to parents defending nests is the potential loss of their own life, and thus, any future reproduction they might expect. If female ducks' probability of survival to breed in subsequent years is higher in wet years than in dry years, it may be better for the ducks to invest less in the current brood in order not to jeopardise future reproduction. This condition would apply if costs of reproduction are negatively correlated with wetland abundance.

There is a large body of evidence that suggests that reproduction involves significant costs to the individual in the form of tradeoffs between reproduction and longevity and/or future fecundity (reviewed in Bell and Koufopanou 1986; Clutton-Brock 1991; Stearns 1992). The costs of reproduction can be behavioural, such as may come from parental care behaviour, or physiological. For example, parents performing parental care behaviour may be more susceptible to predation. A physiological cost may result from that fact that energy channeled

into producing eggs is not available for fat storage for winter survival. There is also substantial evidence that reproduction only significantly compromises future survival when environmental conditions are poor (Bell and Koufopanou 1986; Clutton-Brock 1991), or when the parent is in poor condition. Cichon et al. (1998) found that female collared flycatchers (*Ficedula albicollis*) that were in poor condition were less likely to survive to the next breeding season when broods were experimentally increased, but the same was not true for females in good condition. Schwarzkopf (1993) found that when environmental conditions were poor and food intake was low, female water skinks (*Eulamprus tympanum*) that reproduced did not survive as well as females that did not reproduce. There is also evidence from seabirds that in years of poor food conditions, or when parental foraging ability was experimentally decreased, parents only feed young sufficient not to compromise their own body condition (Sæther et al. 1993; Mauck and Grubb 1995; Pons and Migot 1995; Wernham and Bryant 1998). Thus, there is ample evidence that, particularly for long-lived species, the survival of the parent may have as much or more bearing on decisions regarding reproductive effort, or parental investment, as does the survival of the offspring.

The hypothesis that I propose is that female ducks risk less in defending their nests in wetter years because their costs of reproduction are lower. Because those costs are lower, the females have a higher probability of future reproduction, and thus, they are relatively more valuable to themselves than are their offspring (*sensu* Andersson et al. 1980). Although this hypothesis is consistent with the general tenets of life history theory, it nonetheless represents a novel application of that theory. In the references cited above that documented the costs of reproduction, parents invested less when conditions were poor. However, in the ducks that I studied, parents invested less when conditions were good. Thus, rather than the conventional case of parents favouring themselves

over their offspring when the viability of the offspring is low, in the case of these ducks I am proposing that the parents favoured themselves despite the fact that their offspring had a higher probability of survival.

If the interpretation I have proposed for my results is correct, the cost of reproduction in ducks should be high generally, but lower in wet years than in dry years. At present, there is little evidence available on the cost of reproduction in waterfowl. Indirect evidence suggests that post-breeding molt may have detrimental effects on breeding females in years with low wetlands, and hence, low food availability. Molt requires a significant amount of protein which cannot be stored sufficiently by ducks (Hohman et al. 1992; Krapu and Reinecke 1992). In addition, breeding females do not tend to recover body condition before molting, and may remain on brooding ponds during molt, rather than migrate to safer and more nutritionally productive areas (Hohman et al. 1992; Baldassarre and Bolen 1994). As food availability limits growth in ducklings in years with fewer wetlands, it is similarly likely to have a negative influence on the ability of females to recover body condition during molt and before migration.

There is some evidence that survival of adult ducks may be lower in years of poor water conditions (Nichols et al. 1982; Johnson et al. 1992). There is also evidence that mortality rates of adult female ducks may actually be higher in wetter years for some species (Arnold and Clark 1996). However, none of this information is specific to nesting females. A greater proportion of adult females nest in good years, and hence, as a population, females may be more susceptible to predation and the costs associated with parental care in good years. In poor years, fewer females may choose to nest. Hence, while mortality of an individual nesting female may be higher, if fewer females nest, average female survival may be better. Understanding nest defence behaviour of ducks will require more information on the costs of reproduction generally, and specific information on

how parent and duckling survival vary with wetland conditions. Experiments in which the costs of reproduction are manipulated by supplemental feeding or other means may also help to determine whether the costs of producing and incubating a clutch are responsible for differences in nest defence among years.

Literature Cited

- Afton, A. D. and Paulus, S. L. 1992. Incubation and brood care. *In Ecology and management of breeding waterfowl. Edited by Batt, B. D. J., A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu.* University of Minnesota Press, Minneapolis. pp. 62-108.
- Andersson, M., Wiklund, C. G., and Rundgren, H. 1980. Parental defence of offspring: a model and an example. *Anim. Behav.* 28:536-542.
- Armstrong, W. T. 1986. The influence of clutch size and clutch age on parental behaviour in blue-winged teal and northern shoveler. M.Sc. Thesis, Queen's University, Kingston, Ontario Canada.
- Arnold, T. W. and Clark, R. G. 1996. Survival and philopatry of female dabbling ducks in southcentral Saskatchewan. *J. Wildl. Manage.* 60:560-568.
- Baldassarre, G. A., and Bolen, E. G. 1994. Waterfowl ecology and management. John Wiley & Sons, Inc., New York.
- Ball, I. J., Gilmer, D. S., Cowardin, L. M., and Riechmann, J. H. 1975. Survival of wood duck and mallard broods in north-central Minnesota. *J. Wildl. Manage.* 39:776-780.
- Barash, D. P. 1975. Evolutionary aspects of parental behavior: Distraction behavior of the alpine accentor. *Wilson Bull.* 87(3):367-373.
- Bell, G. and Koufopanou, V. 1986. The cost of reproduction. *Oxford surveys in evolutionary biology* 3: 83-131.
- Berry, W. D., and Feldman, S. 1985. Multiple regression in practice. Sage Publications, Beverly Hills, CA.
- Biermann, G. C. and Robertson, R. J. 1981. An increase in parental investment during the breeding season. *Anim. Behav.* 29:487-489.

- Bjerke, T., Espmark, Y. and Fonstad, T. 1985. Nest defence and parental investment in the Redwing, *Turdus iliacus*. *Ornis Scand.* 16:14-19.
- Blancher, P. J., and Robertson, R. J. 1982. Kingbird aggression: does it deter predation? *Anim. Behav.* 30:929-930.
- Boucher, D. H. 1977. On wasting parental investment. *Am. Nat.* 111:786-788.
- Breitwisch, R. 1988. Sex differences in defence of eggs and nestlings by northern mockingbirds, *Mimus polyglottos*. *Anim. Behav.* 36:62-72.
- Brunton, D. H. 1986. Fatal anti-predator behaviour of a killdeer. *Wilson Bull.* 98:605-607.
- Brunton, D. H. 1990. The effects of nesting stage, sex and type of predator on parental defense by killdeer (*Charadrius vociferus*): testing models of avian parental defense. *Behav. Ecol. Sociobiol.* 26:181-190.
- Bures, S and Pavel, V. 1997. The effect of nestling condition on risk-taking in meadow pipits. *Anim. Behav.* 54:1531-1534.
- Cichon, M., Olejniczak, P., and Gustafsson, L. 1998. The effect of body condition on the cost of reproduction in female collared flycatchers *Ficedula albicollis*. *Ibis* 140:128-130.
- Clark, R. G., Nudds, T. D., and Bailey, R. O. 1991. Populations and nesting success of upland-nesting ducks in relation to cover establishment. *Can. Wild. Serv. Progr. Notes* No. 193.
- Clutton-Brock, T. H. 1991. The evolution of parental care. Princeton University Press, Princeton, New Jersey.
- Coleman, R. M. 1987. Does experience with predators affect parental investment? *Auk* 104:791-792.
- Curio, E. 1975. The functional organisation of anti-predator behaviour in the pied flycatcher: a study of avian visual perception. *Anim. Behav.* 23:1-115.

- Curio, E., Regelman, K., and Zimmerman, U. 1984. The defence of first and second broods by great tit (*Parus major*) parents: a test of predictive sociobiology. *Z. Tierpsychol.* 66:101-127.
- Dale, S. Gustavsen, R, and Slagsvold, T. 1996. Risk taking during parental care: a test of three hypotheses applied to the pied flycatcher. *Behav. Ecol. Sociobiol.* 39:31-42.
- Dufour, K. W., and Weatherhead, P. J. In press. Bilateral symmetry as an indicator of male quality in red-winged blackbirds: associations with measures of health, viability and parental effort. *Behav. Ecol.*
- Dufour, K. W., Ankney, C. D., and Weatherhead, P. J. 1993. Condition and vulnerability to hunting among mallards staging at Lake St. Clair, Ontario. *J. Wildl. Manage.* 57:209-215.
- Dzubin, A. and Gollop, J. B. 1972. Aspects of mallard breeding ecology in Canadian parkland and grassland. *In* Population ecology of migratory birds. U.S. Fish & Wild. Serv. Wildl. Res. Rep. 2. pp 113-152.
- Dzus, E. H., and Clark, R. G. 1997. Overland travel, food abundance, and wetland use by mallards: relationships with offspring survival. *Wilson Bull.* 109:504-515.
- Dzus, E. H., and Clark, R. G. 1998. Brood survival and recruitment of mallards in relation to wetland density and hatching date. *Auk* 115: 311-318.
- Eckert, C. G., and Weatherhead, P. J. 1987. Male characteristics, parental quality and the study of mate choice in the red-winged blackbird (*Agelaius phoeniceus*). *Behav. Ecol. Sociobiol.* 20:35-42.
- Forbes, M. R. L., Clark, R. G., Weatherhead, P. J., and Armstrong, T. 1994. Risk-taking by female ducks: intra- and interspecific tests of nest defense theory. *Behav. Ecol. Sociobiol.* 34:79-85.

- Gloutney, M. L., Clark, R. G., Afton, A. D., and Huff, G. J. 1993. Timing of nest searches for upland nesting waterfowl. *J. Wildl. Manage.* 57:597-601.
- Gramza, A. F. 1967. Responses of brooding nighthawks to a disturbance stimulus. *Auk* 84:72-86.
- Greenwood, H., Clark, R. G., and Weatherhead, P. J. 1986. Condition bias of hunter shot mallards (*Anas platyrhynchos*). *Can. J. Zool.* 64:599-601.
- Greenwood, R. J., Sargeant, A. B., Johnson, D. H., Cowardin, L. M. and Shaffer, T. L. 1995. Factors associated with duck nest success in the prairie pothole region of Canada. *Wildl. Monogr.* 128:1-57.
- Greig-Smith, P. W. 1980. Parental investment in nest defence by stonechats (*Saxicola torquata*). *Anim. Behav.* 28:604-619.
- Hakkarainen, H. and Korpimäki, E. 1994. Nest defence of Tengmalm's owls reflects offspring survival prospects under fluctuating food conditions. *Anim. Behav.* 48:843-849.
- Hatch, M. I. 1997. Variation in song sparrow nest defense: individual consistency and relationship to nest success. *Condor* 99:282-289.
- Hobson, K. A., Bouchart, M. L., and Sealy, S. G. 1988. Responses of naïve yellow warblers to a novel nest predator. *Anim. Behav.* 36:1823-1830.
- Hohman, W. L., Ankney, C. D., and Gordon, D. H. 1992. Ecology and management of postbreeding waterfowl. *In Ecology and management of breeding waterfowl. Edited by Batt, B. D. J., A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu.* University of Minnesota Press, Minneapolis. pp. 128-189.
- Hudson, P. J., and Newborn, D. 1990. Brood defence in a precocial species: variations in the distraction displays of red grouse, *Lagopus lagopus scoticus*. *Anim. Behav.* 40:254-261.

- Johnson, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. *Auk* 96:651-661.
- Johnson, D. H., Nichols, J. D. and Schwartz, M. D. 1992. Population dynamics of breeding waterfowl. *In* Ecology and management of breeding waterfowl. *Edited by* Batt, B. D. J., A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu. University of Minnesota Press, Minneapolis. pp. 446-485.
- Johnson, D. H. and Sargeant, A. B. 1977. Impact of red fox predation on the sex ratio of prairie mallards. U.S. Fish and Wildl. Serv., Wildl. Res. Rep. 6.
- Klett, A. T., Shaffer, T. L., and Johnson, D. H. 1988. Duck nest success in the prairie pothole region. *J. Wildl. Manage.* 52:431-440.
- Knight, R. L. and Temple, S. A. 1986a. Why does intensity of avian nest defense increase during the nesting cycle? *Auk* 103:318-327.
- Knight, R. L. and Temple, S. A. 1986b. Nest defence in the American goldfinch. *Animal Behav.* 34:887-897.
- Krapu, G. L. and Reinecke, K. J. 1992. Foraging ecology and nutrition. *In* Ecology and management of breeding waterfowl. *Edited by* Batt, B. D. J., A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu. University of Minnesota Press, Minneapolis. pp. 1-29.
- Krapu, G. L., Klett, A. T., and Jorde, D. G. 1983. The effect of variable spring water conditions on mallard reproduction. *Auk* 100:689-698.
- Leitch, W. G. and Kaminski, R. M. 1985. Long-term waterfowl trends in Saskatchewan grassland. *J. Wildl. Manage.* 49:212-222.
- Leonard, J. P., Anderson, M. G., Prince, H. H. and Emery, R. B. 1996. Survival and movements of canvasback ducklings. *J. Wildl. Manage.* 60:863-874.
- Mallory, M. L. and Weatherhead, P. J. 1993. Observer effects on common goldeneye nest defense. *Condor* 95:467-469.

- Mallory, M. L., McNichol, D. K., Walton, R. A., and Wayland, M. E. In press. Risk-taking by incubating common goldeneyes and hooded mergansers. *Condor*.
- Martin, K., and Horn, A. G. 1993. Clutch defense by male and female Willow Ptarmigan *Lagopus lagopus*. *Ornis Scand.* 24:261-266.
- Mauck, R. A., and Grubb, Jr., T. C. 1995. Petrel parents shunt all experimentally increased reproductive costs to their offspring. *Anim. Behav.* 49:999-1008.
- Mauser, D. M., Jarvis, R. L. and Gilmer, D. S. 1994. Survival of radio-marked mallard ducklings in northeastern California. *J. Wildl. Manage.* 58:82-88.
- McLean, I. G., Smith, J. N. M., and Stewart, K. G. 1986. Mobbing behaviour, nest exposure, and breeding success in the American robin. *Behaviour* 96:171-186.
- Meilvang, D., Moksnes, A., and Røskft, E. 1997. Nest predation, nesting characteristics and nest defence behaviour of fieldfares and redwings. *J. Avian Biol.* 28:331-337.
- Montgomerie, R. D. and Weatherhead, P. J. 1988. Risks and rewards of nest defence by parent birds. *Q. Rev. Biol.* 63:167-187.
- Nichols, J. D., Pospahala, R. S., and Hines, J. E. 1982. Breeding-ground habitat conditions and the survival of mallards. *J. Wildl. Manage.* 46:80-87.
- Nudds, T. D. 1977. Quantifying the vegetative structure of wildlife cover. *Wildl. Soc. Bull.* 5:113-117.
- Orthmeyer, D. L., and Ball, I. J. 1990. Survival of mallard broods on Benton Lake National Wildlife Refuge in northcentral Montana. *J. Wildl. Manage.* 54:62-66.

- Pasitschniak-Arts, M., and Messier, F. 1995. Risk of predation on waterfowl nests in the Canadian prairies: effects of habitat edges and agricultural practices. *Oikos* 73:347-355.
- Pons, J. and Migot, P. 1995. Life-history strategy of the herring gull: changes in survival and fecundity in a population subjected to various feeding conditions. *J. Anim. Ecol.* 64:592-599.
- Redondo, T. 1989. Avian nest defence: theoretical models and evidence. *Behaviour* 111:161-195.
- Redondo, T., and Carranza, J. 1989. Offspring reproductive value and nest defense in the magpie (*Pica pica*). *Behav. Ecol. Sociobiol.* 25:369-378.
- Regelmann, K. and Curio, E. 1983. Determinants of brood defence in the great tit *Parus major* L. *Behav. Ecol. Sociobiol.* 13:131-145.
- Rice, W. R. 1989. Analysing tables of statistical tests. *Evolution* 43:223-225.
- Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. *Smithson. Contrib. Zool.* 9:1-48.
- Robertson, R. J. and Biermann, G. C. 1979. Parental investment strategies determined by expected benefits. *Z. Tierpsychol.* 50:124-128.
- Rotella, J. J., and Ratti, J. T. 1992a. Mallard brood survival and wetland habitat conditions in southwestern Manitoba. *J. Wildl. Manage.* 56:499-507.
- Rotella, J. J., and Ratti, J. T. 1992b. Mallard brood movements and wetland selection in southwestern Manitoba. *J. Wildl. Manage.* 56:508-515.
- Rytkönen, S., and Soppela, M. 1995. Vicinity of sparrowhawk nest affects willow tit nest defense. *Condor* 97:1074-1078.
- Rytkönen, S., Koivula, K., and Orell, M. 1990. Temporal increase in nest defence intensity of the willow tit (*Parus montanus*): parental investment or methodological artifact? *Behav. Ecol. Sociobiol.* 27:283-286.

- Rytkönen, S., Orell, M., Koivula, K. and Soppela, M. 1995. Correlation between two components of parental investment: nest defence intensity and nestling provisioning effort of willow tits. *Oecologia* 104:386-393.
- Sæther, B., Andersen, R. and Pedersen, H. C. 1993. Regulation of parental effort in a long-lived seabirds: an experimental manipulation of the cost of reproduction in the antarctic petrel, *Thalassoica antarctica*. *Behav. Ecol. Sociobiol.* 33:147-150.
- Sandercock, B. K. 1994. The effect of manipulated brood size on parental defence in a precocial bird, the Willow Ptarmigan. *J. Avian Biol.* 25:281-286.
- Sargeant, A. B. 1972. Red fox spatial characteristics in relation to waterfowl predation. *J. Wildl. Manage.* 36:225-236.
- Sargeant, A. B. and Raveling, D. G. 1992. Mortality during the breeding season. *In Ecology and management of breeding waterfowl. Edited by Batt, B. D. J., A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu.* University of Minnesota Press, Minneapolis. pp. 396-422.
- SAS Institute Inc. 1994. JMP statistics and graphics guide. SAS Institute Inc., Cary, NC.
- Savard, J. L., Smith, G. E. J., and Smith, J. N. M. 1991. Duckling mortality in Barrow's goldeneye and bufflehead broods. *Auk* 108:568-577.
- Schwarzkopf, L. 1994. Costs of reproduction in water skinks. *Ecology* 74:1970-1981.
- Sedinger, J. S. 1992. Ecology of prefledging waterfowl. *In Ecology and management of breeding waterfowl. Edited by Batt, B. D. J., A. D. Afton,*

- M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu. University of Minnesota Press, Minneapolis. pp. 109-127.
- Siderius, J. A. 1993. Nest defense in relation to nesting stage and response of parents to repeated model presentations in the eastern kingbird (*Tyrannus tyrannus*). *Auk* 110:921-923.
- Sjöberg, G. 1994. Factors affecting nest defence in female Canada Geese *Branta canadensis*. *Ibis* 136:129-135.
- Smith, A. G. 1969. Waterfowl-habitat relationships on the Lousana, Alberta, waterfowl study area. *In* Saskatoon wetlands seminar. Can. Wildl. Serv. Rep Ser. 6. pp 116-122. Cited in Baldassarre and Bolen 1994.
- Smith, R. I. 1970. Response of breeding pintails to drought. *J. Wildl. Manage.* 34:943-946.
- Sonerud, G. A. 1988. To distract display or not: grouse hens and foxes. *Oikos* 51:233-237.
- Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford.
- Stevens, J. 1996. Applied multivariate statistics for the social sciences, 3rd ed. Lawrence Erlbaum Associates, Mahwah, New Jersey.
- Stewart, R. E., and Kantrud, H. A. 1973. Ecological distribution of breeding waterfowl populations in North Dakota. *J. Wildl. Manage.* 37:39-50.
- Talent, L. G., Jarvis, R. L., and Krapu, G. L. 1983. Survival of mallard broods in south-central North Dakota. *Condor* 85:74-78.
- Tolonen, P. and Korpimäki, E. 1995. Parental effort of kestrels (*Falco tinnunculus*) in nest defense: effects of laying time, brood size and varying survival prospects of offspring. *Behav. Ecol.* 6:435-441.

- Trivers, R. L. 1972. Parental investment and sexual selection. *In* Sexual selection and the descent of man, 1871-1971. *Edited by* Campbell, B. Aldine Publishing Company, Chicago. pp. 136-179.
- Viñuela J., Amat, J. A., and Ferrer, M. 1995. Nest defence of nesting chinstrap penguins (*Pygoscelis antarctica*) against intruders. *Ethology* 99:323-331.
- Wallin, K. 1987. Defence as parental care in tawny owls (*Strix aluco*). *Behaviour* 102:213-230.
- Weatherhead, P. J. 1979. Do savannah sparrows commit the Concorde fallacy? *Behav. Ecol. Sociobiol.* 5:373-381.
- Weatherhead, P. J. 1982. Risk-taking by red-winged blackbirds and the Concorde fallacy. *Z. Tierpsychol.* 60:199-208.
- Weatherhead, P. J. 1989. Nest defence by song sparrows: methodological and life history considerations. *Behav. Ecol. Sociobiol.* 25:129-136.
- Weatherhead, P. J. 1990. Nest defence as shareable paternal care in red-winged blackbirds. *Anim. Behav.* 39:1173-1178.
- Weller, M. W. 1956. A simple field candler for waterfowl eggs. *J. Wildl. Manage.* 20:111-113.
- Wernham, C. V., and Bryant, D. M. 1998. An experimental study of reduced parental effort and future reproductive success in the puffin, *Fratercula arctica*. *J. Anim. Ecol.* 67:25-40.
- Westmoreland, D. 1989. Offspring age and nest defence in mourning doves; a test of two hypotheses. *Anim. Behav.* 38:1062-1066.
- Westneat, D. F. 1989. Intensity of nest defense in Indigo Buntings increases with stage and not number of visits. *Auk* 106:747-749.
- Wiklund, C. G. 1990. Offspring protection by merlin *Falco columbarius* females; the importance of brood size and expected offspring survival for defense of young. *Behav. Ecol. Sociobiol.* 26:217-223.

- Winkler, D. W. 1991. Parental investment decision rules in tree swallows: parental defense, abandonment, and the so-called Concorde Fallacy. *Behav. Ecol.* 2:133-142.
- Winkler, D. W. 1992. Causes and consequences of variation in parental defense behavior by tree swallows. *Condor* 94:502-520.
- Zar, J. H. 1984. *Biostatistical Analysis*, 2nd ed. Prentice Hall, New Jersey.

IMAGE EVALUATION TEST TARGET (QA-3)

APPLIED IMAGE, Inc
1653 East Main Street
Rochester, NY 14609 USA
Phone: 716/482-0300
Fax: 716/288-5989

© 1993, Applied Image, Inc., All Rights Reserved