Factors affecting adult female crèche attendance and duckling survival of common eiders in the southern Bay of Fundy and northern Gulf of Maine

by

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Dedication

To Patrick and Derek - if only all adoptions could turn out so well!

Abstract

In addition to studying female condition and brood ecology of common eiders (*Somateria mollissima*), I examined the impact of great black-backed (*Larus marinus*) gull predation on survival of common eider ducklings, between hatching and fledging, in relation to different levels of gull control on the Wolves Archipelago in the southern Bay of Fundy and on Petit Manan National Wildlife Refuge (PMNWR) in the northern Gulf of Maine. Clutch size and crèche (groups containing any number of adult female(s) and duckling(s), two or more of which are parentally unrelated) attendance in common eiders was related to body condition. Body condition at clutch initiation was strongly correlated with within-season variation in clutch size and laying date, and the cost of incubation did not increase with clutch size. My results did not support the "incubation-cost hypothesis" that clutch size is determined by the interaction between the allocation of body reserves to egg production, incubation and care of chicks. I argue that clutch size and the likelihood that females tend their own brood are both determined by pre-laying body condition which supports the "egg-production hypothesis" that clutch size is limited by a hen's ability to allocate nutrient reserves to egg laying.

Body condition of tending females was higher than that of abandoning females regardless of the point at which they were captured in the incubation period. Whether or not a female abandoned her nest/ducklings depended upon her nutrient reserves at the beginning of nest initiation. Females which cared for their own ducklings and/or adopted ducklings lost only 32% of their pre-incubation body reserves, whereas females which abandoned their clutches and ducklings lost 35% and 37%, respectively. My results did not support the predictions of the *alternative reproductive strategy,* which states that post-hatch brood amalgamation is maintained in a population as a mixed evolutionarily stable strategy; rather females abandoned their brood because of depleted energy reserves, i.e.*energetic stress*, and the ability to aquire these reserves may be related to *age or experience.*

Duckling survival to fledgling was higher within the Petit Manan National Wildlife Refuge in the Gulf of Maine (12%) than on the Wolves Archipelago in the Bay of Fundy (6%). The relatively large number of ducklings associated with Petit Manan accounted for a large proportion of the surviving ducklings and may reflect lower predation rates by great black-backed gulls as a result of gull control measures on Petit Manan/Green Island. Daily survival rate of ducklings was higher in on PMNWR (DSR = 0.92) than on the Wolves Archipelago (DSR = 0.35) ($p < 0.001$). There was no difference in daily survival rate (DSR) of ducklings hatched on the Wolves Archipelago between 1995 and 1997, despite limited gull control in 1996. Previous low estimates of eider duckling mortality on the Wolves Archipelago, Bay of Fundy cannot be explained by movements of broods to the mainland coast. The recovery of radio-transmitters attached to eider ducklings and subsequently retrieved from great black-backed gull pellets suggested that traditional methods of estimating the number of eider ducklings eaten by gulls from the remains found in pellets at gull nests and loafing areas underestimates the true number eaten by a factor of 5-17.

The breeding population of common eiders in the Bay of Fundy has remained stable over the last decade. However, the number of ducklings surviving to fledging in the Bay of Fundy decreased from > 14% of the adult breeding population prior to 1991 to < 10% between 1995 and 1998. The current levels of recruitment observed for the eider population in the Bay of Fundy are not enough to offset the estimated 13% mortality rate for adult female eiders originating in the Atlantic Coast subpopulation. Persistently low duckling production of eiders in the Bay of Fundy could result in gradual shifts in the population structure, and ultimately in declines in population size.

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Introduction

Chapter 1

1.1. Background

Post-hatch brood amalgamation or crèching behaviour, whereby a percentage of the females abandon their young to other birds, is common among Anatidae and occurs in several species with self-feeding young (Eadie *et al.* 1988). Common eiders (*Somateria mollissima*) use three strategies during brood care: (1) complete abandonment of the young, (ii) care for the young by one female alone, and (iii) parental care shared between two or three females resulting in a stable crèche which lasts for several weeks (Gorman and Milne 1972, Bedard and Munro 1976, Munro and Bedard 1977). Broods of common eiders are strongly attracted to each other, and adoption and abandoning of ducklings occur in the first days after hatching. Within 3-7 days, strong bonds are established between the female(s) and the ducklings (Bedard and Munro 1976, Koryakin 1982), although larger, unstable crèches are also formed during feeding and resting later in the rearing period (Gorman and Milne 1972, Schmutz *et al.* 1982). In addition to brood-caring females, females without young often assist brood-caring females in defending a brood during predator attacks. The origin of these females is uncertain and some authors have suggested that they originate from the nest failing and/or a non-breeding cohort (Munro and Bedard 1977).

The formation of crèches by common eiders occurs in the Gulf of St. Lawrence (*S.m. dresseri*) (Munro and Bedard 1977) and Scotland (*S.m. mollissima*) (Gorman and Milne 1972), but is uncommon in the Arctic (*S.m. sedentaria*) (Cooch 1965). These differences have been attributed to differences in nesting densities and predation (Gorman and Milne 1972). Bedard and Munro (1976) found that about 20% of common eider females abandoned their brood to others, whereas Bustnes and Erikstad (1991) found that 60% of females abandoned their broods. Gorman and Milne (1972), however, concluded that most females abandon their young completely after a short period of parental care, because the food of females was spatially separated from that of ducklings.

Conflicting data from Scotland (Milne 1963) and North America (McAloney

1973, Cooch 1965) suggest that factors affecting the post-hatch survival and the bond between mother and young are still not well understood. Several hypotheses have been put forward to explain post-hatch brood amalgamation (see Eadie *et al.* 1988 for review), but the determinants remain poorly known (Rohwer and Freeman 1989, Afton and Paulus 1992, Sayler 1992). Several authors have suggested that the body condition is a determining factor in parental care in female ducks (Kear 1970, Gorman and Milne 1972, Williams 1974, Eadie *et al.* 1988, Kehoe 1989) and that females in poor condition more readily abandon their young (Eadie *et al.* 1988, Kehoe 1989). While abandonment leads to a lower survival rate of the female's own young (Bustnes and Erikstad 1991), it may benefit lifetime reproduction by increasing the likelihood of the females' own survival (Eadie *et al.* 1988). Hypotheses put forward to explain crèching behaviour for brood-caring females include increased reproductive success of adoptive parents, adopted young and/or genetic parents (Eadie *et al.* 1988). Brood-caring females may enhance the probability of their own or related young surviving by exploiting fostered young (Eadie and Lumsden 1985, Hamilton 1971). Advantages that accrue directly to ducklings may include reduced predation (Munro and Bedard 1977) or increased survival through monopolization of the best feeding areas by large crèches (Williams 1974). Thus, the extent to which eiders crèche has the potential to directly affect duckling survival and subsequent recruitment to a population.

Common eiders breeding in eastern North America, abundant at first European contact, were reduced to remnant levels by indiscriminate hunting and egg collecting during the 19th century (Gross 1944). With better protection and the regulation of hunting under the Migratory Birds Convention, numbers increased substantially. Few studies, however, have examined the recruitment of fledglings to North American eider populations. The number of eider fledglings in a population can be highly variable from year to year, despite relatively stable numbers in breeding pairs and hatchlings produced (Swennen 1983). High duckling mortality is common in eiders (Bauer and Glutz von

Blotzheim 1969), and factors involved in the extremes of fledging output include predation, weather, condition at hatch, food supply and disease (McAloney 1973, Mendenhall and Milne 1985, Ahlund and Gotmark 1989). In general, eiders show delayed sexual maturity (Mendall 1968), strong homing (Wakeley and Mendall 1976), and low recruitment rates (Reed and Erskine 1986), suggesting adaptation to a relatively stable environment. Thus, any changes to the environment that affect their survival could have major effects on the status of the population.

One such change is the exposure of eiders to predators. The range of great black-backed gulls (*Larus marinus*) and numbers of herring gulls (*Larus argentatus*) and common eiders have expanded considerably along the Atlantic coast of North America since the 1920's (Drury 1973, 1974). These gulls are predators on eider eggs and young (Ahlen and Andersson 1970, Bourget 1973, Campbell 1975), yet increases in the numbers of both herring gulls and common eiders in the St. Lawrence estuary demonstrate that herring gull predation on eider eggs or ducklings need not prevent eider populations from increasing (Munro and Bedard 1977). However, great black-backed gulls are more predatory than herring gulls on eider eggs and young (Bourget 1973), and therefore, have the potential to substantially impact the recruitment of ducklings to an eider population.

In eastern Canada, historical and current information is too sparse to allow a precise assessment of great black-backed gull populations. There is considerable controversy as to whether the present populations of great black-backed gulls in the Bay of Fundy are population increases resulting from a combination of increased protection (under the Migratory Birds Convention of 1916) and exogenous food sources, or range expansions. Boardman (1862) wrote of great black-backed gulls in the Bay of Fundy: "Resident. Not plenty. A few breed about the islands." whereas Audubon (1835) had to travel to Labrador to observe them. Evidently the great black-backed gull did not exist in the numbers that it does today. In the southern reaches of its range, the eider now faces a predator that historically was scarce or absent.

The breeding population of the common eider has remained relatively constant over the last decade, ranging from 8,000 to 10,000 breeding pairs in New Brunswick (Erskine and Smith 1986, Erskine 1992) and 28,000 breeding pairs along the coast of Maine (Krohn *et al.* 1992). Aerial surveys conducted by NBDNRE (New Brunswick Department of Natural Resources and Energy) identified the largest concentrations of eider ducklings in areas immediately adjacent to the breeding colonies, with the exception of the Wolves Archipelago where common eiders nest in association with large numbers of great black-backed gulls. It is unlikely that the lack of ducklings around the Wolves Archipelago could be attributed to differences in numbers of ducklings or in human disturbance. Nesting habitat on the Wolves Archipelago is similar to several other colonies in the Bay of Fundy and hatch success for this colony has been documented as high as 80-90% (Hicklin 1989, Gilliland 1990).

Hicklin (1989) suggested that predation by great black-backed gulls accounted for the low duckling recruitment on the Wolves Archipelago. Gilliland (1990), however, estimated < 10% predation based predominantly on the analysis of pellets collected at gull nests and loafing areas, and suggested that the lack of ducklings observed around the Wolves Archipelago was not due to low recruitment resulting from gull predation, but rather reflected the movement of ducklings away from the Wolves Archipelago. Minot (1976) found that eider broods left their offshore nesting islands and moved to the rockweed-covered shorelines of Grand Manan. McAloney (1973) and Guignion (1967) found that eider broods left the rugged exposed shore of their offshore nesting islands for the more sheltered bays of the mainland coast.

Eiders have been shown to nest in association with a variety of other bird species, most commonly gulls (Gotmark and Ahlund 1988). This association may be beneficial for the eiders (e.g., Young and Titman 1988). Alternatively, nesting associations may be an ecological trap (Dwenychuk and Boag 1972). The gulls may be "allowing" the eiders to nest successfully so they can consume the ducklings once hatched. Contradictory results have been obtained in other studies involving nesting ducks and gulls (Young and Titman 1986). A study showing a positive relationship between nesting in gull colonies and recruitment (not hatching success) would confirm that eiders nesting in gull colonies benefit from the association (Robertson 1995).

Between 1995 and 1997, I examined brood ecology of common eiders with specific reference to brood amalgamation, post-hatch movements, and duckling survival on the Wolves Archipelago in the Bay of Fundy. However, high predation rates by great black-backed gulls on eider ducklings precluded the study of brood amalgamation, despite gull control measures undertaken in 1996. Recognizing the need for a site with higher duckling survival to examine post-hatch brood amalgamation, I expanded the study in 1997 and 1998 to include a common eider colony on Green Island, in the Gulf of Maine. Green Island is part of a two-island archipelago which includes Petit Manan Island, a U.S. National Wildlife Refuge (PMNWR). Between 1984 and 1990, a gull-control program, employing the use of avicide DRC 1339, was instituted on Petit Manan and Green Island by the U.S. Fish and Wildlife Service. Human presence has been maintained on Petit Manan every summer since 1984 to monitor the tern population and to actively discourage re-settlement of gulls. In 1997 and 1998, all breeding pairs of great black-backed gulls were eliminated from Green Island by trapping and killing at least one member of each pair, and destroying any gull nests remaining after unsuccessful attempts to trap the pair. This allowed me to determine the extent to which thriving populations of large gulls are placing increased pressure on the annual production of common eiders, while at the same time allowing me to return my original research objectives looking at factors affecting adult female crèche attendance.

1.2. Overview of Chapters

I have divided the main objectives of my thesis into four sub-objectives, which correspond to the first four chapters of my thesis. All chapters have been or will be submitted to various journals for publication. Individuals who contributed extensively to field logistics or finances of various project components were additionally acknowledged by authorship as reflected in several chapters. These individuals did not contribute to the actual writing of the manuscripts. For continuity of style, all chapters are written according to specifications for the Canadian Journal of Zoology. Each chapter has been written to stand alone, e.g. I have provided the scientific name of species whenever birds, plants, or other organisms are first mentioned in the text of each chapter. In Chapter 2, I investigate **the effect of female condition on incubation and crèche attendance in common eiders**. In determining the body condition of hens captured during incubation I was able to incidentally re-examine **the effect of female condition on clutch size and laying date in common eiders** in Chapter 3.

With the addition of a study area free of breeding gulls in 1997, I was able to compare duckling mortality in the absence of breeding gulls (at PMNWR) with mortality in the presence of breeding gulls (Wolves Archipelago). This allowed me to assess **the effect of gull control on survival of eider ducklings** in Chapter 4. In addition to monitoring post-hatch movements and survival of ducklings, the use of radio-transmitters allowed me to assess the efficacy of traditional methods used (i.e., analysis of regurgitated pellets) to estimate predation rates on eiders by gulls in Chapter 5. In Chapter 6, I report on **the status and productivity of common eiders in relation to the status of great black-backed gulls and herring gulls in the southern Bay of Fundy and northern Gulf of Maine**. I evaluated **the effects of capture and tagging on nest success of common eiders** associated with nasal-tagging and implanting intra-abdominal radio-transmitters into adult females captured during incubation throughout the course of this study in Chapter 7. Chapter 8 is a comprehensive discussion of my major conclusions and suggests areas for further research.

Gull control efforts on the Wolves Archipelago in 1997 provided a large sample of great black-backed gulls. This provided me with the opportunity to gather mophological data on the specimens. Gulls were culled throughout the incubation period so that I could examine weight change and size of endogenous nutrient reserves in male and female great black-backed gulls during breeding. In Appendix I and II of my thesis, I provide a method for **sex determination of great black-backed gulls using morphometric characters**, and report on **the use of energy, fat and protein reserves by breeding great black-backed gulls**, respectively. These appendices on gulls have been included in this thesis on eiders because my work identified the biology of these gulls as very important to eiders and I feel it is important to document the work I was able to do to begin to improve our understanding of the biology of the eiders' major predator.

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The effect of female condition on incubation and crèche attendance in common eiders

Chapter 2

Mawhinney, K., and A. W. Diamond. 1999. The effect of female condition on incubation and crèche attendance in common eiders. Auk: *Submitted.*

Abstract

We examined the relationship between female condition of common eider hens captured during incubation and subsequent membership in a crèche. In addition, we artificially extended and reduced the incubation period of females by switching clutches from a sample from known age nests initiated 5 days apart, to determine the body condition at which nests or ducklings were abandoned. Females tending a crèche were in better condition than abandoning females regardless of the point at which they were captured in the incubation period. Whether a female eider abandoned her nest/ducklings was a state-dependent decision related to her nutrient reserves at arrival on the breeding grounds. Females who cared for ducklings lost only 32% of their pre-incubation body reserves at the time of hatch, where females which abandoned their clutches and ducklings lost 35% and 37%, respectively. 'Aunties' were females in good condition that hatched and lost their own ducklings or their clutch early in incubation such that they were in good condition when ducklings in the colony hatched. Our results do not support the predictions of the *alternative reproductive strategy,* which states that post-hatch brood amalgamation is maintained in a population as a mixed evolutionarily stable strategy. We suggest that that females abandon their brood because of depleted energy reserves, i.e.*energetic stress*, and that the ability to aquire these reserves may be related to *age or experience*.

2.1. Introduction

In birds with a long life expectancy, one breeding season represents a relatively small contribution to life-time reproductive success, and the amount of effort allocated to current reproduction represents a trade-off between current and future reproductive success and survival (Roff 1992, Stearns 1992). McNamara and Houston (1996) stressed the significance of an organism's physiological state (i.e., body condition) for life history decisions. Among other things, fat reserves and foraging skills have been listed as possible parameters of an organism's state (Heinsohn 1991, Witter and Cuthill 1993, McNamara and Houston 1996). An individual with large energy reserves should allocate more to present reproduction than an individual with smaller energy reserves or poorer foraging skills.

Adult female common eiders (*Somateria mollissima*) have a high annual survival rate (Coulson 1984, Kremmentz *et al.* 1996); and when nesting for the first time they have an expectation of breeding of about ten years (Coulson 1984). Females arriving on the breeding grounds must have enough energy reserves to produce a clutch and sustain them through a 26 day fast during incubation, during which they lose up to 46% of their body mass (Korschgen 1977, Parker and Holm 1990). Incidents of nest abandonment by female eiders late in the incubation period (Tinbergen 1958, Korschgen 1977, Bustnes and Erikstad 1991) have been related to depleted nutrient reserves (Korschgen 1977, Bustnes and Erikstad 1991). If a female abandons her clutch prior to hatch, her breeding attempt fails, and she will not breed again until the following year. However, continued incubation may lead to reduced future fecundity because of increased mortality risk. Increased mortality related to depleted energy reserves in the period immediately following hatch (Baillie and Milne 1982, Coulson 1984), and the incidence of hens starving to death while incubating a clutch, have both been documented for common eiders (Korschgen 1977).

Ankney and MacInnes (1978) found that lesser snow geese (*Chen caerulescens caerulescens*) abandoning clutches weighed less than birds which successfully hatched nests, and that muscle protein was greatly depleted in females which had apparently starved to death during incubation. Olsson (1997) found that male King Penguins (*Aptenodytes patagonicus*) entered protein catabolism and abandoned eggs, suggesting that they reached a "critical body mass" and were not willing to continue losing mass. Critical body mass has been defined as mass at which the transition from lipids to proteins as the main fuel for metabolism occurs (Cherel *et al.* 1988, 1991). When a bird reaches a critical body mass, the cost of fasting increases considerably because protein is a less efficient fuel than fat (Groscolas 1990). To continue using protein as fuel when fat reserves are depleted would mean increased risk of mortality due to starvation. Birds with altricial young (e.g. penguins) must save some reserves to search for food for both themselves and their young immediately after hatching (Olsson 1997). Birds with precocial young, such as eiders, may, however, be able to deplete their body reserves further during incubation because they need not feed their young and/or can abandon their young to the care of another female or crèche (Munro and Bedard 1977, Bustnes and Erikstad 1991). Crèches are groups containing any number of adult female(s) and duckling(s), two or more of which are parentally unrelated (Bedard and Munro 1976).

The breeding stress that eiders face is extreme (Korschgen 1977). Females which stay with their own young and/or adopt young must have enough energy reserves remaining after incubation to sustain them during brood rearing. The care of young entails spending more time watching for predators, requires the expenditure of energy defending and brooding the young, and allows less time for feeding (Munro and Bedard 1977, Bustnes and Erikstad 1991). Giving up young after hatching is potentially costly in terms of reproductive success, since the ducklings from brood-tending females survive better than ducklings from brood abandoners (Nastase 1983, Bustnes and Erikstad 1991).

However, it may benefit lifetime reproduction by increasing the likelihood of the females' own survival (Eadie *et al.* 1988).

Several authors have suggested that the body condition of ducks is a determining factor in parental care (Kear 1970, Gorman and Milne 1977, Williams 1974, Eadie *et al.* 1988, Kehoe 1989), and females in poor condition more readily abandon their young (Eadie *et al.* 1988, Kehoe 1989). State-dependent decisions to abandon a clutch or brood or to stay with their own and/or adopted young include consideration of remaining energy reserves and ability to replenish exhausted body reserves afterwards (i.e., foraging skills). Bustnes and Erikstad (1991) suggested that whether a female eider cared for young seemed to depend on her body mass (condition) at hatching, and suggested that females in poor condition more readily abandoned their young. The objective of this study was to examine the relationship between body weight corrected for structural size (hereafter body condition, Whyte and Bolen 1984) and subsequent membership in a crèche of common eider hens captured during incubation on two study areas in the Gulf of Maine. In addition, we artificially extended and reduced the incubation period of females to determine the body condition at which nests or ducklings were abandoned.

2.2. Study Area

The Wolves Archipelago (44°56'N, 66°44'W) is a group of 5 islands located 12 km offshore from Beaver Harbour, New Brunswick. The most northerly island, East Wolf, is the largest (2039 ha), followed, north to south, by Green Rock (20 ha), Spruce Island (78 ha), Flatpot Island (233 ha) and South Wolf (425 ha). The dominant vegetation on the islands, with the exception of Green Rock, is balsam fir (*Abies balsamea*)/Spruce (*Picea* spp.). The dominant vegetation of Green Rock is grass (Gramineae spp.) and wild raspberry (*Rubus idaeus*). Breeding seabirds include common eiders, double-crested cormorants (*Phalacrocorax auritus*), black guillemots (*Cepphus grylle*), great black-backed gulls (*Larus marinus*) and herring gulls (*L. argentatus*).

Recent additions include a colony of black-legged kittiwakes *Rissa tridactyla* (Kehoe 1994) and razorbills (*Alca torda*) (Mawhinney and Sears 1996).

Green Island (5 hectares) (44°30'N, 68°30'W) is located 25 km east of Bar Harbour in the Gulf of Maine, U.S.A. The island is treeless with thin peaty soil, and vegetation consists mainly of grasses. Breeding species include common eiders, great black-backed gulls, herring gulls, black guillemots and one pair of American oystercatchers (*Haematopus palliatus*) (Mawhinney *et al.* 1999a).

2.3. Methods

Common eider hens from known nests in the Wolves Archipelago (1995-1997) and on Green Island (1997-1998) were captured with drop door nest traps (Weller 1957), or as they flushed from the nest (Mawhinney *et al.* 1999b). Each bird was weighed to the nearest 0.1 g with a spring balance and six measures of structural size recorded: (1) head + bill length, the maximum distance from the bill tip to the posterior extremity of the occipital process; (2) culmen, from the anterior end of feathering on top of the middle of the bill to the end of the nail; (3) wing chord, with the wing flattened and flexed at the wrist, from the wrist to the tip of the wing; (4) tarsus length, measured with the leg flexed, from the pit at the rear of the junction of the tibiotarsus and the tarsometatarus to the distal end of the tibiotarsus; (5) keel length, the distance between the notch at the furculum and the posterior point along the median of the sternum; and (6) total length, from the tip of the tail to the tip of the bill with the bird stretched on its back. All measurements were taken to the nearest 0.1 mm with calipers except wing and total length, which were measured to the nearest mm with a flat stopped ruler. Each bird was then marked individually with a plastic nasal tag (Lokemoen and Sharp 1985) and a standard U.S.F.W.S. aluminum band and released.

The number of eggs from each marked hen's nest was recorded and nests were visited regularly throughout the breeding season to monitor presence, nest contents, and evidence of predation. Hatch date of these females was calculated from direct observations of clutch initiation during visits to nests while laying was in progress and/or by candling the eggs (Weller 1956). An incubation period of 26 days and an interval of 24 hours between the laying of eggs were used to predict hatching dates (Choate 1966, Milne 1974). Incubation starts with laying of the second egg, and is independent of the actual number of eggs in the nest and the final clutch size (Swennen *et al.* 1993). The nests were revisited every two days during hatching to confirm hatch date.

In 1997, the incubation period of 10 nasal-tagged females was extended artificially, and the incubation period of 10 nasal-tagged females reduced by switching the clutches from a sample of known age nests initiated 5 days apart on Green Island. This procedure was repeated on another 20 nests in 1998. However, the incubation period of 5 of 10 females estimated to be in poor condition were artificially extended by an additional 5 days to determine body condition at which nests were abandoned. The post-hatch movements of all nasal-tagged females were monitored and when located they were classified as abandoners, tenders or aunties according to their behaviour. Females within 0-10 m (attending) were distinguished from those females more than 10 m (not attending) away from a brood. Abandoners are females that are observed giving up their own young, while tenders are females that care for their young and/or adopted young (Bustnes and Erikstad 1991). Aunties are females without young of their own, which assist brood-caring females in defending a brood.

The structural size of each bird was determined by the first principal component (PC1) scores from an analysis on the correlation matrix of log-transformed morphological variables (head + bill, culmen, wing, tarsus, keel, total) (Alisauskas and Ankney 1987, Hanson *et al.* 1990). Body weight (hereafter body condition) was adjusted for variation in structural size by two techniques. The simplest method was to include PC1 scores (Rising and Somers 1989, Freedman and Jackson 1990) as a covariate in the statistical model. The other method involved regressing weight on the PC1 score and using the residuals for each bird to calculate a new value, Y_i, which is corrected for body size. The equation is as follows: corrected body weight = residual + mean body weight, or $Y_i = Y_{obs} - (a + b(PC1)) + Y_{obs})$ (Alisauskas and Ankney 1987, Hanson *et al.* 1990). This technique was used for the purpose of illustrating changes in body condition during incubation.

Analyses of covariance (ANCOVA, SYSTAT, Wilkinson 1988) were used to determine whether body condition during incubation varied between years within each study area and between study areas. ANCOVA was performed to determine whether crèche attendance by hens varied with body condition during incubation. Regression analyses were used to examine significant relationships predicted by ANCOVA models. ANCOVA procedures were based on type III sums of squares. This procedure tests for the effect of an independent variable in the model on the dependent variable by adjusting for the effects of all other independent variables (SAS Institute Inc. 1990). Higher order interactions were excluded from the statistical model if they were non-significant and had no biological importance.

Body condition at hatch or nest abandonment was estimated for each hen by subtracting the daily loss in body condition (25 g, calculated by regressing body condition on incubation, Fig. 2.1) for each day remaining in days of incubation (*body condition at hatch = body condition at original capture - (number of days remaining in incubation x 25 g)*). Body condition at the beginning of incubation was estimated for each hen by adding 25 g for each day incubating to body condition at capture. Loss (%) of body condition was estimated for hens which were observed tending a brood/crèche or abandoning a nest or brood by subtracting body condition at hatch or nest abandonment divided by body condition at beginning of incubation from 100 (*% loss = 100 - (body condition at hatch/body condition at beginning of incubation*). Analyses of variance

(ANOVA) were used to determine if hatch weights differed between tenders, abandoners and aunties, and to determine whether loss of body condition differed between females which tended and abandoned broods. Paired t-tests were used to test differences between estimated body condition of hens with extended incubation periods which abandoned their nests, estimated body condition of hens with extended incubation periods which hatched nests, estimated body condition of hens with reduced incubation which hatched nests and estimated body condition of hens with reduced incubation which tended broods. Results were considered significant if $p \leq 0.05$.

2.4. Results

Incubation status was known for 209 (85 in 1995, 85 in 1996 and 39 in 1997) adult females captured on the Wolves Archipelago and 138 (66 in 1997 and 72 in 1998) captured on Green Island. The structural measurements of eider hens did not load equally on the first principle component axis (PC1), and only head, tarsus and keel were important determinants of structural size. PC1 accounted for 47% of the variation in structural measurements and was characterized by the following eigenvectors: head 0.56; tarsus 0.76; keel 0.73.

Body condition of hens decreased significantly as incubation progressed (Table 2.1, Fig. 2.1(i)). Changes in body condition of hens during incubation did not vary between years on the Wolves Archipelago (ANCOVA $F = 1.28, p = 0.28$) or Green Island (ANCOVA $F = 0.99, p = 0.32$), did not differ between study areas (Table 2.1) and were therefore grouped for subsequent analyses. Body weight of common eider hens varied with structural size (Table 2.1). Body weight (Y) increased with structural size (X), but the variance explained by the relationship was very low ($Y = 1.61 + 0.07X$, $r^2 = 0.07$).

The status of a female in a crèche was known for only 83 females due to high predation rates by great black-backed gulls on eider ducklings in both study areas

(Mawhinney and Diamond 1999a). There were significant interactions between crèche attendance, days into incubation and body size (Table 2.2). Structural size (Y) of adult females decreased as incubation (X) progressed ($Y = 0.22 - 0.02X$, $p = 0.012$), however, the explained variance of this relationship was very low ($r^2 = 0.02$). Females tending crèches were structurally smaller ($\bar{x}$PC1 = - 0.27 ± 0.97 SD) than aunties ($\bar{x}$PC1 = 0.25 ± 0.86 SD), which were smaller than abandoning females ($\bar{x}$PC1 = 0.37 ± 1.04 SD) ($F = 3.64$, $p = 0.03$).

Crèche attendance was dependent on body condition of common eider hens during incubation (Table 2.2). The body condition of tending females was higher than that of females which abandoned broods, while body condition of aunties varied regardless at which point they were captured in the incubation period (Fig. 2.(ii)). Body condition at hatch varied between females ($F = 33.59$, $p = 0.001$). Body condition at hatch was higher for females tending crèches ($\bar{x} = 1.41$ ± 0.08 SD, n = 33) than for females abandoning broods ($\bar{x} = 1.22$ ± 0.08 SD, n = 24) ($F = 8.19$, $p = 0.001$). Females in poor condition which later became aunties had their nests depredated and did not continue to use energy reserves to complete the incubation period. Body condition of aunties (estimated from date of nest predation) ($\bar{x} = 1.49$ ± 0.14 SD, n = 26) was higher than that of females tending a crèche ($F = 7.59$, $p = 0.008$). Loss (%) of body condition was greater for females which abandoned broods ($\bar{x} = 35\%$ ± 1.5 SD, n = 33) than for those which tended ($\bar{x} = 32\%$ ± 1.2 SD, n = 33) broods ($F = 81.85$, $p = 0.001$).

All hens with artificially reduced incubation periods which were observed with hatched ducklings tended their own and adopted ducklings throughout the brood-rearing period (Table 2.3). In contrast, hens with artificially extended incubation periods abandoned their nest prior to hatch, or those observed with hatched ducklings abandoned them to another female within 2 days of hatch (Table 2.3). Estimated body condition of females with artificially extended incubation periods at the point at which they abandoned their nests was significantly lower than that at hatch for females which successfully hatched ducklings (Table 2.3). Loss (%) of body condition for females which abandoned nests was 37% ± 2.2 SD (n = 8).

The estimated body condition at hatch of females with artificially reduced incubation periods was significantly higher than that of females with artificially extended incubation periods which abandoned and hatched nests, and than females with artificially reduced incubation periods that were not observed with live ducklings (Table 2.4). Estimated body condition at hatch did not differ between females with artificially extended incubation periods which successfully hatched nests and females with artificially reduced incubation periods that were not observed with live ducklings (Table 2.4).

2.5. Discussion

The results of this study suggest that abandonment of the clutch and ducklings is associated with a critical body condition, whereas the body condition of tending females was higher than that of abandoning females regardless of the point at which they are captured in the incubation period. Females which abandoned their clutches and ducklings lost 35% and 37% of their pre-incubation body reserves, respectively. Females which cared for their own ducklings and/or adopted ducklings lost only 32% of their pre-incubation body reserves. A critical theshold of depletion of energy reserves linked to clutch abandonment has been found in penguins (Olsson 1997), geese (Aldrich and Raveling 1983) and procellariiforms (Chaurand and Weimerskirch 1994, Weimerskirch 1995).

Gorman and Milne (1977) concluded that most females abandon their young completely after a short period of parental care, but no other authors (Munro and Bedard 1977, Bustnes and Erikstad 1991) reached similar conclusions. Our results support Bustnes and Erikstad (1991) in that we found that only those females that hatched young were observed to be the care-givers of young. However, using multiple measures of body size, we were able to provide clear evidence that whether or not a female cared for young was dependent on body condition. Bustnes and Erikstad (1991) did not find significant differences in the body condition of brood-abandoning and brood-tending females; we suggest that the nature of the measurement (estimated weight/keel length^3) they used to estimate body condition was inappropriate. Single linear measurements cover only part of the overall skeletal size and may lead to misinterpretation of trends present, as well as significant loss of information concerning variation in overall structural morphology (Green 1986).

Some authors have suggested that aunties originate from the nest-failing (Munro and Bedard 1977) and/or non-breeding cohorts (Schmutz *et al.* 1982). We found that aunties were females in good condition that hatched and lost their own ducklings, or females that lost their clutch early in incubation such that they were in good condition when ducklings in the colony hatched. However, not all females that hatched in good condition and lost their own ducklings/clutch became aunties. Hypotheses put forward to explain crèching behaviour of brood-caring females include increased reproductive success of adoptive parents, adopted young and/or genetic parents. Crèching behaviour of aunties, however, can be explained by kin selection only if they are closely related to the mothers of the broods in the crèche (Eadie *et al.* 1988). Perhaps those females which did not become aunties were not related to any of the tending females with live ducklings.

Once a female abandoned a nest or left a crèche, she was never seen to return to it. In contrast, aunties feeding and assisting with the defence of crèches, would leave for several days at a time throughout the brood rearing period. During these recesses, they were observed further offshore feeding in the sub-tidal zone. These females were likely able to replenish energy reserves during these recesses from brood care, suggesting they did not have the same energy and/or feeding constraints as females which were the primary tenders of a crèche. The physical recovery of females caring for young may be limited because females change their habitat and feed with ducklings on periwinkles (*Littorina* spp.) in the intertidal zone (Cantin *et al.* 1974, Minot 1980), whereas females without young are able to feed on common mussels (*Mytilus mytilus*) in the subtidal zone (Schmutz *et al.* 1982).

Bedard and Munro (1977) found that about 20% of common eider females abandoned their brood to others, whereas Bustnes and Erikstad (1991) found that 60% of females abandoned their broods. Given the high predation rates by great black-backed gulls on eider ducklings, we did not attempt to quantify the rate of brood abandonment in this study (Mawhinney and Diamond 1999a). The extent to which crèching behaviour varies between populations (Bedard and Munro 1977, Bustnes and Erikstad 1991), however, may vary in different populations for different reasons, such as age-related differences in population structure or variability in winter habitat. Nutrient reserves acquired by hens prior to the breeding season depend on conditions encountered on the wintering grounds including weather (Guillemette 1991), resource availability (Guillemette *et al.* 1992, Guillemette *et al.* 1996), age (Spur and Milne 1976a) and pair formation (Spur and Milne 1976b).

The male eider plays an important role in increasing the female's food intake prior to laying by protecting her from disturbance (Ashcroft 1976). The numbers and biomass of the prey species of eiders are generally lowest in the spring (Milne and Dunnet 1972) and females that are not paired or are only in the process of forming pairs may suffer interference to their feeding by males (Milne 1974). Therefore, the duration of the pair bond and the experience of the male, as well as her own feeding efficiency, are likely to affect the size of the female's reserves at laying. Spur and Milne (1976b) showed that young birds formed pair bonds later in the winter than older ones, and suggested that this was because older birds reunited with previous partners in the autumn. First year female eiders have lighter winter weights than adults and do not form pairs (Milne 1974) and late-paired females either do not breed or breed late (Spur andMilne 1976).

Our results do not support the predictions of the *alternative reproductive strategy* which states that post-hatch brood amalgamation could be maintained in a population as a mixed ESS (Eadie *et al.* 1988). According to Parker (1984), a mixed ESS can be achieved in only two ways: (i) individuals exhibit genetically fixed strategies (polymorphism), or (ii) individuals use strategies randomly within ESS probabilities. If individuals show different behaviours (i.e., abandon a brood in one year and tend broods or crèches the next year), there is no genetic polymorphism. Furthermore, if changes in individual behaviours can be related to any environmental or phenotypic cue, then the whole mixed ESS hypothesis can be rejected as a plausible explanation for such behaviour. Abandoning and adoption of young were not obligate individual strategies but changed between years (Bustnes and Erikstad 1991), and whether or not a female abandoned her nest/ducklings were state-dependent decisions dependent upon nutrient reserves (i.e., phenotypic variation) of common eider hens at the beginning of nest initiation. We suggest that females abandon their brood because of depleted energy reserves, i.e. *energetic stress* and that this may be related to age, i.e. *age or experience* hypothesis (Eadie et al. 1988).

Aldrich and Raveling (1983) found that experience rather than age was the important variable affecting acquisition of reserves in Canada geese, and that inexperienced females were unable to gain enough reserves to provide for maximum nest attentiveness during incubation. We provide clear evidence that whether a female eider cared for young was dependent on her body condition, and that females in poor condition more readily abandoned their young. The age at first breeding for most eiders in

Scotland is 4 years, but some females breed at 2 and 3 years (26% and 45%, respectively) (Baillie and Milne 1982). Two-year-old females start incubation with lower reserves than older birds, and laying dates of eiders become progressively earlier over the first few years of breeding (after which they do not vary with age) and clutch size decreased with increased laying date (Baillie and Milne 1982). Body condition at clutch initiation determines within-season variation in clutch size and laying date (Mawhinney and Diamond 1999b). Whether older females also start incubation with lower reserves is difficult to address given the logistics required to follow marked individuals which are long-lived. However, the survival rate of female eiders decreases progressively in females after 17 years (Coulson 1984) and studies have shown a decline in the breeding performance of older birds (Kear 1973, Coulson *et al.* 1976).

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Table 2.1. Results of ANCOVA to determine factors affecting body weight of common eiders during incubation on the Wolves Archipelago, New Brunswick (1995-1997) and Green Island, Maine (1997-1998).

	Dependent variable = body weight	
Source of variation	F	*p*
Body size (PC1)	40.26	0.001
Days into incubation	1152.7	0.001
Study area	2.13	0.15

Table 2.2. Results of ANCOVA to determine if crèche attendance by common eider hens on the Wolves Archipelago, New Brunswick (1995-1997) and Green Island, Maine (1997-1998) varied with body condition during incubation.

	Dependent variable = body weight	
Source of variation	F	*p*
Body size (PC1)	1.92	0.017
Days into incubation	285.79	0.001
Crèche attendance	9.21	0.001
Body size x Days into incubation	0.4	0.53
Body size x Crèche attendance	11.62	0.001
Days into incubation x Crèche attendance	3.83	0.026
Body size x Days into incubation x Crèche attendance	8.97	0.001

Table 2.3. Fate of nests from nasal-tagged common eider hens with artificially reduced and extended incubation periods.

	1997 (n = 10)		1998 (n = 10)	
	Incubation reduced	Incubation extended	Incubation reduced	Incubation extended
Fate of nests				
Hatched	9	5	8	4
Predated	1	2	2	1
Abandoned	0	3	0	5
Brood attendance				
Tended	3	0	4	0
Auntie	2	0	2	0
Abandoned	0	3	0	2
Unknown	4	2	2	0

Table 2.4. Estimated body condition (mean ± SD) of common eider hens with artificially reduced and extended incubation periods.

	Estimated body condition of common eiders			
Incubation	At nest abandonment (n = 8)	Hatched nests/brood abandoned (n = 9)	Hatched nests/fate of brood unknown (n = 6)	Broods tended (n = 11)
Reduced	$1.16^a \pm 0.02$ (Range = 1.1 - 1.2)	$1.25^b \pm 0.03$ (Range = 1.2 - 1.3)		
Extended			$1.29^b \pm 0.06$ (Range = 1.2 - 1.3)	$1.42^c \pm 0.05$ (Range = 1.3 - 1.5)

Values which share a letter are not significantly different (T-test, $p > 0.05$).

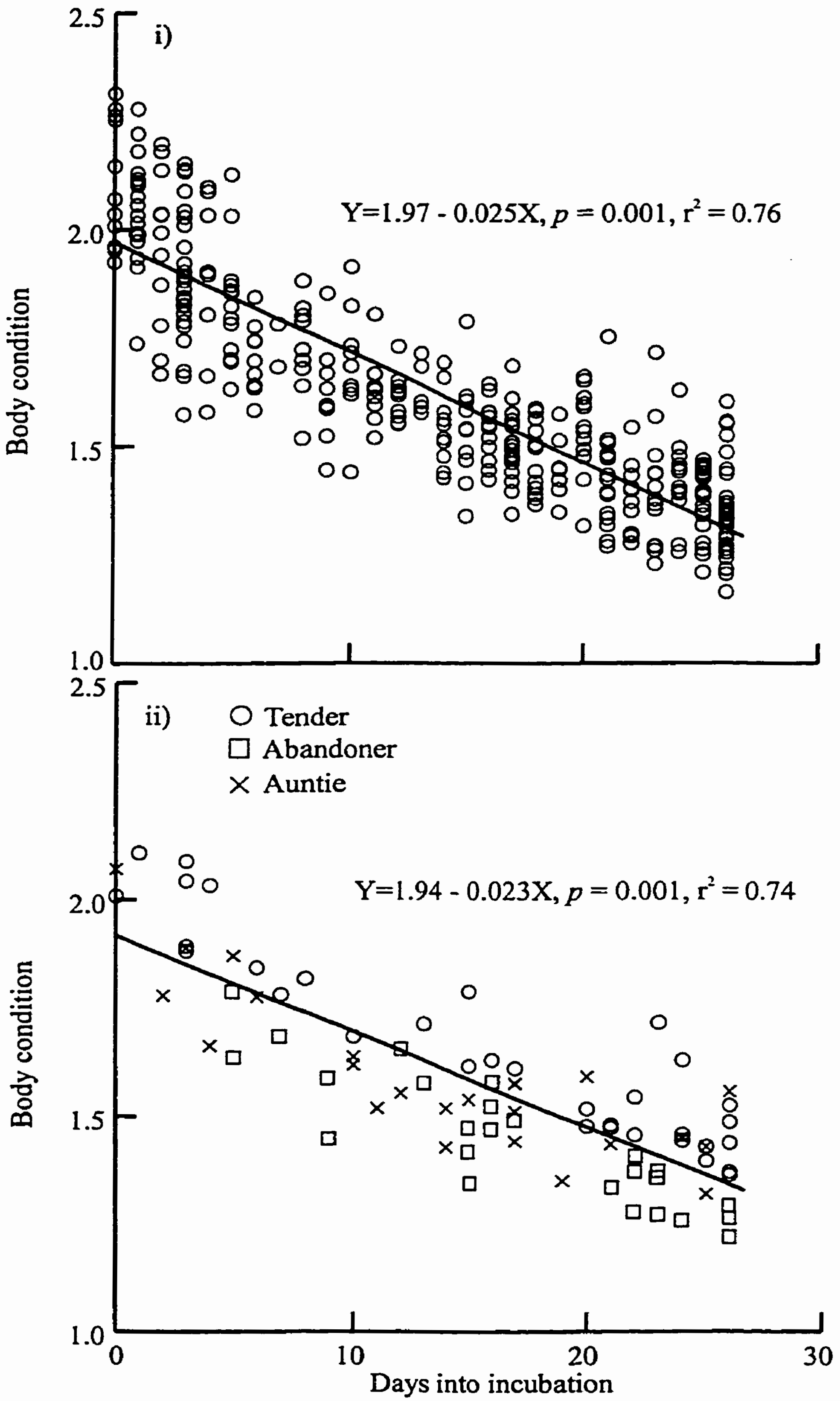

Fig. 2.1. Relationship between body condition (weight (kg) corrected for structural size (PC1)) and i) incubation and ii) subsequent creche attendance in common eiders.

The effect of female condition on clutch size and laying date in common eiders

Chapter 3

Mawhinney, K., C. W. Robbins, and A. W. Diamond. 1999. The effect of female condition on clutch size and laying date in common eiders. J. Avian Biol: *Submitted.*

Abstract

We re-examined the relationship between female condition and clutch size in common eiders and provide evidence which supports the "egg-production hypothesis" that clutch size is limited by a hen's ability to allocate nutrient reserves to egg laying. Clutch size of common eider hens in the Gulf of Maine was related to body condition at clutch initiation and the cost of incubation did not increase with clutch size. Body condition at clutch initiation was strongly correlated with within-season variation in clutch size and laying date. Our results do not support the "incubation-cost hypothesis" that clutch size is determined by the interaction between the allocation of body reserves to egg production, incubation and care of chicks. We argue that clutch size and the likelihood that females tend their own brood are both determined by pre-laying body condition.

3.1. Introduction

The importance of nutrient reserves (lipid, protein and minerals) for reproduction has been most clearly demonstrated in common eiders (*Somateria mollissima*) (Korschgen 1977, Parker and Holm 1990); and arctic-nesting lesser snow geese (*Chen caerulescens caerulescens*) (Ankney and MacInnes 1978), which require reserves for egg production and the metabolic demands of the female during incubation (see Arnold and Rohwer 1991 for review). Common eiders terminate feeding during laying and incubation and lose up to 46% of their body mass from prelaying to hatching (Korschgen 1977, Parker and Holm 1990). Of the total energy at hand before laying began, 33% was used during laying, 35% during incubation and 32% remained at hatching. The body mass of female common eiders increases by about 20% before egg laying (Gorman and Milne 1971). Weight gained by female common eiders before laying was equal to that lost during laying (Parker and Holm 1990), suggesting that increased body reserves in females served breeding directly as capital costs for clutch formation. Lack's (1967, 1968) egg-production hypothesis suggests that clutch size is limited by a hen's ability to allocate nutrient reserves to egg laying. However, recent studies have developed the incubation-cost hypothesis which suggests that optimal clutch size is determined by the interaction between the allocation of body reserves to egg production, incubation (Erikstad 1986, Gloutney and Clark 1991) and care of chicks (Lessells 1986, Bustnes and Erikstad 1991).

Despite compelling evidence that egg production is limited by body reserves (Erikstad and Bustnes 1994) and clutch size is determined before laying starts (Swennen *et al.* 1993), Erikstad *et al.* (1993) suggested that body reserves alone could not determine the clutch size in common eiders because the explained variance ($r^2 = 0.09$) of the relationship between clutch size and female hatching mass was very low. We disagree that this was even a valid test for three reasons. Firstly, they correlated clutch size with hatching mass, but according to their incubation-cost hypothesis (Erikstad *et al.* 1993), females producing large clutches allocate relatively more body reserves to incubation than those producing small clutches to shorten the incubation period. Therefore, mass at the onset of incubation (or termination of laying) as a response variable should have been measured.

Secondly, Erikstad *et al.* (1993) did not control for variation in body size when comparing differences in body mass. Although fat accounts for the greatest variation in body mass (Witter and Cuthill 1993) and fluctuations in overall weight can be a reliable indicator of changes in fat reserves (McEwan and Whitehead 1984, Johnson *et al.* 1985), structurally larger birds may contain more fat than smaller birds because they are bigger, not because they are in better condition. In live birds, body weight corrected for structural size has been widely recognized as a condition index because changes in body weight are due largely to changes in total body fat (Bailey 1979, Reinecke *et al.* 1982, Chappel and Titman 1983, Whyte and Bolen 1984).

Finally, Erikstad *et al.* (1993) did not account for potential variation in egg size associated with individual clutches. Differences in female condition are a potential source of annual variation in egg size (Croxall *et al.* 1992). Previous studies have found no relationship between body weight (Laurila and Hario 1988) or body size (Swennen and Van der Meer 1995) and egg size in common eiders. However, several studies have demonstrated significant annual variation in egg size (Flint and Sedinger 1992, Robertson 1995), while others have not (Erikstad *et al.* 1985, Grant 1991, Smith *et al.* 1993).

A strong negative correlation between laying date and clutch size within and between years has been shown in many species (Klomp 1970, Rohwer 1992), and can account for much of the variation in clutch size (Meijer *et al.* 1990). Milne (1976) found a weak positive correlation between winter body weight of female eiders and clutch size the following spring and suggested that females in better condition tended to lay earlier (Spur and Milne 1976a). In addition, the clutch size of eiders decreased as the season progressed (Spur and Milne 1976a). Late-arriving females in poor condition may reduce clutch size and/or egg quality (size) in an attempt to retain sufficient reserves for fasting during incubation. If egg size is correlated with clutch size or laying date, and these traits vary annually, then egg size will also show annual variation. Alternatively, annual differences in clutch size and egg size may be associated with annual variation in body condition.

Common eider hens captured during incubation on two study areas in the Gulf of Maine provided us with the opportunity to examine the relationship between body weight corrected for structural size (hereafter body condition, Whyte and Bolen 1984) and clutch size, incidentally to other research objectives (Mawhinney and Diamond 1999). The objectives of this study were: i) to determine if clutch size and egg size (weight) of common eiders were related to body condition at clutch initiation; ii) to determine if body condition at clutch initiation varied with laying date; and iii) to examine the relationship between clutch size and cost of incubation.

3.2. Study Area

The Wolves Archipelago (44°56'N, 66°44'W) is a group of 5 islands located 12 km offshore from Beaver Harbour, New Brunswick. The most northerly island, East Wolf, is the largest (2039 ha), followed, north to south, by Green Rock (20 ha), Spruce Island (78 ha), Flatpot Island (233 ha) and South Wolf (425 ha). The dominant vegetation on the islands, with the exception of Green Rock, is balsam fir (*Abies balsamea*)/spruce (*Picea* spp.). The dominant vegetation of Green Rock is grass (Gramineae spp.) and wild raspberry (*Rubus idaeus*). Breeding seabirds include common eiders, double-crested cormorants (*Phalacrocorax auritus*), black guillemots (*Cepphus grylle*), great black-backed gulls (*Larus marinus*) and herring gulls (*Larus argentatus*).

Recent additions include a colony of black-legged kittiwakes (Kehoe 1994) and razorbills (*Alca torda*) (Mawhinney and Sears 1996).

Green Island (5 hectares) (44°30'N, 68°30'W) is located 25 km east of Bar Harbour in the Gulf of Maine, U.S.A. The island is treeless with thin peaty soil, and vegetation consists mainly of grasses. Breeding species include common eiders, great black-backed gulls, herring gulls, black guillemots and one pair of American oystercatchers (*Haematopus palliatus*) (Mawhinney *et al.* 1999).

3.3. Methods

Common eider hens from known nests in the Wolves Archipelago (1996 and 1997) and on Green Island (1997 and 1998) were captured with drop door nest traps (Weller 1957), or as they flushed from the nest. Each bird was weighed to the nearest 0.1 g with a spring balance and six measures of structural size recorded: (1) head + bill length, the maximum distance from the bill tip to the posterior extremity of the occipital process; (2) culmen, from the anterior end of feathering on top of the middle of the bill to the posterior end of the nail; (3) wing chord, with the wing flattened and flexed at the wrist, from the wrist to the tip of the wing; (4) tarsus length, measured with the leg flexed, from the pit at the junction of the tibiotarsus and the tarsometatarus to the distal end of the tibiotarsus; (5) keel length, the distance between the notch at the furculum and the posterior point along the median of the sternum; and (6) total length, from the tip of the tail to the tip of the bill with the bird stretched on its back. All measurements were taken to the nearest 0.1 mm with calipers except wing and total length, which were measured to the nearest mm with a flat stopped ruler. Each bird was then marked individually with plastic nasal tags (Lokemoen and Sharp 1985) and standard U.S.F.W.S. aluminum bands and released.

The number of eggs from each marked hen's nest was recorded, and nests were visited regularly throughout the breeding season to monitor presence, nest contents, and evidence of predation. If the laying sequence of the captured hen's nest was known, the length and breadth of each egg in a clutch were measured to 0.1 mm using dial calipers. The fresh weight of each egg was calculated using: weight (W) = 0.5 V + 10.46, where W = fresh weight of each egg and V = volume index cm^3 = length x $(breadth)^2$ (Baillie and Milne 1982). The average fresh weight of each egg in a clutch was then calculated for each clutch. Known parasitic clutches (nests in which > 1 female laid eggs) were excluded from the analysis.

Structural size of each bird was determined by the first principal component (PC1) scores from an analysis on the correlation matrix of log transformed morphological variables (head + bill, culmen, wing, tarsus, keel, total) (Alisauskas and Ankney 1987, Hanson *et al.* 1990). Body weight (Y_{obs}) was adjusted for variation in structural size by regressing weight on the PC1 score and using the residuals for each bird to calculate a new value, Y_i, which is corrected for body size. The equation is as follows: corrected body weight = residual + mean body weight, or $Y_i = Y_{obs} - ((a + b(PC1)) + Y_{obs})$ (Alisauskas and Ankney 1987, Hanson *et al.* 1990).

Body condition at clutch initiation was estimated for each hen by adding 25.0 g of body weight corrected for structural size (Mawhinney and Diamond 1999) for each day the hen had been incubating and the calculated weight for each egg the hen had laid. Clutch initiation dates were estimated from direct observations of clutch initiation during visits to nests while laying was in progress. An incubation period of 26 days (Choate 1966, Milne 1974), and an interval of 24 hours between the laying of eggs were used to estimate clutch initiation dates. Permanent egg attendance starts from the laying of the second egg and is independent of the actual number of eggs in the nest and the final clutch size (Swennen *et al.* 1993). Data from hens captured more than once in each season were pooled, and we calculated daily loss in body condition during incubation as *(body condition at original capture - body condition at recapture)/number of days* *between capture and recapture.*

Common eiders began to initiate clutches on 10 May 1996 and 18 May 1997 on the Wolves Archipelago and on 4 May 1997 and 15 May 1998 on Green Island. Clutch initiation dates of each nest were subtracted from the initiation date of the first clutch found in each year, to correct for differences related to annual variation in nesting phenology. Analyses of covariance (ANCOVA, SYSTAT, Wilkinson 1988) were performed to test for the independent effects of body condition at clutch initiation, initiation date and year on clutch size for each study area. ANCOVA's were used to determine if body condition at clutch initiation varied with initiation date for each study area. Analyses of variance were used to detemine if body condition at clutch initiation varied between study areas. Mean egg weight of 3-6 egg clutches were compared with an ANCOVA to determine if egg weight varied with clutch size, year and study area. Clutches with < 3 and > 7 eggs were eliminated from analysis due to small sample size. Simple linear regression (SLR) was used to determine if fresh egg weight was correlated with body condition at clutch initiation. ANOVA was used to determine if daily loss in body condition during incubation varied with clutch size.

ANCOVA procedures were based on type III sums of squares. This procedure tests for the effect of an independent variable in the model on the dependent variable by adjusting for the effects of all other independent variables (SAS Institute Inc. 1990). Higher order interactions were excluded from the statistical model if they were non-significant and had no biological importance. Results were considered significant if $p < 0.05$.

3.4. Results

Nest initiation dates were known for 92 (60 in 1996 and 32 in 1997) adult females captured on the Wolves Archipelago and 81 (46 in 1997 and 35 in 1998) captured on Green Island. The structural measurements of eider hens did not load equally on the first principal component axis (PC1) and only head, tarsus and keel were important determinants of structural size. PC1 accounted for 51% of the variation in structural measurements and was characterized by the following eigenvectors: head 0.58; tarsus 0.80; keel 0.75.

Clutch size did not vary between years (ANCOVA $F_1 = 0.8, p = 0.3$) or with clutch initiation date ($F = 1.0, p = 0.3$) but did vary with body condition at clutch initiation ($F = 66.2, p = 0.001$) on the Wolves Archipelago. Clutch size did not vary with year (ANCOVA $F_1 = 3.3, p = 0.1$) or clutch initiation date ($F = 1.3, p = 0.3$) but did vary with body condition at clutch initiation ($F = 82.8, p = 0.001$) on Green Island. Clutch size did not vary between study areas (ANOVA $F_1 = 1.0, p = 0.3$). Clutch size increased with body condition at clutch initiation on both the Wolves Archipelago and Green Island (Fig. 3.1).

Mean egg weight did not vary between years (ANCOVA Wolves Archipelago: $F_1 = 0.4, p = 0.5$; Green Island: $F_1 = 0.3, p = 0.5$), with clutch size (ANCOVA Wolves Archipelago: $F_1 = 0.3, p = 0.6$; Green Island: $F_1 = 1.0, p = 0.3$), or between study areas (ANCOVA $F_1 = 1.0, p = 0.3$). Mean egg weight was not correlated to body condition at clutch initiation (SLR $F = 0.05, p = 0.8$). Mean egg weight was 114 g ± 0.006 SD (n = 170).

Body condition at clutch initiation varied with initiation date ($F_1 = 4.7, p = 0.03$) on the Wolves Archipelago and there was a significant interaction between clutch initiation date and year (ANCOVA $F_1 = 4.1, p = 0.05$). Body condition at clutch initiation was higher for hens initiating clutches earlier in the 1996 breeding season but did not vary in 1997 (Fig. 3.2 (i)). Body condition at clutch initiation varied between years on Green Island (ANCOVA $F_1 = 6.0, p = 0.02$) and with initiation date ($F = 17.9, p = 0.001$). In both years, body condition at clutch initiation declined as the season progressed (Fig. 3.2 (ii)). Body condition at clutch initiation was lower on Green Island in 1997 ($\bar{x}$ = 2.5 kg ± 0.17 SD, n = 45) than in 1998 ($\bar{x}$ = 2.6 kg ± 0.24 SD, n = 36). However, body condition at clutch initiation did not vary between the Wolves Archipelago ($\bar{x}$ = 2.5 kg ± 0.18 SD, n = 92) and Green Island (ANOVA $F_1 = 0.3, p = 0.6$). Loss in body condition during incubation did not vary with clutch size (ANOVA $F_4 = 0.6, p = 0.6$). Mean loss in body condition per day during incubation was 25.4 g/day ± 0.7 (n = 37).

3.5. Discussion

Clutch size of common eider hens in the Gulf of Maine was related to body condition at clutch initiation. In addition, the cost of incubation (measured as the loss in body condition) to individual hens did not increase with clutch size or differ between the two study areas (Mawhinney and Diamond 1999). With the exception of Erikstad and Tveraa (1995), the only study that has demonstrated increased cost of incubation related to clutch size in waterfowl was of parasitized nests in wood ducks *Aix sponsa* (Hepp *et al.* 1990). In natural clutches of wood ducks individual variation in body mass loss was not explained by variation in clutch size (Harvey *et al.* 1989), and other studies of waterfowl have demonstrated that the loss of body mass during incubation does not vary with clutch size (Rohwer 1985).

Energetic costs of incubation have been related to costs involved in reheating eggs after feeding recesses in passerines (Haftorn and Reinertsen 1985, Beibach 1986). Beibach (1986) found that energy costs of rewarming eggs increased with increased length of preceding inattentive periods and lower temperature, but not with clutch size. Several studies have reported no effect of clutch size on the metabolic costs of incubation (Haftorn and Reinertsen 1985, Weathers 1985, Gloutney *et al.* 1996). Female common eiders leave the nest for only about 4 minutes every 2nd or 3rd day to drink, and they insulate their nests with down and cover their eggs when they leave their eggs (Erikstad and Tveraa 1995). Egg temperatures drop only about 1°C during these short breaks

(Mehlum 1991), suggesting the cost of reheating eggs is small.

Erikstad and Tveraa (1995) suggested that females producing large clutches, shorten their incubation period (although not significantly) by allocating more body reserves to incubation to reduce the risk of nest predation. Another possible interpretation is that reduced predation on these nests may be related to increased nest attentiveness associated with the larger body reserves of these hens (Aldrich and Raveling 1983). Common eider females with a large body mass at hatching also have a large body mass at the start of and throughout the incubation period (Mawhinney and Diamond 1999). Common eider hens in poor condition late in incubation may become inattentive to, or abandon, the nest (Korschgen 1977, Bustnes and Erikstad 1991, Swennen *et al.* 1993). Swennen *et al.* (1993) noted that in eiders nearly all eggs lost to predators are lost when the female leaves the nest.

If females use their levels of nutrient reserves as the proximate cue to terminate egg-laying (Ryder 1970, Ankney and MacInnes 1978, Drent and Daan 1980) for future allocation to incubation and the care of chicks (Erikstad *et al.* 1993, Erikstad and Bustnes 1994) then they should not respond to artificially extended incubation periods. In our study females were found dead on or near nests (n = 10) and others responded to artificially extended incubation periods by remaining on the nest up to 7 days to successfully hatch ducklings (Mawhinney and Diamond 1999). The incidence of hens starving to death while incubating a clutch has been documented for eiders (Korschgen 1977) and arctic-nesting geese (Ankney and MacInnes 1978).

It has been well documented that clutch size (Klomp 1970, Milne 1974, Rohwer 1992) and body condition (Spur and Milne 1976a) of hens initiating clutches decreases as the season progresses. Erikstad *et al.* (1993) also found significant relationships between clutch size, body mass and laying date. They performed separate analyses for each because some variables were not available for all females and a simultaneous test of all variables in combination would have restricted sample sizes. In our study, body condition of common eider hens at clutch initiation determined within-season variation in clutch size and laying date. Clutch size did not differ between years, but delayed nesting resulted in reduced body condition of hens initiating clutches on Green Island in 1998 (Fig. 3.2). Weather conditions encountered by common eiders on the breeding grounds can cause significant delays in nest initiation (Hario and Selin 1988), and body reserves may decline while birds wait for nesting sites to become available (Parker and Holm 1990). Reduced clutch sizes resulting from delaying nesting have been documented in arctic-nesting geese and eiders (Barry 1962, Ahlen and Anderson 1980).

Robertson (1995) suggested that the proximate mechanisms affecting clutch and egg size are different. Egg size variation was correlated with the ambient temperatures during the laying period, whereas clutch size variation was correlated with laying date. Since egg size decreases and metabolic costs increase with decreasing temperature, egg size may be more closely related to metabolic rate (Williams *et al.* 1993). Egg size in common eiders is highly repeatable and heritable (Laurila and Hario 1988) and we found no evidence to suggest a trade-off between egg size and clutch size. Egg size did not vary within clutch size, year or study area and was not correlated with female condition.

According to the egg-production hypothesis (Ankney *et al.* 1991), females should reduce their body reserves during egg laying to a fixed threshold independent of clutch size, and the cost of incubating eggs should not increase with clutch size. Body condition at or near the end of laying shows considerable variation in the size of reserves in common eider hens (Mawhinney and Diamond 1999), and in females of other waterfowl species (Ankney and Alisauskas 1991). Ankney and Alisauskas (1991) hypothesized that the fact that some females stop laying with considerably more reserves than others is related to genetic polymorphisms among females relative to their tactics for completing incubation and brood care.

Eiders have a parental care system in which some females abandon their young soon after hatching while others care for their own young and also adopt young from brood-abandoning females (Munro and Bedard 1977, Bustnes and Erikstad 1991). Giving up young after hatching is costly in terms of reproductive success, since the ducklings from brood-tending females survive better than ducklings from brood abandoners (Nastase 1983, Bustnes and Erikstad 1991). The likelihood that females should tend their brood is related not only to body mass at hatch (Bustnes and Erikstad 1991, Mawhinney and Diamond 1999) but also to clutch size (Bustnes and Erikstad 1991). Females hatching larger clutches, which are determined by body condition, tend their brood at a lower body mass than females hatching small broods (Bustnes and Erikstad 1991).

Our results do not support the incubation-cost hypothesis (Erikstad *et al.* 1993). In contrast to Erikstad *et al.* (1993), we argue that clutch size and the likelihood that females tend their own crèche are both determined by pre-laying body condition. Abandoning and adoption of young are not obligate individual strategies but change between years (Bustnes and Erikstad 1991) and depend on body condition at hatch (Bustnes and Erikstad 1991, Mawhinney and Diamond 1999), which itself is dependent on pre-laying condition (Mawhinney and Diamond 1999). Nutrient reserves acquired by hens prior to the breeding season depend on conditions encountered on the wintering grounds including weather (Guillemette 1991), resource availability (Guillemette *et al.* 1992, Guillemette *et al.* 1996), age (Spur and Milne 1976a) and pair formation (Spur and Milne 1976b).

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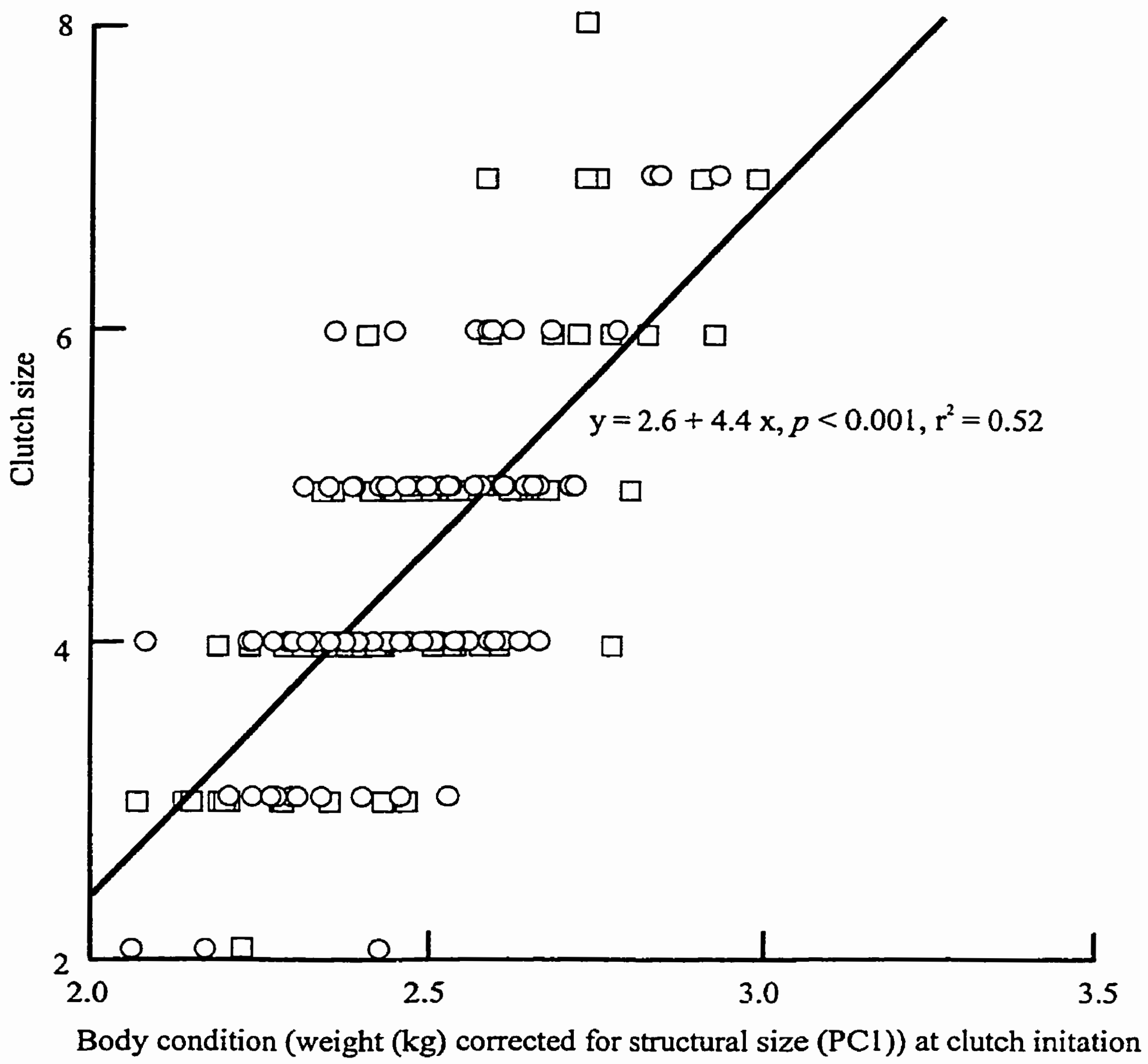

Fig. 3.1. Relationship between clutch size and body condition (weight (kg) corrected for structural size (PC1)) at clutch initiation for common eiders on the Wolves Archipelago, 1996 and 1997 (circles), and Green Island, 1997 and 1998 (squares).

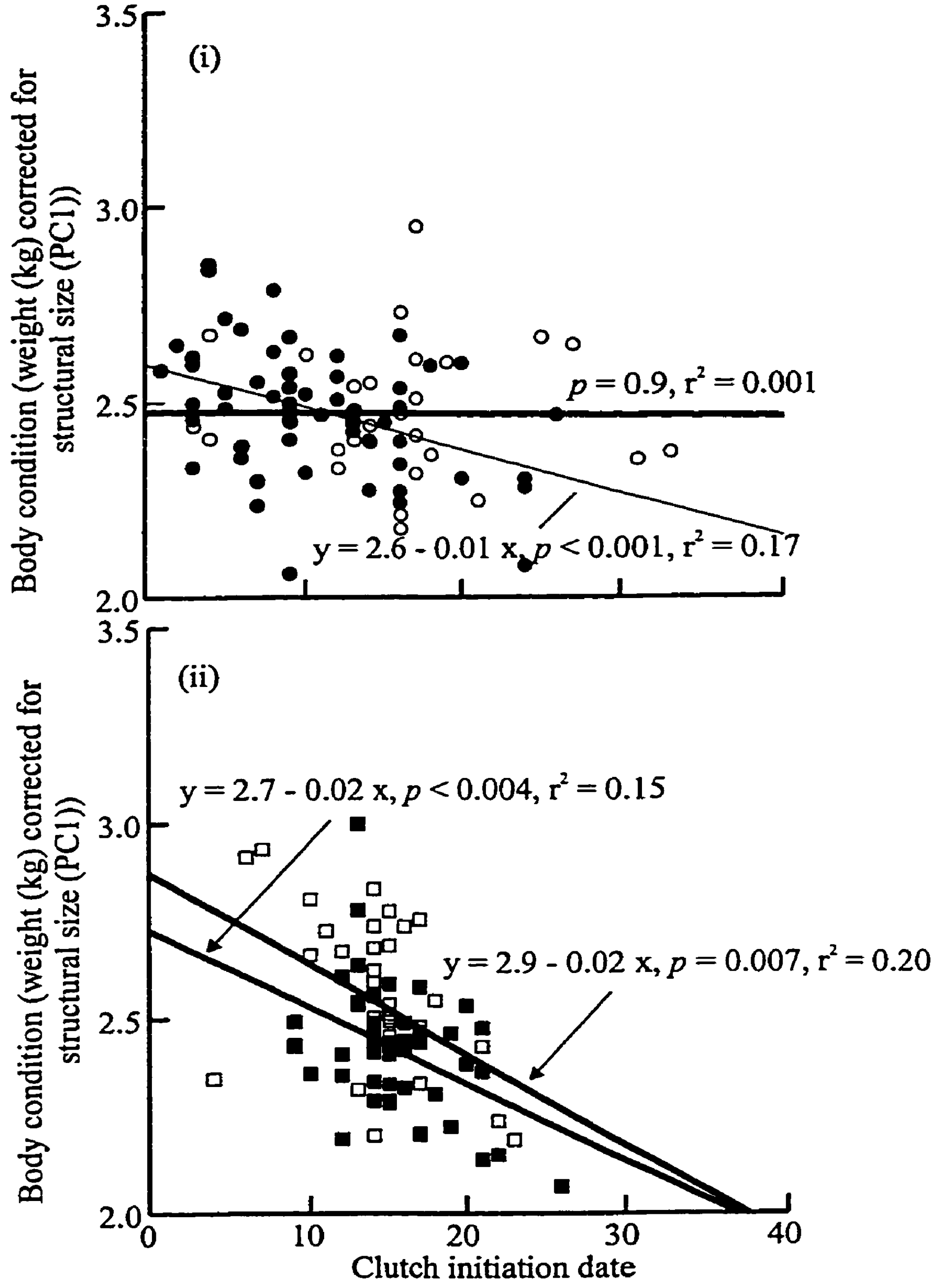

Fig. 3.2. Relationship between body condition (weight (kg) corrected for structural size (PC1)) at clutch initiation and clutch initiation date (corrected by subtracting initiation date for each nest from the initiation date of the first clutch found in each year) for common eiders on (i) the Wolves Archipelago, 1996 (closed circles) and 1997 (open circles), and (ii) Green Island, 1997 (closed squares) and 1998 (open squares).

The effect of gull control on survival of eider ducklings

Chapter 4

Mawhinney, K., and A. W. Diamond. 1999. The effect of gull control on survival of eider ducklings. J. Wildl. Manage: *Submitted.*

Abstract

We examined the impact of great black-backed gull predation on survival of common eider ducklings, between hatching and fledging, in relation to different levels of gull control on the Wolves Archipelago in the southern Bay of Fundy and on Petit Manan National Wildlife Refuge (PMNWR) in the northern Gulf of Maine. There was no difference in daily survival rate (DSR) of ducklings hatched on the Wolves Archipelago between 1995 and 1997, despite limited gull control in 1996. Spraying of gull eggs with an oil emulsion prevented them from hatching, but adult gulls from these nests still depredated eider ducklings. Not enough gulls were killed to reduce predation pressure on eider ducklings hatching from these islands. Total gull control through the elimination of breeding pairs and destruction of nests and eggs was effective in discouraging gulls from renesting and daily survival rate of ducklings was higher on PMNWR (DSR = 0.92) than on the Wolves Archipelago (DSR = 0.35) ($p < 0.001$). The overall numbers of ducklings surviving to fledging was considerably higher in PMNWR (23 - 24% of the breeding pairs in 1997 and 1998), than on the Wolves Archipelago in 1995 - 1998 (< 5% of the breeding pairs in all years). The number of ducklings surviving to fledging on the Wolves Archipelago was not correlated with the commercial catches of herring as an alternative food source for predatory gulls.

4.1 Introduction

The great black-backed gull (*Larus marinus*) constitutes 25% of the large gull population breeding in the southern Bay of Fundy (Diamond *et al.* 1999, Mawhinney *et al.* 1999b) and the northern Gulf of Maine (Drury 1973, 1974, Erwin 1979, Schauffler 1998) and is becoming increasingly important in relation to the numbers of other species. Elsewhere, thriving populations of large gulls are placing increased pressure on the annual production of a number of seabird species (Harris 1966, Thomas 1972, Harris 1980, Burger and Gochfeld 1994, Gilchrist and Gaston 1997). However, the dietary flexibility and larger size of great black-backed gulls makes them better foraging competitors (Furness *et al.* 1992) and more effective predators of seabirds than other species of gulls (Bourget 1973, Harris 1980, Buckley 1990, Russell and Montevecchi 1996).

High predation by great black-backed gulls on common eider (*Somateria mollissima*) ducklings in 1995 precluded a brood ecology study on the Wolves Archipelago (Mawhinney and Diamond 1999). Surveys suggested that although number of common eiders breeding in the Bay of Fundy were unchanged since the late 1980's (ca. 8,500 pairs), the number of ducklings surviving to fledging had declined dramatically (Mawhinney *et al.* 1999b). We proposed culling great black-backed gulls on the Wolves Archipelago (Fig. 1) to increase survival of eider broods in 1996. Canadian Wildlife Service recognized the importance of ensuring brood survival, but suggested that the goal to ensure brood survival could best be increased by preventing the gulls from producing any chicks, eliminating the need for gulls to secure food for their chicks when ducklings hatch and move to sea. In light of these concerns, we revised our original study design to a combination of culling and reducing gull production, and refocused the study to assess the efficacy of limited control as a management action to increase eider recruitment.

In 1997, we expanded the study to include Green Island, in the Gulf of Maine. Green Island is part of a two-island archipelago within the Petit Manan National Wildlife Refuge (PMNWR) (Fig. 1). Between 1984 and 1990, a gull-control program employing the use of the avicide DRC 1339 was instituted on Petit Manan and Green Island by the U.S. Fish and Wildlife Service. Human presence has been maintained on Petit Manan every summer since 1984 to monitor the tern (*Sterna* spp.) population and to actively discourage re-settlement of gulls (Anderson and Devlin 1998). In 1997 and 1998, breeding pairs of great black-backed gulls that had re-settled on Green Island were successfully eliminated by killing at least one member of each pair, and destroying remaining gull nests after successive attempts to trap the pair were unsuccessful.

Most studies of the impact of predation by large gulls have focused on terns (Hatch 1970, Lock 1975, Shealer and Burger 1992, Yorio and Quintana 1997), alcids (Alcidae) (Harris 1980, Nettleship 1972, Gilchrist and Gaston 1997) and black-legged kittiwakes (*Rissa tridactyla*) (Burger and Gochfeld 1994), rather than eiders (Mendall and Milne 1985, Swennen 1989). An understanding of this impact may become important should gull numbers, and subsequent predation rates, increase such that management actions become necessary. The present account quantifies the impact of great black-backed gull (hereafter gull) predation on survival of eider ducklings, between hatching and fledging, in relation to various levels of gull control. We also examined whether the number of ducklings surviving to fledge was related to commercial catches of herring (*Clupea harengus*) stocks from weirs around the Wolves Archipelago for the same years. Herring caught by weirs reflect annual changes in availability (Stephenson *et al.* 1993) and are the major alternative source of food for gulls (Gilliland 1990).

4.2 Study Area

The Wolves Archipelago (44°56'N, 66°44'W) is a group of 5 islands located 12 km offshore from Beaver Harbour, New Brunswick (Fig. 4.1). The most northerly island, East Wolf, is the largest (2039 ha), followed, north to south, by Green Rock (20 ha), Spruce Island (78 ha), Flatpot Island (233 ha) and South Wolf (425 ha). The dominant vegetation on the islands, with the exception of Green Rock, is balsam fir (*Abies balsamea*)/spruce (*Picea* spp.). The dominant vegetation of Green Rock is grass (Gramineae spp.) and wild raspberry (*Rubus idaeus*). Breeding seabirds include common eiders, great black-backed gulls, double-crested dormorants (*Phalacrocorax auritus*), black guillemots (*Cepphus grylle*) and herring gulls (*Larus argentatus*). Recent additions include a colony of black-legged kittiwakes (Kehoe 1994) and two pairs of razorbills (*Alca torda*) (Mawhinney and Sears 1996).

Green Island (5 hectares) (44°30'N, 68°30'W) and Petit Manan Island (6.5 hectares), are located 25 km east of Bar Harbour in the Gulf of Maine, U.S.A. (Fig. 4.1). The islands are connected by a bar at low tide (Fig. 4.1). Both are treeless with thin peaty soil, and vegetation consists mainly of grasses. Breeding species in addition to common eiders and great black-backed gulls, include terns, Atlantic puffins (*Fratercula artica*), razorbills, black guillemots, laughing gulls (*L. atricilla*), herring gulls (Anderson and Devlin 1997) and one pair of American oystercatchers (*Haematopus palliatus*) (Mawhinney *et al.* 1999a).

4.3 Methods

4.3.1. Brood ecology of the common eider

All 5 islands of the Wolves Archipelago were searched systematically for common eider nests following initiation of egg-laying in late April/early May, and were visited weekly throughout the 1995, 1996 and 1997 breeding seasons. Green Island was searched systematically every 5 days for eider nests following egg laying in late April/early May in 1997 and 1998. The eggs within each nest were marked individually with a black felt marker to indicate the nest and number in the laying sequence, and the clutch size was recorded. All eider nests were marked with coloured vinyl flagging on the Wolves Archipelago. On Green Island, a combination of poor nesting cover and high density of eider nests, made it impossible to flag all eider nests. With the exception of Green Island in 1997, the total number of nests on each island was estimated using ratios of nests with marked eggs to those with unmarked eggs in nests counted along a transect north to south on the island 3 weeks into incubation (Walsh *et al.* 1995). On Green Island in 1997 (2 June), a total count of eider nests was conducted by three observers walking in tandem until the entire island was covered.

In mid- to-late incubation adult females were captured with modified Weller nest traps (Weller 1957), or as they flushed from the nest. Each bird was marked individually with plastic nasal pieces (Lokemoen and Sharp 1985) and standard U.S.F.W.S. aluminum bands. The nests of these females were marked with vinyl flagging (or with a different color of flagging tape on the Wolves Archipelago) and were visited regularly throughout the breeding season to monitor presence, nest contents, and evidence of predation. The hatch date of these females was calculated from direct observations of clutch initiation during visits to nests while laying was in progress and/or by candling the eggs (Weller 1956). An incubation period of 26 days, and an interval of 24 hours between the laying of eggs (Choate 1966, Milne 1974) were used to estimate expected hatching dates. Permanent egg attendance starts from the laying of the second egg and is independent of the actual number of eggs in the nest and the final clutch size (Swennen *et al.* 1993). Hatching dates of nests of nasal-tagged females were confirmed by direct observation of ducklings in the nest. At hatch, one duckling from each clutch (Wolves Archipelago: 41 in 1995, 55 in 1996, 21 in 1997; Green Island: 30 in 1997) was fitted with an external radio transmitter (Model 384, 150 MHZ, Advanced Telemetry Systems, Isanti, MN) (Mauser and Jarvis 1991).

Duckling survival was monitored by surveying the water around all islands of the Wolves Archipelago at least twice each week until 4 weeks after peak hatch, and weekly thereafter. Numbers of nasal-marked females and ducklings fitted with radio-transmitters, and the total number of ducklings on the water, were counted in 1995 through 1997. Number and age (Gollop and Marshall 1954) of ducklings and other adult females were recorded for all broods. Surveys were conducted until the youngest ducklings were at least of 35 days old (Class IIc). Number of ducklings surviving to this age-class is considered a reliable index of recruitment because they have survived most of the rearing period (Ringelmen and Longcore 1982; Savard *et al.* 1991; Flint and Grand 1997). Weekly brood surveys were also conducted on the Wolves Archipelago in 1998 to determine if brood survival was higher when researcher disturbance on the breeding colonies was restricted to gull counts conducted in early May. Coastal surveys were conducted in 1995 and 1996, at 10 and 20 days following hatch, to determine if long-distance movements were made by ducklings hatched from hens marked on the Wolves Archipelago. The water around Petit Manan and Green Island was surveyed daily until 4 weeks after hatch and weekly thereafter in 1997 and 1998. Coastal surveys were conducted every 7 - 10 days to determine long distance movements the broods hatched from hens marked on Green Island.

Aerial surveys were also conducted in the southern Bay of Fundy along the New Brunswick coast from Saint John west to St. Andrews and extended to all coastal and offshore islands and the Grand Manan Archipelago, 2, 6 and 7 weeks post-hatch to monitor ducklings fitted with radio transmitters in 1995 through 1997. Flights were conducted in the northern Gulf of Maine between Schoodic Point and Jordan's Delight four weeks post-hatch to monitor ducklings fitted with radio transmitters in 1997. Flights were conducted from a Cessna 150 in New Brunswick and a Cessna 120 in Maine. The aircraft were flown parallel with the coast at a height of 75 m and a speed of 160 km/hr on a course approximately 120 m offshore between 1.5 hours before and after high tide.

In all years and at both study sites, some radio-transmitters were neither recovered nor detected on live ducklings during monitoring flights throughout of the Bay of Fundy (1995, n = 8; 1996, n = 11; 1997, n = 5) or in the northern Gulf of Maine (1997, n = 4). The lost transmitters may represent gull predations regurgitated in unrecoverable areas (Mawhinney and Diamond 1999). However, we cannot eliminate the possibility that these radios may have simply failed, and they were therefore eliminated from subsequent analysis.

Ducklings > 25 days became progressively more difficult to locate, as they fed further offshore or left the study area altogether. We analyzed duckling survival to 25 days relative to age, beginning with age 0 as the hatch date. We assumed that all mortalities occurred at the mid-point of the observation interval. We used the methods of Flint *et al.* (1995) to estimate the daily survival rate (DSR) of ducklings. This technique allows for mixing of young among broods and does not require the assumption that the survival probability of ducklings within broods was independent. We calculated a base DSR assuming constant survival from 0 to 25 days for each year and compared DSRs among treatment groups (broods with radio-tagged ducklings and broods of marked hens) and years following the methods of Sauer and Williams (1989). We examined whether the number of ducklings surviving to fledge was related to commercial catches of herring stocks from weirs around the Wolves Archipelago for the same years using simple linear regression (SLR)(SYSTAT, Wilkinson 1988).

The importance of amphipods and *Littorina* spp. to young eider ducklings has been well documented (Pethon 1967, McAloney 1973, Cantin *et al.* 1974). To determine if rockweed (fucoid spp.) habitats used by ducklings were related to prey abundance, shorelines identified as important areas for eider broods, and areas with similar shorelines where ducklings were not observed, were sampled for available invertebrates (Fig. 4.1). Rockweed within a 10 cm x 10 cm quadrat was sampled for attached interstitial invertebrates along two transects running parallel to the shoreline, 3 metres below mean low tide and at mid-tide. From each of the two transects, 3 samples were taken within one metre of one another at 3 stations spaced 35 metres apart, for a total of 9 samples/transect. These samples were washed and immediately preserved in 95% ethanol. All species in a sample were identified (Littorina: *Littorina obtusa*, *L. saxatilus*, *L. littorea*; Amphipods: *Calliopius laeviusculus*, *Marinogammarus finmarchicus*, *M. obtusatus*, *M. stoerensis*, unknown gammarid amphipods) with the aid of a dissecting microscope, and counted. *Littorina* were measured, and preferred size classes (3-5mm) taken by ducklings in the area (Hamilton 1997) were counted. Non-parametric Mann Whitney-U and Kruskal-Wallis tests were used to determine if prey abundance differed within and between rockweed habitats used by ducklings.

4.3.2. Great black-backed gulls

All islands in the Wolves Archipelago were searched systematically for gull nests following initiation of egg laying in mid-April/early May in 1995-1998. Nests were marked with numbered wooden stakes, and their locations recorded. In 1996, gulls were eliminated through a combination of shooting and nest trapping on Spruce and Flatpot Island (Table 4.1), where eider nests, and therefore potential duckling production, were highest. Adult gulls nesting on these two islands were captured on the nest (sea-bird traps, Mills and Ryder 1979) and killed by cervical dislocation. Gulls were trapped in mid- to late-April, prior to eider nest initiation; any gulls remaining on these two islands by late May were shot or had their nests destroyed.

The clutches of gulls on South Wolf Island and Green Rock were sprayed with a mixture of dye (Rhodamine B, Green Rock; Malachite Green, South Wolf) and white mineral oil (65% in water) 2 to 3 times during the incubation period to prevent hatching (Morris and Siderius 1990) (Table 4.1). The dyes color-marked incubating adults which helped to facilitate identification of gulls observed depredating ducklings. Thereafter, nests were visited regularly throughout the breeding season and checked for presence of incubating adult and fate (successful or unsuccessful). Re-colonization of the study area by breeding gulls was monitored in subsequent breeding seasons (1997 and 1998).

Green Island was searched systematically for great black-backed gulls nests when egg laying started in late April/early May in 1997 and 1998. One adult from each pair was captured on the nest (sea bird traps, Mills and Ryder 1979) and killed by cervical dislocation. Gull nests left on the island by late May were destroyed after successive attempts to trap the pair were unsuccessful. In 1998, the number of non-breeding adult gulls loafing on Green Island following gull control was counted twice each day (05:00-09:00; 15:00-18:00) throughout the breeding season from the 37.5 metre lighthouse tower on Petit Manan Island. Analyses of variance (ANOVA, SYSTAT, Wilkinson 1988) were used to test whether the number of gulls loafing on Green Island varied with time of day and hatching phenology (pre-hatch = following gull control and prior to eider duckling hatch; hatch = date of first known hatch to last known hatch of eider ducklings; post-hatch = following last known hatch date of eider ducklings) .

4.4. Results

4.4.1. Brood ecology of the common eider

Apart from two ducklings radio-tagged in 1996, all transmitters that were recovered from radio-tagged ducklings on the Wolves Archipelago in 1995 (n = 34), 1996 (n = 46) and 1997 (n = 16), had been depredated by great black-backed gulls. In 1996, one duckling radio-tagged on Green Rock appeared to have died enroute to the water, and another on Spruce was found dead in the nest. Of the 30 ducklings radio-tagged on Green Island in 1997, 22 were depredated by great black-backed gulls, 2 fledged in the immediate vicinity of Petit Manan Island, and 2 fledged in brood-rearing areas, 6 km from their hatching island.

Between 1995 and 1997, 392 (176 in 1995, 126 in 1996 and 90 in 1997) adult females breeding on the Wolves Archipelago were captured and nasal-tagged. Only one was observed with a surviving brood in 1995, 2 in 1996 and 3 in 1997. Of 263 (132 in 1997 and 131 in 1998) adult females captured and nasal-tagged on Green Island, 21 (12 in 1997 and 9 in 1998) were observed with ducklings. Daily survival rate (DSR) of radio-tagged ducklings did not differ from that of ducklings from broods of marked hens on the Wolves Archipelago ($\chi^2_1 = 0.0030, p < 0.99$ for 1996; $\chi^2_1 = 0.011, p < 0.90$ for 1996; $\chi^2_1 = 0.63, p < 0.50$ for 1997) or Green Island in 1997 ($\chi^2_1 = 0.53, p < 0.50$). There was no difference in DSR of ducklings among years on the Wolves Archipelago ($\chi^2_2 = 1.09, p < 0.75$) and Green Island ($\chi^2_1 = 0.0083, p < 0.95$). Daily survival rate of ducklings hatched on the Wolves Archipelago was lower than for those hatched on Green Island ($\chi^2_1 = 31.21, p < 0.001$, Table 4.2).

All radio-tagged ducklings were depredated by gulls within the first week of hatch and brood surveys corroborated that ducklings were the most vulnerable within the first week of hatch (class 1A, Gollop and Marshall 1954). Class 1A ducklings were regularly observed on the water around the islands of the Wolves Archipelago during hatch in each year, but very few survived to subsequent age classes (Table 4.3). The number of ducklings observed surviving to fledging on the Wolves Archipelago between 1995 and 1998 was not related to the catch per unit effort of commercial herring landings in July - August (SLR: $F_3 = 0.35, p = 0.59$).

The overall number of ducklings fledged per breeding pair was considerably higher in the Petit Manan/Green Island Archipelago in 1997 and 1998, than on the Wolves Archipelago in 1995 to 1997 (Table 4.2). One-hundred and eighty-five (185) and 198 ducklings fledged in the immediate vicinity of the breeding colony in 1997 and 1998, respectively. Nasal-tagged females with ducklings (n = 1 in 1997 and n = 5 in 1998) were observed along the mainland coast at Petit Manan Point and other coastal islands further inshore (Bois Bubert, Douglas Islands) (Fig. 4.1). Broods along the coastline observed with nasal-tagged hens accounted for an additional 5 ducklings in

1997 and 50 ducklings in 1998. Broods with nasal-tagged females from the Wolves were not observed along the mainland coast between 1995 and 1998.

Littorina density did not vary between coves within an island among the Wolves ($p > 0.05$ in all cases) or between islands (K-W test statistic = 1.2, $p = 0.89$) on the Wolves Archipelago in 1996 ($\bar{x} = 15$ *Littorina* / 10 cm^2 ± 36 SD, n = 412). The abundance of amphipods did not vary between coves within an island ($p > 0.05$ in all cases) or between islands (K-W test statistic = 4.5, $p = 0.34$) on the Wolves Archipelago ($\bar{x} = 2$ amphipods / 10 cm^2 ± 4 SD, n = 412).

The abundance of *Littorina* did not vary between coves on Green Island (K-W test statistic = 0.8, $p = 0.68$) and did not vary between islands (K-W test statistic = 1.3×10^3, $p = 0.146$)(3 *Littorina* / 10cm^2 ± 7 SD, n = 108). *Littorina* varied between coves on Petit Manan (K-W test statistic = 17.9, $p = 0.001$) and were more abundant on the south and west cove ($\bar{x} =$ 5 *Littorina* / 10cm^2 ± 8 SD, n = 36). *Littorina* were absent in the north cove. Amphipoda abundance tended to be higher, though not significantly so (K-W test statistic = 1.1, $p = 0.08$) on Green Island ($\bar{x} = 12$ amphipods / 10 cm^2 ± 14 SD, n = 54) than on Petit Manan ($\bar{x} = 8$ amphipods / 10 cm^2 ± 19 SD, n = 54). However, on Petit Manan, amphipods were more abundant ($\bar{x} = 22$ amphipods / 10 cm^2 ± 14 SD, n = 18), though not significantly (K-W test statistic = 3.2, $p = 0.21$) on the north cove, where *Littorina* were absent.

4.4.2. Great black-backed gulls

In 1996, 245 great black-backed gulls were killed on Spruce Island and Flatpot Island by 29 May, 126 by nest-trapping and 119 by shooting. Of the gulls nest-trapped, 16 pairs and 94 (26 males and 68 females) gulls of a pair were taken from individual nests. Eleven great black-backed gull pairs abandoned their nests altogether as a result of nest-trapping activity and 7 nests were destroyed late in the incubation period after successive attempts to trap or shoot the pairs were unsuccessful. Gulls recolonized

Flatpot and Spruce Island in 1997 and 1998 following the elimination of breeding pairs from these islands in 1995, but the overall number of gulls nesting on the Wolves Archipelago declined in each breeding season following gull control (Table 4.1).

All gull eggs on Green Rock and South Wolf were prevented from hatching in 1996, but most gulls were still incubating on 26 and 28 May, respectively. In 1995, hatching of great black-backed gull nests had been completed by 21 May (unpublished data), and in 1996, most nests on East Wolf, the control island, were hatched by 16 May. Color-marked gulls from both Green Rock and South Wolf island were observed loafing on Flatpot Island and Spruce Island and were seen taking eider ducklings. Twelve gulls (of which three were colour-marked) loafing on exposed rocks identified as gull specialist locations (Gilliland 1990), on Flatpot Island and Spruce Island, were shot in June (when eider broods were on the water) and were replaced by other gulls within 2 days.

Twenty-five gulls were eliminated from Green Island by nest trapping by 11 May 1997. Three gull pairs abandoned their nests altogether following nest-trapping activity and 19 nests were destroyed late in the incubation period after unsuccessful attempts to trap them. Despite the fact that all breeding pairs (25) were eliminated from Green Island prior to eider nest initiation, 40 - 65 gulls were consistently observed loafing in areas on Green Island throughout the eider breeding season and during peak duckling hatch. In 1998, 48 gulls were eliminated by nest trapping from Green Island by 28 May. Eleven pairs abandoned their nests altogether following nest-trapping activity, 3 nests were destroyed late in the incubation period after unsuccessful attempts to trap them and 4 nests were depredated. The number of adult gulls loafing on Green Island did not vary with hatch of eider ducklings on Green Island ($\bar{x} = 36 \pm 9$ SD, n = 25) (ANOVA: $F_2 = 0.69, p = 0.51$). The number of gulls loafing on Green Island in late afternoon did not differ (ANOVA: $F_2 = 0.72, p = 0.50$) from early in the day during pre-hatch ($\bar{x} = 24 \pm 12$

SD, n = 7) and post-hatch ($\bar{x} = 33 \pm 12$ SD, n = 3) but was higher during hatch ($\bar{x} = 95 \pm 16$ SD, n = 10) (ANOVA: $F_2 = 41.05, p < 0.001$).

4.5. Discussion

Our estimates of duckling survival on Petit Manan/Green Island, where breeding pairs of gulls were eliminated, were considerably higher than that on the Wolves Archipelago, where there was limited or no gull control. Ducklings fledged from PMNWR were an important source of recruits for the local breeding population of common eiders in the Gulf of Maine (Mawhinney *et al.* 1999b). Duckling survival on the Wolves Archipelago was considerably lower than that reported for common eiders in Scotland (Mendenhall and Milne 1985) (10.4%) and for waterfowl in general (10-68%) (Reed 1975, Ringelman and Longcore 1982, Talent *et al.* 1983, Lokemoen *et al.* 1990, Savard *et al.* 1991, Flint and Grand 1997). The current levels of recruitment in the Bay of Fundy population are not enough to offset the estimated 13% mortality rate of adult female eiders originating in the Atlantic Coast (Krementz *et al.* 1996). However, the population of common eiders on the Wolves Archipelago has remained stable (ca. 700-800 breeding pairs) over the last decade despite the low production of fledglings in the same period (see Hicklin 1989, Mawhinney *et al.* 1999b). Low production of ducklings on the Wolves Archipelago may be balanced by high adult survival (Krementz *et al.* 1996) and some immigration from other local breeding colonies in Passamaquoddy Bay (unpublished data); similar patterns of low duckling production balanced by a high adult survival and some immigration has been documented in other eider populations (. Baillie 1981, Swennen 1983, Ahlund and Gotmark 1989).

Gilliland (1990) suggested that gull predation on eider ducklings from the Wolves Archipelago in 1988 and 1989 accounted for < 10% of duckling mortality, and suggested that females were moving ducklings away from the Wolves Archipelago to coastal brood rearing areas. However, Gilliland's (1990) estimates of gull predation were based on duckling remains found in association with gull nests and loafing areas. Mark-recapture ratios from radio-transmitters retrieved from ducklings depredated by great black-backed gulls suggest that gull predation on eider ducklings is considerably higher than that accounted for by nest debris associated with gull nests and loafing areas alone (Mawhinney and Diamond 1999). Also, we found no evidence to suggest that ducklings hatched on the Wolves Archipelago were moving to coastal brood-rearing areas. In contrast, ducklings hatched on Green Island were observed in coastal brood-rearing areas 6 km from their hatching island, along the mainland coast at Petit Manan Point and other coastal islands further inshore.

In general, it has been suggested that gull predation on common eider ducklings is greater during years when alternative food items are more scarce for gulls (Beetz 1916, Beloposki 1957, Gilliland 1990). Mendenhall and Milne (1985) observed unusually high survival rates among common eider ducklings in 1 year of their study when alternative food sources for gulls were abundant. However, Orians and Janzen (1974) suggested that ducklings will always be preferred as food over invertebrates or fish; and Swennen (1989) found that inspection of broods by foraging gulls was as frequent in years with high eider fledging success as in years with poor success. The number of ducklings surviving to fledge on the Wolves Archipelago was not correlated with the commercial catches of herring. We suggest that gull predation of eider ducklings on the Wolves Archipelago does not depend on the availability of alternative prey.

Mendenhall and Milne (1985) estimated ducklings to be vulnerable to gull predation 12.4 hours/day (finding no predation on resting young and assuming no predation at night). However, in both New Brunswick and Maine, gull predation attempts were observed at all times of the day during the entire brood-rearing period (June to August), and the retrieval of transmitters from marked ducklings suggests that predation may occur at night; in several cases, a transmitter was retrieved in a gull pellet the morning after a ducklings was observed alive on the water the prior evening. A considerable proportion of feeding takes place at night in several gull species (Witt *et al.* 1981, Burger and Staine 1993, Castilla and Perez 1995) and great black-backed gulls are able to forage from 16-24 hours a day, in a wide ranges of light conditions (Hatch 1970, Nocera and Kress 1996).

Poor breeding performance caused by investigator disturbance and attributed to other causes may initiate unwarranted concern and misallocation of conservation resources (Rodway *et al.* 1996). In addition, disturbance by boats can markedly raise gull predation on eider ducklings (McAloney 1973, Ahlund and Gotmark 1989). Hens observed with broods on the water around the Wolves Archipelago were given a wide berth in order to limit observer-induced predation during boat surveys, and the number of ducklings fledged did not increase in 1998, when researcher disturbance on the Wolves Archipelago was limited to a few weeks in early May. Boating associated with fishing activities around the Wolves Archipelago is most intense from mid-July to mid-September, well after ducklings have hatched. Recreational boating is limited to a few local areas within the Bay of Fundy, and it is unlikely that boating activity occurred frequently enough to account for the overall low fledgling success in the Bay of Fundy (Mawhinney *et al.* 1999b).

The pattern we observed of high predation by gulls early in brood rearing, has been well documented in common eiders elsewhere (Mendenhall and Milne 1985, Ahlund and Gotmark 1989, Swennen 1989). Predation by gulls is an extremely important factor in duckling mortality (Mendenhall and Milne 1985, Ahlund and Gotmark 1989, Swennen 1989), and any mechanism that reduced mortality from predation would be selectively advantageous. In both Maine and New Brunswick, post-hatch movement by hens with surviving broods away from their hatching islands was not related to prey abundance; rather we interpret it as a tactic adopted by hens to avoid predation by moving ducklings away from the largest concentrations of great black-backed gulls. Surviving ducklings hatched from Spruce and Flatpot Island, in the Wolves Archipelago, were observed only around the north-east tip of East Wolf and the south-west end of South Wolf, where the number of breeding gulls was lower (Table 4.1). Surviving ducklings hatched from Green Island were observed around Petit Manan which was gull-free or other brood-rearing areas away from the two-island archipelago. Once on Petit Manan, broods spread out along the entire coastline during high tide, and during low tide, adult females brought ducklings (1-20 days old) to feed at the north tip of the island (Fig. 4.1) where the abundance of amphipods was highest.

4.5.1. Management implications

We demonstrated that limited gull control was not an effective management action to increase eider recruitment on the Wolves Archipelago. Reducing gull production was not effective in clearing the islands of nesting gulls nor did it reduce the number of nesting pairs on these islands during the study period. The adult birds retained territories and continued to prey on eider ducklings on their own nesting islands, as well as those islands cleared of breeding pairs earlier in the breeding season. The spraying of eggs with an oil emulsion had the desired effect of preventing eggs from hatching, but did not reduce gull predation on eider duckling.

Limiting reproductive output can be an effective method of control for herring gulls (Gross 1951, Wanless *et al.* 1996) but not for lesser black-backed gulls (*L. fuscus*) (Wanless *et al.* 1996). Increases in Maine herring gull populations were halted by coastal measures in the 1940's and 1950's (Gross 1951), but the work was discontinued for financial reasons (Graham and Ayres 1975). Herring gull immigrants were deterred from nesting on Isle of May both in years when reproductive output was controlled and the colony was subjected to considerable disturbance, and in later seasons when no clutches were destroyed (Wanless *et al.* 1996). However, limiting reproductive output is not an effective method to control lesser black-backed gulls which have higher adult survival and immigration rates (Wanless *et al.* 1996). We do not know how effective it might be with great black-backed gulls. Neither adult survival or immigration rates are known, but the breeding population on the Wolves Archipelago continued to decline for several years following the single year of control by culling.

Gulls on the Wolves Archipelago were shot prior to the initiation of eiders nesting and well into incubation to reduce the likelihood of nest abandonment by eiders. However, persistent shooting of gulls on the Wolves Archipelago led to their becoming wary and progressively more difficult to shoot. Shooting does not seem to be a successful method of reducing colonies of gulls because only a small number of gulls in a colony can normally be shot and there is little consequent effect on the breeding success of the colony (Thomas 1972). In addition, the noise and/or disturbance incurred from using guns may be deleterious to other bird species because it may give the gulls opportunities to steal unguarded eggs and chicks (Wanless *et al.* 1996). Culling gulls trapped on the nest was extremely effective in eliminating breeding pairs locally, but not enough gulls from the Archipelago were killed to be effective in reducing predation pressure on eider ducklings hatching from these islands. In cases where gull control is deemed necessary, control measures taken should ensure that enough gulls are eliminated to be effective.

It has been suggested that most eider ducklings are depredated by great black-backed gull 'specialists' and that the removal of such gulls would alleviate the duckling mortality associated with them (Gilliland 1990). On the Wolves Archipelago, great black-backed gulls that specialized on ducklings used nest locations on high grassy areas and rocks that afforded them clear access to duckling broods (Gilliland 1990). Great black-backed gulls using these areas on Flatpot Island and Spruce Island during brood surveys in 1996 were shot, but were replaced by other gulls by the following brood survey (i.e., within 2 days). Clearly, 'specialization' on eating eider ducklings was a function of the nest site, not of individual differences in gull behaviour. Spear (1993) also found that 'specialist' in western gulls were replaced quickly, and feeding territory and to a lesser degree the number of specialists appeared to covary annually with the number of guillemots and cormorants nests in the colony.

Large numbers of adult gulls have been killed at many colonies over the past 20 years. Although in most cases this has resulted in a rapid and substantial reduction in the breeding population of the colony concerned, the method has been judged to be less effective than expected, mainly because culls tend to reduce nest density and thus provide conditions which are extremely attractive to recruits (Bruyns 1958, Thomas 1972, Chabrzyk and Coulson 1976, Duncan 1981, Spaans *et al.* 1991). In herring gulls, however, large scale culling has been shown to disrupt the dynamics of recruitment over a wide area, producing a knock-out effect whereby birds deterred from breeding in a culled colony emigrate to other colonies (Duncan 1981, Coulson 1991). There appeared to be no immigration or recruitment of great black-backed gulls to the Wolves Archipelago in breeding seasons subsequent to gull control rather, the number of gulls nesting declined with each subsequent breeding season. Perhaps researcher disturbance on the colony was enough to deter gulls from nesting on the Wolves Archipelago in years following the cull.

In Maine, total gull control through the elimination of breeding pairs and destruction of nests and eggs was effective in discouraging gulls from renesting, but some non-nesting gulls remained on Green Island throughout the breeding season. The success of the gull control on this eider colony was largely a result of the gull-free refuge for broods provided by Petit Manan. The management effort at Petit Manan has focused on terns and requires human presence to actively discourage resettlement of gulls (Anderson and Devlin 1998). Eiders are less tolerant of disturbance and human presence on their breeding colonies often leads to abandonment of nests (Sabean 1972) and even the colony (Hilden 1964). Eiders breeding on Ship Island in Maine prior to 1995 abandoned the island and moved to a neighbouring island (Trumpet) when human presence was maintained on Ship Island for management efforts focused on tern restoration in 1996 (B. Allen pers. comm.). Perhaps the best we can do for eiders is to eliminate breeding pairs of gulls from nesting islands that are close to islands, such as those provided on colonies managed for terns, which provide a gull-free refuge with sufficient rearing habitat for eider broods.

We suggest that in cases where great black-backed gulls are nesting on small islands crowded with nesting eiders, and especially where the gulls' consumption of ducklings is known to be excessive (i.e., to exceed recruitment), immediate local control may be justified, provided that gull reduction programs are exercised on a local level where control measures can be effective (i.e., adjacent to gull-free brood-rearing habitat). Local control should be conducted only at major colonies of seabirds to ensure high productivity and a sufficient supply of new individuals to the breeding colony. This would ensure a highly productive central stock that would contribute to the sustainability of the population and help to offset population declines caused by gulls elsewhere (Lock 1975).

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Table 4.1. Number of great black-backed gull (*Larus marinus*) nests on the Wolves Archipelago, 1995-1998.

	Year			
Island	1995	1996	1997	1998
South Wolf	122	131[a]	112	88
Flatpot	109	87[b]	78	41
Spruce	75	69[b]	39	38
Green Rock	98	95[a]	108	68
East Wolf	28	46	28	14
Total	432	428	365	249

[a] Eggs sprayed with oil emulsion to prevent hatch.

[b] At least one member of each breeding pair killed.

Table 4.2. Estimated daily survival of common eider ducklings (uncorrected for total brood loss) on the Wolves Archipelago, New Brunswick, 1995-1997 and Green Island, Maine (1997-1998).

Variable	Wolves Archipelago	Petit Manan/Green Island
Duckling exposure days	1868	4720
Broods observed	318	120
Estimated DSR[a]	0.3478	0.9237
SE[b]	0.0576	0.0271
Proportion surviving to 25 days[c](%)	3.41×10^{-10}	13.76

[a] Estimated daily survival rate (DSR) following Flint *et al.* (1995).

[b] Standard error (SE) based on variance calculated among DSRs for each brood (Flint *et al.* 1995).

[c] DSR raised to power of 25 days, assuming constant survival.

Table 4.3. Estimated number of common eider (*Somateria mollissima*) nests and ducklings fledged on the Wolves Archipelago, 1995, 1996, 1997, 1998 and on Green Island, 1997 and 1998.

	Year	Nests[a]	Ducklings fledged	Ducklings fledged per pair
Wolves Archipelago	1995	770	12	0.016
	1996	756	8	0.011
	1997	843	46	0.055
	1998	709[b]	14	0.02
Green Island	1997	800[c]	194	0.24
	1998	1086	248	0.23

[a] Based on ratios of nests with marked eggs to those with unmarked eggs of nests counted three weeks into incubation.

[b] Based on breeding pair survey (Mawhinney *et al.* 1999b).

[c] Total count.

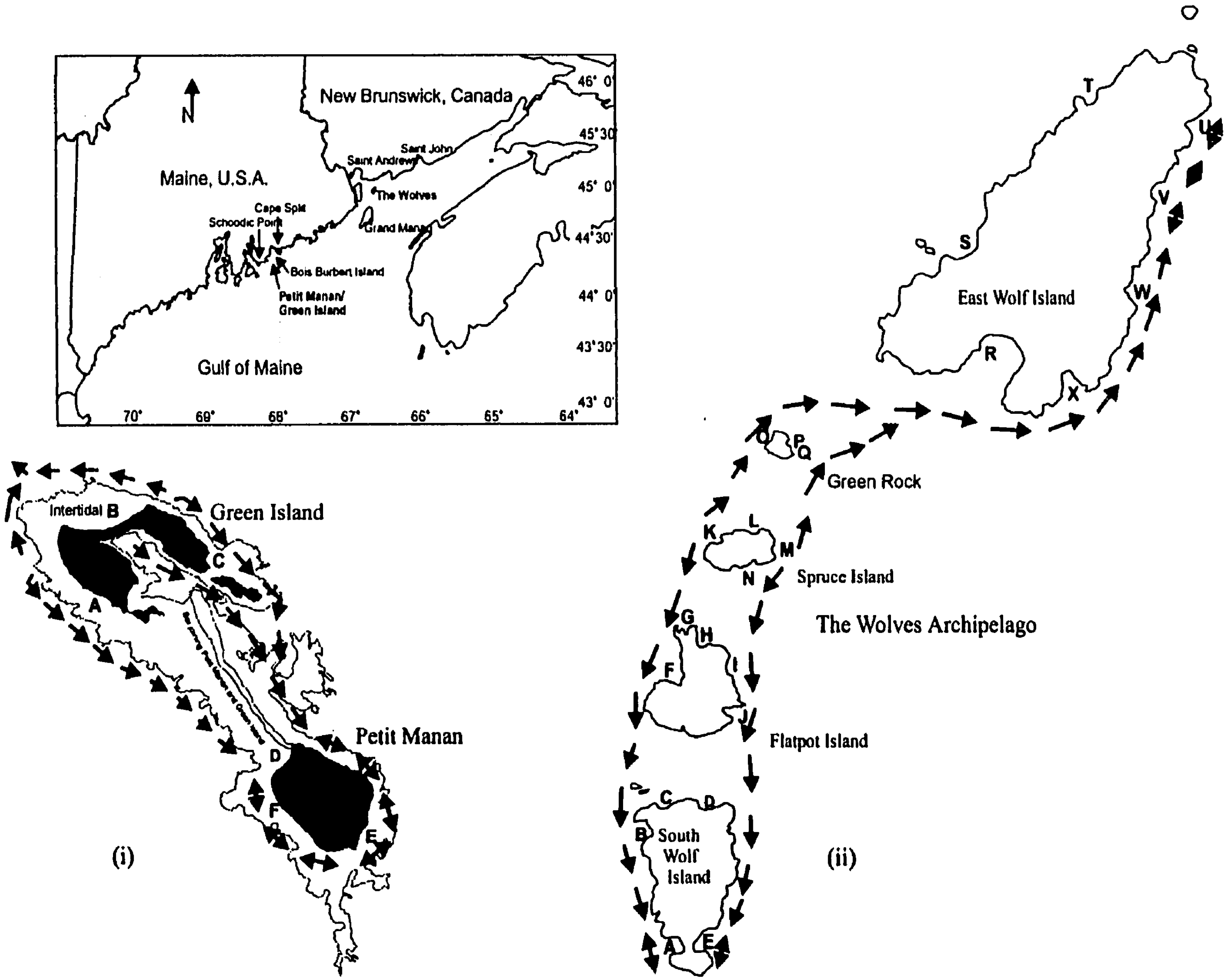

Fig. 4.1: Location of the study areas in the Gulf of Maine: (i) Petit Manan and Green Island, U.S.A. and; (ii) The Wolves Archipelago, Canada. Letters indicate coves from which invertebrate samples were collected. Arrows depict the movement of hens with broods from their nesting islands.

Using radio-transmitters to improve estimates of gull predation on common eider ducklings

Chapter 5

Mawhinney, K., and A. W. Diamond. 1999. Using radio-transmitters to improve estimates of gull predation on eider ducklings. Condor 101: 824-831.

Abstract

We quantified the efficacy of using pellet numbers to estimate predation rates on common eider (*Somateria mollissima*) ducklings by great black-backed gulls (*Larus marinus*) using eider ducklings fitted with radio transmitters. Ducklings fitted with radio-transmitters were no more vulnerable to gull predation than were other ducklings. The recovery of radio-transmitters attached to eider ducklings and subsequently retrieved from great black-backed gull pellets suggests that traditional methods of estimating the number of eider ducklings eaten by gulls from the remains found in pellets at gull nests and loafing areas underestimates the true number eaten by a factor of 5-17. Previous low estimates of eider duckling mortality on the Wolves Archipelago, Bay of Fundy cannot be explained by movements of broods to the mainland coast.

5.1. Introduction

Large gulls (*Larus* spp.) are important predators of the eggs and young of other seabirds (Thomas 1972, Gilchrist and Gaston 1997). Studies of the impact of predation by great black-backed gulls (*Larus marinus*) have focused on terns (*Sterna* spp.) (Shealer and Burger 1992), auks (Alcidae) (Harris 1980), and black-legged kittiwakes (*Rissa tridactyla*) (Burger and Gochfeld 1994). Harris (1980) found that 30-40 pairs of great black-backed gulls took about 2,700 adult Atlantic puffins (*Fratercula arctica*) from a colony of 40,000 pairs during a breeding season; yet Beaman (1978) found that only 400 puffins were taken from a colony of 8,000 pairs by a neighboring colony of 1,800 pairs of great black-backed gulls. Clearly, there is no simple relationship between the numbers of gulls and the extent of their predation at nearby colonies of other seabirds.

The range of great black-backed gulls and numbers of herring gulls (*L. argentatus*) and great black-backed gulls have expanded considerably along the Atlantic coast of North America since the 1920s (Erskine 1992). Common eider (*Somateria mollissima*) populations began increasing after they were protected under the Migratory Birds Convention in 1916 (Gross 1944). Simultaneous increases in the numbers of both herring gulls and common eiders in the St. Lawrence estuary demonstrate that herring gull predation on eider eggs or ducklings need not prevent eider populations from increasing (Munro and Bédard 1977). However, great black-backed gulls are relative newcomers to eastern Canada, their ranges have expanded southward as garbage and fisheries offal became more abundant (Belant *et al.* 1993), and they are more predatory than herring gulls. Great black-backed gulls are known to prey on common eider eggs and young at the nest site (Ahlén and Åndersson 1970, Bourget 1973) and ducklings on the water (Munro and Bédard 1977, Swennen 1989). The common eider now faces a predator that historically was scarce or absent, and whose impact on egg and duckling survival has not been assessed.

Gilliland (1990) suggested that gull predation in an eider colony accounted for less than 10% of duckling mortality. This estimate was based primarily on the number of duckling remains in pellets (indigestible residue) associated with gull nests and loafing areas. Information gained from studies of regurgitated pellets has been widely used to study the impact of predation by cormorants on fish populations (Derby and Lovvorn 1997), and by great skuas (*Catharacta skua*) (Furness 1981) and great black-backed gulls (Furness 1981, Harris 1980) on other seabirds. In addition, pellets have been widely used to study diet and to monitor variation in the use of certain prey items by gulls (Nogales *et al.* 1995, Oro *et al.* 1997). However, if gulls move from their normal feeding or roosting area, pellets may be unobtainable, and there are marked differences in the ease with which pellets can be found depending on the presence and age of chicks and the vegetation adjacent to the breeding site. In this paper we quantify the efficacy of pellets in estimating predation rates on radio-tagged common eider ducklings by great black-backed gulls under a variety of conditions.

5.2. Study Area

The Wolves Archipelago (44°56'N, 66°44'W) is a group of 5 islands, 12 km offshore from Beaver Harbour, New Brunswick, Canada in the Bay of Fundy. The islands range from 20 - 2,039 ha in area; most are forested with balsam fir (*Abies balsama*) and spruce (*Picea* spp.) but the smallest, Green Rock, is dominantly grasses (Gramineae spp.) and wild raspberry (*Rubus idaeus*). In addition to common eiders and great black-backed gulls, other breeding seabirds include double-crested cormorants (*Phalacrocorax auritus*), black guillemots (*Cepphus grylle*), and herring gulls. Recent additions include a colony of black-legged kittiwakes (Kehoe 1994) and two pairs of razorbills (*Alca torda*) (Mawhinney and Sears 1996).

Petit Manan Island and Green Island (44°30'N, 68°30'W), 25 km east of Bar Harbor, are part of a National Wildlife Refuge in the Gulf of Maine, U.S.A. The islands are connected by a bar at low tide. Both are treeless with thin peaty soil, and vegetation consists mainly of grasses. The removal of gulls in 1984 was followed within 3 weeks by the return of terns (*Sterna* spp.), Atlantic puffins, razorbills, eiders and other seabirds after a 4-year absence (Anderson and Devlin 1998). In 1997, 35 great black-backed gulls pairs that had recolonized Green Island were eliminated, but up to 40-65 adult gulls were observed loafing on Green Island throughout the breeding season.

5.3. Methods

The study was initiated in 1995 on the Wolves Archipelago, New Brunswick (hereafter 'the Wolves') where common eiders and great black-backed gulls nest in close proximity. In 1996, we carried out limited gull control on 4 of the 5 islands on the Wolves to assess possible methods to reduce gull predation rates; breeding gulls were killed on two islands, and gull clutches were sprayed with oil to prevent hatch on the other two islands. In 1997, work continued on the Wolves and was initiated on an eider colony on Petit Manan and Green Island. Gull control measures had been undertaken on Petit Manan and Green Island in 1984 to facilitate tern restoration (Anderson and Devlin 1998), and Petit Manan Island has since been maintained free of gulls; we studied the eider colony on Green Island.

5.3.1. Common eiders

Eider colonies in both New Brunswick (1995-1997) and Maine (1997) were searched systematically for eider nests when egg laying started in late April/early May. Nests were marked individually with vinyl flagging and were visited weekly throughout the breeding season. Hatch dates were calculated from direct observations of clutch initiation during visits to nests while laying was in progress and/or the eggs of these clutches were candled (Weller 1956). Incubation periods of 24-25 days and an egg-laying interval of 24 hr (Korschgen 1977) were used to predict hatching dates.

At hatching, ducklings were tagged with standard aluminum web-tags (in 1995 and 1996 only). Each duckling was sexed by cloacal inspection and weighed to the nearest 0.1 g with a spring balance. One duckling from each clutch (41 in 1995, 55 in 1996, and 20 in 1997 from the Wolves; 30 in 1997 from Green Island) was fitted with an external radio transmitter (Model 384, 150 MHZ, Advanced Telemetry Systems, Isanti, Minnesota). The transmitters measured 19 x 8 x 11 mm and weighed 1.9 g (0.03% of duckling body mass). Extending from the rear of the transmitter was a 14 cm long antenna made of 0.54 mm diameter nylon coated stainless steel wire. Protruding 12 mm from the front of the transmitter was an anchor made of 0.61 mm diameter stainless steel wire formed into 2 projecting prongs. A 3-4 mm incision was made in the skin perpendicular to the body axis and the stainless steel anchor was inserted under the skin. Sutures were placed through the skin under the transmitter, and the ends were drawn over the top of the transmitter, tied and fastened with cyanoacrylate glue (Mauser and Jarvis 1991). Radio-tagged ducklings were monitored by boat at least 3 times each week, and weekly coastal surveys were conducted along the mainland to determine production and/or long distance movements. In 1995 and 1996, aerial brood surveys were conducted in the Bay of Fundy at 2, 6, and 7 weeks after peak hatch to estimate the number of ducklings produced and to monitor radio-tagged ducklings from the Wolves Archipelago. These surveys covered the New Brunswick coast from Saint John west to St. Andrews and extended to all coastal and offshore islands and the Grand Manan Archipelago. In 1997, a monitoring flight was conducted 6 weeks after peak hatch along the mainland coast of Maine from Schoodic Point to Cape Split, including Green Island, Petit Manan, and all coastal islands in the Gulf of Maine. On all flights, the aircraft was flown at a height of 75 m and speed of 160 $kmhr^{-1}$ approximately 120 m offshore between 1.5 hr before and after high tide. The number of all eiders observed with 8 x 30 binoculars on the 500 m survey path were recorded using a global positioning system (GPS) and marked on 1:50,000 topographic maps.

To determine whether our sample of ducklings that were radio-tagged was biased, analyses of variance (ANOVA, SYSTAT, Wilkinson 1988) were used to determine whether the body mass of ducklings hatched (1) on the Wolves Archipelago varied with sex, year, and/or differed between radio-tagged and untagged ducklings, (2) on Green Island varied with sex and/or differed between radio-tagged and untagged ducklings, and (3) varied between the two study areas (the Wolves and Green Island) and/or differed between radio-tagged and untagged ducklings. We used an alpha of 0.05 in all tests and values reported are means ± SD.

5.3.2. Great black-backed gulls

All islands in the Wolves Archipelago were searched systematically for great black-backed gulls (hereafter, gulls) nests when egg laying started in mid April/early May in 1995-1997. Nests were marked with numbered wooden stakes. Gull debris (indigestible residue and other prey items not eaten) around the nest sites and loafing areas in both study areas was removed prior to the hatching of eider ducklings. Thereafter, gull debris was collected from nest sites and loafing areas regularly throughout the breeding season until the eider ducklings fledged. In the lab, gull debris was washed and sorted; the minimum number of ducklings in each sample was determined by dividing the maximum number of duplicate body parts by their frequency of occurrence in a single duckling (e.g., two for tarsometatarsus, one for maxilla). This is the standard method used to estimate the number of prey items eaten by gulls (Nogales *et al.* 1995, Oro *et al.* 1997). We were able to test the assumption that remnants of all ducklings depredated are regurgitated around gull nests or loafing areas (Gilliland 1990) using the remains of ducklings marked with transmitters.

The minimum number of ducklings killed was estimated independently using mark-recapture ratios determined from retrieved transmitters. We determined the total number of ducklings that were depredated using the formula, $a = x/y$, where x is equal to the proportion (%) of transmitters retrieved from gull nests and loafing areas, and y is equal to x divided by the number of transmitters retrieved from depredated ducklings. Simple binomial variance estimates ($\sigma = (p(1-p)/n)^{1/2}$) were calculated and applied to the count of the number of the ducklings in debris (variance of total estimate = binomial variance x number of ducklings counted in debris); and 95% confidence intervals (CI) ($p \pm 1.96\sigma$) were calculated (Sokal and Rohlf 1981). We compared the proportion of gull pellets associated with gull nests and loafing areas between years and study sites using a general Chi-square statistic that addresses an unambiguous null hypothesis of homogeneity among rates (Sauer and Williams 1989). With this statistic, specific hypotheses of homogeneity can be simultaneously tested using contrasts.

5.4. Results

5.4.1. Duckling characteristics

In 1995 and 1996, 1,271 and 1,068 ducklings, respectively, were web-tagged on the Wolves Archipelago; a total of 353 ducklings were weighed and sexed between 1995 and 1997, and a total of 68 ducklings were weighed and sexed on Green Island in 1997. The weights of ducklings hatched on the Wolves Archipelago did not vary with sex or between radio-tagged and untagged ducklings (sex: $F_{1,1} = 1.3$, $P > 0.3$; marker: $F_{1,1} = 1.1$, $P > 0.3$). Weights did, however, vary between years ($F_2 = 10.8$, $p < 0.001$). Ducklings hatched in 1996 were the heaviest ($\bar{x} = 79.6 \pm 7.2$ g, $n = 157$), followed by those hatched in 1995 ($\bar{x} = 76.4 \pm 5.5$ g, $n = 127$), and 1997 ($\bar{x} = 75.4 \pm 6.3$ g, $n = 69$). The weights of ducklings hatched on Green Island did not vary with sex or between radio-tagged and untagged ducklings (sex: $F_{1,1} = 1.1$, $P > 0.3$; marker: $F_{1,1} = 0.2$, $p > 0.7$). The weights of ducklings hatched on Green Island and the Wolves in 1997 did not vary between radio-tagged and untagged ducklings ($F_{1,1} = 2.1$, $P > 0.2$) but did vary between study sites ($F_{1,1} = 17.1$, $p < 0.001$). Ducklings hatched on Green Island were heavier ($\bar{x} = 79.3 \pm 5.1$ g, $n = 68$) than those hatched on the Wolves Archipelago.

5.4.2. Recovery of radio-transmitters

In all years and at both study sites, 13-24% of radio-transmitters were not recovered (Table 5.1) and were not detected on live ducklings during monitoring flights throughout the Bay of Fundy (1995-1996) or in the northern Gulf of Maine (1997). With the exception of two ducklings radio-tagged in 1996, all transmitters that were recovered on the Wolves Archipelago between 1995 and 1997, were from radio-tagged ducklings depredated by great black-backed gulls. In 1996, one duckling radio-tagged on Green Rock appeared to have died enroute to the water, and another on Spruce was found dead in the nest. Of the 30 ducklings radio-tagged on Green Island in 1997, 22 were depredated by great black-backed gulls, 2 fledged in the immediate vicinity of Petit Manan Island, and 2 fledged in brood-rearing areas off Bois Bubert Island, 6 km from their hatching island.

In both study areas, all pellets that were retrieved containing ducklings were tightly packed and also contained down and bone fragments. When retrieved, radio-transmitters were buried inside the pellets and the antennas were damaged (broken off or coiled) as a result of ingestion by the gull. Of all the transmitters found in gull pellets on the Wolves Archipelago, only 8 (4 in 1995 and 4 in 1996) contained the corresponding web tag, whereas none of the duckling remains found in the pellets associated with gull nests and loafing areas contained web tags.

The proportion of radio-transmitters recovered from gull pellets at nests and loafing areas on the Wolves Archipelago did not differ between 1995 (18%) and 1997 (17%) ($\chi^2_1 = 2.7, p > 0.05$), but in 1996, no gull pellets containing transmitters were found in association with gull nests, and the proportion found at loafing areas (6-7%) was significantly lower than in 1995 and 1997 ($\chi^2_1 = 14.6, p < 0.01$). The proportion of radio-transmitters recovered from gull pellets at nests and loafing areas on the Wolves Archipelago in 1995 and 1997 did not differ from that on Green Island in 1997 (14%)

($\chi^2_3 = 2.4, p > 0.05$).

A large proportion of transmitters retrieved in gull pellets were located beneath the water (Table 5.1). Whereas most were retrieved in gull pellets in the intertidal (13-27%), others were in deeper water and were unrecoverable (Table 5.1). In 1996 on the Wolves Archipelago and in 1997 on Green Island, the proportion of transmitters located beneath the high water levels was similar ($\chi^2_1 = 0.0, p > 0.05$), but higher than on the Wolves Archipelago in 1995 and 1997 ($\chi^2_3 = 14.6, p < 0.01$) (Table 5.1). The proportion of transmitters located beneath high water was similar in 1995 and 1997 on the Wolves Archipelago ($\chi^2_1 = 0.6, p > 0.05$). The remainder of those transmitters retrieved away from gulls nests or loafing areas, on both the Wolves Archipelago and Green Island (Table 5.1), were found in gull pellets scattered throughout the vegetation (forest floor, raspberry, tall grass) of the various islands. These pellets would not have been found during a routine survey of nest debris or loafing areas.

The mark-recapture ratios from the transmitters suggest that gull predation on eider ducklings in this population was 5 to 14 times higher than that accounted for by duckling remains found in gull pellets at gull nests and loafing areas (Table 5.2). If we assume that the radio transmitters that were located but not recoverable below the low tide water were from ducklings depredated by gulls, the ratios of the number of ducklings radio-tagged suggest that gull predation on eider ducklings was 6 to 17 times higher to those subsequently retrieved (Table 5.2).

5.5. Discussion

5.5.1. Duckling characteristics

Our use of mark-recapture ratios of depredated duckling remains in gull pellets rests on our assumption that ducklings marked with radio-transmitters are no more or less vulnerable to gull predation than unmarked ducklings. This assumption is intrinsically difficult to test, but particularly so at the Wolves where virtually all the ducklings produced at this colony were eaten by gulls. As an indirect test we compared weights of radio-tagged and untagged ducklings because a large part of the ducklings vulnerability to predation has been attributed to poor condition at hatch or low hatch weights (Mendenhall and Milne 1985, Swennen 1989).

Despite year and site differences in duckling weights, there was nothing in our observations to suggest that there was any *a priori* bias that would make radio-tagged ducklings more vulnerable to predation by gulls. Initial weights of tagged ducklings were similar to those weights of untagged ducklings. Survival rates of broods with ducklings fitted with radio transmitters did not differ from that of broods with unmarked ducklings in all years and in both study areas (unpubl. data). Young broods were most vulnerable and ducklings were depredated within the first 7 days following hatching. In most cases, if a brood was attacked by great black-backed gulls, the entire brood of ducklings was taken. Less than 25 ducklings fledged of the more than 2,000 hatched from the Wolves Archipelago in 1995, 1996, and 1997 (unpubl. data). In Maine, where overall duckling survival was considerably higher, only four ducklings fitted with transmitters survived to fledge. In addition, one of the surviving ducklings fitted with a transmitter was one of only two ducklings that survived from an initial brood of four ducklings.

5.5.2. Recovery of transmitters

Only a small proportion of gull pellets containing ducklings were located around gull nests and loafing areas. There is no evidence to suggest that the remains of ducklings with radio-transmitters were predisposed to turn up in areas other than gull nests and loafing sites. Additional pellets containing ducklings and other regurgitated food items also were found in the areas away from gull nests and loafing areas. Other studies also have found that total predation of other seabirds cannot be accounted for by gull debris alone. Harris (1980) suggested the impact of a great black-backed gull population on puffins in a Shetland colony must have been even higher than that measured because some corpses and pellets were on unreachable rocks, dropped in the sea, and presumably overlooked. Furness (1981) suggested that only unfledged young which remain on the island, or species which do not feed at sea, are likely to be fully represented in the regurgitated pellets of great skuas nesting in Britain.

Mark-recapture ratios of the number of ducklings radio-tagged to those subsequently retrieved suggest that gull predation on common eider ducklings was considerably higher than that accounted for by duckling remains found in gull pellets at gull nests and loafing areas. We have no evidence that gulls regurgitated pellets containing radio transmitters differently from those without transmitters. When located, the transmitters were buried well inside tightly packed pellets and were surrounded by down and bone fragments and often contained the body parts of more than one duckling. Pellets containing ducklings and other prey items were often found in association with pellets located by using radio-telemetry and would not have been found in routine checks of gull nests and loafing areas. The radio-transmitters themselves were less than 2 cm in their largest dimension and represented only a small proportion of the total volume of the pellets, and were in some cases smaller than the larger tarsometarsus bones found in the regurgitations containing older ducklings. Web tags were rarely detected in gull pellets and are likely passed through the gull and excreted in the faeces. Web tags were much smaller (< 4 mm) than the smallest tarsometatarsus bones used to identify ducklings in the regurgitations. The use of bird pellets to determine dietary intake is generally acknowledged to under-represent small undigestible body parts such as mandible and invertebrate casings, or soft-bodied and readily digestible food items such as invertebrates and small fish (Annett and Pierotti 1989).

Gilliland (1990) suggested that the lack of ducklings around the Wolves in 1988 and 1989, despite apparently low predation rates by gulls, could be accounted for by hens moving ducklings away from the Wolves to coastal brood-rearing areas. This occurred in Maine, where both marked females with broods and females with radio-tagged ducklings, were found in coastal brood-rearing areas 6 km from their hatching islands. However, in all 3 years on the Wolves, radio-tagged ducklings (except two that died ashore in 1996) were depredated by gulls, and none were detected on monitoring flights throughout the Bay of Fundy up to 7 weeks after peak hatch.

The absence of gull chicks and active gull nests on the Wolves Archipelago in 1996 and Green Island in 1997 did not eliminate gull predation on eider ducklings (unpubl. data). In addition, the retrieval of transmitters from ducklings depredated by gulls was more difficult when the gulls did not remain on a breeding territory; a smaller proportion of the transmitters was found in association with gull loafing areas, and higher proportions were found scattered in the vegetation throughout the islands and in the sea, in 1996 than in 1995 and 1997 when gulls were breeding normally. Fewer ducklings were found in pellets at nest sites and traditional loafing areas on the Wolves in 1996, when gulls were controlled, than in 1995 and 1997 when the gulls breeding on the colony had active nests to maintain.

Hartley (1948) stressed that pellets should not be used in food studies until preliminary trials have established their quantitative and qualitative adequacy. As a result of gull control activities in 1996, the number of active gull nests on the Wolves was slightly lower in 1997 than in 1995. However, the proportion of the transmitters found in pellets associated with gulls' nests and loafing areas in 1997 was similar to that found in 1995. This suggests that these ratios provide a good index for quantifying the number of ducklings taken from the colony by great black-backed gulls with active breeding territories. It is unlikely that any of the pellets containing duckling remains found in this study were from eider ducklings depredated by herring gulls, as has been observed in other areas (Ahlén and Åndersson 1970, Bourget 1973). We never observed herring gulls attempting to capture common eider ducklings in either Maine or New Brunswick, and transmitters and pellets were never found in association with active herring gull nests despite the presence of active nests on two islands in the Wolves Archipelago in 1996 and Green Island in 1997. Bourget (1973) also found that great black-backed gulls were the main cause of loss of common eider eggs and young in a mixed gull colony.

The mark-recapture ratios cited in this study can give only a minimum estimate of the number of ducklings depredated, because not all transmitters on depredated ducklings were located. For example, of two predations of tagged ducklings observed in 1996, only one was later retrieved. In all years of this study, a large proportion of transmitters retrieved in gull pellets were found beneath high tide. The signals of these radio-transmitters could be received only at low tide. Some of these transmitters were subsequently retrieved at low tide, but in both 1995 and 1997, a few transmitters were in water so deep that they could not be recovered. The ducklings found in these pellets would not have been found during a routine survey of nest debris littered around the nest sites and/or loafing areas. Therefore, we have no way of knowing how representative the pellets with radio transmitters were of the actual number of ducklings that were depredated by gulls, and subsequently, regurgitated as pellets into the water. In addition, we feel that the lost transmitters may in fact represent gull predations regurgitated in unrecoverable areas. However, we cannot eliminate the possibility that these radio transmitters may have simply failed. Although pellets have been used to monitor variation in the use of certain prey items, our data demonstrate that they cannot be used to accurately assess the impact of gull predation on common eider ducklings.

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Table 5.1. Fate of radio-tagged common eider ducklings on the Wolves Archipelago, New Brunswick, 1995-1997 and Green Island, Maine, 1997.

	Wolves			Green Island
	1995	1996	1997	1997
No. ducklings tagged	41	55	21	30
No. transmitters lost (%)	8 (19)	11 (20)	5 (24)	4 (13)
No. transmitters not recovered below low tide	1	4	2	0
No. transmitters recovered on island tagged	22	34	11	22
No. transmitters recovered on other island	10	8	5	0
No. transmitters recovered in association with gull nests/loafing area (%)	6 (19)	3 (7)	3 (19)	3 (14)
No. transmitters recovered in vegetation (%)	21 (66)	28 (67)	11 (69)	13 (59)
No. transmitters recovered in intertidal (%)	5 (15)	11 (26)	2 (13)	6 (27)
Radio-tagged ducklings fledged	0	0	0	4

Table 5.2. Estimated number of common eider ducklings depredated by great black-backed gulls on the Wolves Archipelago, 1988-1989 (Gilliland 1990), 1995-1997; and Green Island 1997. Ducklings depredated in 1988 and 1989 were estimated using mark-recapture ratios from 1995.

	Total ducklings		
	Estimated from pellets	Estimated using ratios from recoverable transmitters (95% CI)	Estimated using ratios from all transmitters relocated
Wolves Archipelago			
1988	189	995 (591-4,725)	1050
1989	147	775 (459-3,675)	817
1995	184	968 (575-4,600)	1022
1996	74	1057 (493-9,250)	1233
1997	164	863 (421-8,333)	965
Petit Manan/Green Island			
1997	127	907 (454-9,333)	907

Status and productivity of common eiders in relation to great black-backed gulls and herring gulls in the southern Bay of Fundy and the northern Gulf of Maine

Chapter 6

Mawhinney, K., A. W. Diamond, P. Kehoe and N. Benjamin. 1999. Status and productivity of common eiders in relation to great black-backed gulls and herring gulls in the southern Bay of Fundy and the northern Gulf of Maine. Waterbirds 22: 253-262.

Abstract

The breeding population of common eiders (*Somateria mollissima*) in the Bay of Fundy has remained stable over the last decade, ranging from 8,000 to 10,000 breeding pairs. However, the number of ducklings surviving to fledging in the Bay of Fundy decreased from > 14% of the adult breeding population prior to 1991 to < 10% between 1995 and 1998. Although the breeding population in the Grand Manan Archipelago decreased over the decade, these colonies produced more ducklings that survived to fledgling in the Bay of Fundy between 1995 and 1998 and represented an important source of potential recruits (44-87%) to the eider population. Higher duckling production in the Grand Manan Archipelago cannot be attributed to higher hatch success, but may reflect lower predation rates by great black-backed gulls (*L. marinus*). The number of ducklings observed during aerial surveys was not correlated with commercial catches of herring (*Clupea harengus*), an alternative food source for predatory gulls. Duckling survival to fledgling was higher for a local breeding population in the Gulf of Maine (12%) than in the Bay of Fundy (6%). The relatively large number of ducklings associated with a two-island archipelago within the Petit Manan National Wildlife Refuge accounted for a large proportion of the surviving ducklings and may reflect lower predation rates by great black-backed gulls as a result of gull control measures. The current populations of herring gulls (*Larus argentatus*) and great black-backed gulls breeding in the Bay of Fundy in New Brunswick are estimated at 5,367 pairs (5,011-7,282: 95% CI) and 1,771 pairs (1,685-1,868: 95% CI) respectively. Assuming that the age structure of gulls in this region is similar to that of the expanding New England population, the total number of individuals, including non-breeding gulls in the Bay of Fundy probably exceeded 19,550 (18,780-21,593: 95 %CI) in 1998.

6.1. Introduction

With the exception of a tiny population in the Bay of Chaleur, most common eiders (*Somateria mollissima*) in the province of New Brunswick breed on islands in the mouth of the Bay of Fundy in mixed colonies with great black-backed (*Larus marinus*) and herring (*L. argentatus*) gulls (Kehoe 1994). Common eider - gull interactions have been found to range from beneficial (Schamel 1977, Gerell 1985) to neutral (Pimlott 1952, Gotmark and Ahlund 1988) and detrimental (Bourget 1973, van Dijk 1986). Gulls are predators on eider eggs and young at the nest site (Ahlen and Andersson 1970, Bourget 1973, Campbell 1975, van Dijk 1986); however, when nesting in mixed colonies, eiders may benefit from protection against other avian predators (e.g., Young and Titman 1988).

Aerial counts of the highly-visible males have been successfully employed in Maine (Mendall 1968), Scandinavia (Almkvist *et al.* 1975), Labrador and the Maritime Provinces (Lock 1986) to census common eiders with an accuracy of 1.1:1 adult males per nest (Lock 1986). Based on aerial counts, the breeding population of common eiders in the Bay of Fundy remained stable through the 1980s (Erskine 1992) with the largest breeding colonies in the Wolves Archipelago, the Grand Manan Archipelago, Maces Bay, and Passamaquoddy Bay (Bowes 1994; Kehoe 1994). However, little is known about the recruitment of fledglings to this population. Elsewhere, the number of eider fledglings in a population can be highly variable from year to year, despite relatively stable numbers of breeding pairs and hatchlings (Swennen 1989).

In 1987, the New Brunswick Department of Natural Resources and Energy began to conduct aerial counts of ducklings on the water to ascertain eider recruitment in the Bay of Fundy. However, the accuracy of these surveys was never assessed. Surveys were conducted six to seven weeks post-hatch to ensure that ducklings surveyed were a minimum of 35 days old ("Class IIc", Gollop and Marshall 1954). The number of ducklings surviving to this age-class is considered a reliable index of recruitment (Ringelmen and Longcore 1982, Savard *et al.* 1991, Flint and Grand 1997). Surveys were conducted 1.5 hours before and after high tide to ensure that all broods were accounted for, because they are on open water at this time, as the rockweed-covered shoreline is flooded (Minot 1976), and there is no emergent vegetation. Adult females with young broods will often move several kilometers from hatching islands and brood rearing areas, and once established in a brood-rearing area do not venture more than 30 m from land (McAloney 1973, Minot 1976).

The largest concentrations of eider ducklings in the Bay of Fundy were associated with the Grand Manan Archipelago (Bowes 1994). Low duckling production associated with the Wolves Archipelago in the Bay of Fundy was attributed to predation by great black-backed gulls (*Larus marinus*) (Hicklin 1989, Mawhinney and Diamond 1999). Gull predation on common eider ducklings may be greater during years when alternative food items are more scarce (Beetz 1916; Beloposki 1957, Gilliland 1990). Mendenhall and Milne (1985) observed unusually high survival rates among common eider ducklings in one year of their study when alternative food sources for gulls were abundant. However, Orians and Janzen (1974) suggested that ducklings will always be preferred as food over invertebrates or fish; and Swennen (1989) found that inspection of eider crèches by foraging gulls was as frequent in years with high eider fledging success as in years with poor success. Gilliland (1990) suggested that on the Wolves Archipelago, in 1988 and 1989, great black-backed gulls diverted foraging pressure from ducklings to abundant herring (*Clupea harengus*) stocks.

This paper reports the current status of breeding populations and productivity of common eiders in the Bay of Fundy and the upper Gulf of Maine in 1998. Gull populations (great black-backed and herring gulls) in the Bay of Fundy were estimated through a combination of aerial counts, aerial photography and ground-based nest counts

(Kadlec and Drury 1968, Dolbeer *et al.* 1997, Frederick *et al.* 1996). The efficacy of aerial surveys of common eider ducklings was evaluated with collateral ground counts on the water in the Bay of Fundy and the Gulf of Maine. We also examined whether the number of ducklings was related to the major alternative source of food for gulls, i.e., availability of herring in the Bay of Fundy.

6.2. Methods

6.2.1. Common eiders

Males attend females until at least one week after nest initiation (McKinney 1961, Milne 1963, Sabean 1972). Accordingly we conducted breeding pair surveys one week following the peak of nest initiation. Because weather conditions encountered by common eiders on the breeding grounds can cause significant changes in the breeding schedule (Hario and Selin 1988), surveys were timed according to the nesting phenology of common eiders breeding in Passamaquoddy Bay in 1987, 1990 and 1994 (Bowes 1994), and on the Wolves Archipelago in the Bay of Fundy for each of the survey years between 1995 and 1998 (Mawhinney and Diamond 1999) (Table 6. 1). Surveys in New Brunswick were conducted in May 1987, 1990, 1994, 1995, 1996 and 1998, along the coast from Saint John west to St. Andrews, including all coastal and offshore islands and the Grand Manan Archipelago (Fig. 6. 1).

In 1998, common eiders breeding in the Gulf of Maine between Schoodic Point and Jordan's Delight were also censused (Fig. 6.2). The survey was timed according to the nesting phenology of common eiders breeding on Green Island in the Gulf of Maine (Mawhinney and Diamond 1999). Aerial brood surveys were conducted in New Brunswick (1987, 1990, 1991, 1995, 1996 and 1998) and in the Gulf of Maine in 1998. To determine the accuracy of aerial surveys, ground surveys for broods were conducted simultaneously from a small motor boat around the Wolves Archipelago in 1995, 1996 and 1998 and Petit Manan and Green Island in 1998. Aerial surveys were conducted from a Cessna 150 in New Brunswick and a Cessna 120 in Maine. The aircraft were flown following the coast at a height of 75 m and a speed of 160 km/hr on a course approximately 120 m offshore, between 1.5 hours before and after high tide. The numbers of adult male eiders observed on the survey path were recorded and marked on a 1:50,000 topographic map during breeding pair surveys; and the number and age of ducklings was recorded for all broods and marked on a 1:50,000 topographic map during brood surveys. The relationship between the numbers of breeding pairs and ducklings observed over time was examined using linear regression (Wilkinson 1988). The numbers of ducklings observed were regressed on the catch per unit effort of commercial catches of herring stocks in the Bay of Fundy for the same years. Herring landings in the fishing weirs provide an excellent index of annual changes in the availability of herring in the Bay of Fundy (Stephenson *et al.* 1993).

6.2.2. Great black-backed gulls and herring gulls

In 1998, we searched for all gull colonies in the Bay of Fundy along the same flight path flown for the common eider breeding pair survey, in a Cessna 172 fixed-wing aircraft at an altitude of 125 meters. Aerial visual estimates were made on 25 and 26 May 1998 when gulls were in late incubation. Counts of gulls were made by two observers and the ratios of great black-backed gulls (GBBG) to herring gulls (HG) were estimated. The locations of all colonies were recorded on 1:50,000 topographic maps. Color photographs were taken of nine islands identified with gull colonies, at an altitude of 300 meters. Photographs were taken through an opening in the aircraft floor, with a 70 mm Hasselblad camera (150mm lens, 70mm back, Kodak E100S Ektachrome film). The original film was magnified 4X and each gull image was identified to species and counted.

Twelve islands with nesting gulls were systematically surveyed from 24-30 May by observers walking in tandem until the entire island was covered. Great black-backed and herring gull nests were identified and marked with wooden popsicle sticks. The total numbers of nests for each island were estimated using mark-relocate ratios of marked to unmarked nests counted along a transect running through all habitat types on each island following the initial survey (Walsh *et al.* 1995). Because ground counts of nests are considered the most reliable technique for estimating or censusing colonial nesting species, it is the standard with which the other estimates (aerial visual estimates and photographs) were compared (Wilkinson 1991). We examined three relationships: (1) gulls counted on photographs and ground counts of nests, (2) gulls counted on photographs and visual estimates of gulls, and (3) visual estimates of gulls and ground counts of nests.

6.3. Results

6.3.1. Common eiders

The breeding population of common eiders in the Bay of Fundy has remained stable ($p = 0.94$, $r^2 = 0.02$) over the last decade, ranging from 9,843 breeding pairs in 1987 to 8,278 in 1995, 9,798 in 1996 and 8,768 in 1998 (Table 6.1). Overall, the number of ducklings surviving to fledging in the Bay of Fundy declined significantly ($p < 0.026$, $r^2 = 0.83$) from 900-1,500/year prior to 1991 to less than 800 in 1996 and less than 500 in 1995 and 1998 (Table 6.1). The large concentrations of eider ducklings associated with the Grand Manan Archipelago (Table 6.1) declined considerably between 1987 and 1998 (Table 6.1). Prior to 1991, ducklings produced from islands in this archipelago varied in their contribution to the overall number of ducklings produced in the Bay of Fundy (80% in 1987 to 33% in 1990 and 60% in 1991). The proportion increased from 45% in 1995 to 57% in 1996 and 87% in 1998 while the proportion of adults breeding in this region has remained stable, ranging from 37%-46% during the same time period.

The ratios of the numbers of ducklings observed during aerial surveys to those observed on the water ranged from 0.89 to 1.08, averaging 0.99:1 overall (Table 6.2).

The number of ducklings observed during aerial surveys was not related to the catch per unit effort of commercial herring landings in the Bay of Fundy for the overall breeding season (May-August $p = 0.61$, $r = 0.27$), nor for any given month of the breeding season (May $p = 0.71$, $r = 0.34$; June $p = 0.48$, $r = 0.97$; July $p = 0.93$, $r = 0.30$; August $p = 0.39$, $r = 0.15$).

The breeding population of common eiders in the Gulf of Maine from Schoodic Point to Jordan's Delight was 5,417 (Fig. 6.2). The number of ducklings surviving to fledging was 314, of which 198 were found immediately around Petit Manan and Green Island. Because we did not cover areas west of Schoodic Point during the aerial brood survey and no ducklings were observed between Schoodic Point and Cranberry Point, we feel that these ducklings likely represent ducklings produced from the 2,579 adult breeding pairs observed between Cranberry Point and Jordan's Delight and not those produced from the 2,838 pairs of common eiders breeding on Schoodic Island.

Duckling production between Cranberry Point and Jordan's Delight was approximately 12% of the adult breeding population in this region, with the largest concentration of ducklings observed around Petit Manan and Green Island. At least five additional broods (including more than 50 ducklings) along the coastline were produced from hens nasal-tagged on Green Island (Mawhinney and Diamond 1999). Seventy-nine percent (248) of the 314 ducklings that survived in this region were produced from the 1,200 breeding pairs of common eiders on Petit Manan and Green islands. The remaining 66 ducklings represent a production rate of only five percent of the remaining 1,379 common eiders breeding in this region.

6.3.2. Great black-backed gulls and herring gulls

Of 137 islands surveyed, 53 had breeding colonies of gulls (White Horse Island, east of Campobello was missed in this survey). Aerial photographs were taken of nine nesting islands and nest counts were conducted on 12 islands. The ratio of the number of gulls counted in photographs to those estimated visually was 1.35 (± 0.23: 95% Confidence Intervals (CI), N = 9) for great black-backed gulls and 1.65 (± 0.34: 95% CI, N = 9) for herring gulls. The ratio of territorial gulls counted on photographs to the number of nests in a colony was the least reliable at 2.48 (± 1.24: 95% CI, N = 6) for great black-backed gulls and 1.91 (± 0.54: 95% CI, N = 6) for herring gulls. Of 12 islands censused on the ground, 83-100% of great black-backed gull nests and 50-100% of herring gull nests were found on the first count. The ratios of the number of gulls estimated visually to those counted on the ground in a colony were the most reliable and were similar for both species: 1.01 (± 0.026: 95% CI, N = 12) for great black-backed gulls and 0.90 (± 0.085: 95% CI, N = 12) for herring gulls, for an overall ratio of 0.95 (± 0.046: 95% CI, N = 24). The number of breeding pairs in a colony (Table 6.3) was derived using the ratios derived from the number of gulls estimated visually to those counted on the ground.

The breeding population of gulls in the Bay of Fundy in New Brunswick was estimated at 7,519 pairs (7,223-8,305: 95% CI) in the 1998 breeding season, of which 1,771 (1,685-1,868: 95% CI) were great black-backed gulls and 5,367 (5,011-7,282: 95% CI) were herring gulls. The ratio of herring gulls to great black-backed gulls was considerably higher in the Grand Manan Archipelago (15: 1) than in the Musquash/St. George/St. Stephen (0.7: 1) and Campobello (4: 1) regions of the Bay of Fundy.

6.4. Discussion

The breeding population of common eiders in the Bay of Fundy remained stable over the last decade, ranging from 8,000 to 10,000 pairs. However, the number of ducklings surviving to fledging in the Bay of Fundy has declined from > 14% of the adult breeding population prior to 1991 to < 10% since 1995 (1995, 4%; 1996, 8%; 1998, 6%). The number of ducklings observed during aerial surveys was not correlated to the commercial catches of herring, the main prey species of great black-backed gulls in the

Bay of Fundy (Gilliland 1990). We therefore suggest that predation on eider ducklings does not seem to depend on the availability of alternative food for their major predator. Despite a decline in overall numbers, eider ducklings observed in Grand Manan Archipelago between 1995 and 1998 represented an important source of potential recruits (44-87%) to the eider population in the Bay of Fundy. The higher productivity of ducklings in this archipelago may reflect lower overall predation rates by gulls. Herring gulls are more abundant than great black-backed gulls in the Grand Manan Archipelago, compared to the rest of the Bay of Fundy.

Duckling survival was higher for the local breeding population of common eiders in the Gulf of Maine (12%) than in the Bay of Fundy (6%) and was driven by the large number of ducklings associated with Petit Manan and Green Island. Within the Petit Manan National Wildlife Refuge, this higher productivity may reflect lower predation rates by great black-backed gulls as a result of gull control measures. Between 1984 and 1990, a gull-control program employing the use of avicide DRC 1339 was instituted on Petit Manan and Green Island by the U.S. Fish and Wildlife Service. Humans have been present on Petit Manan every summer since 1984 to monitor the tern population and to discourage resettlement of gulls (Anderson and Devlin 1998). In 1997 and 1998, all breeding pairs of great black-backed gulls that had resettled on Green Island were successfully eliminated as part of a study to assess the efficacy of gull control as a management action to increase eider recruitment (Mawhinney and Diamond 1999). The low productivity of eider ducklings from the other colonies in this region (Mawhinney and Diamond 1999) likely reflects predation by the breeding populations of great black-backed gulls also established at those colonies (Schauffler 1998).

Counts from photographs and visual estimates of the numbers of territorial gulls are generally reliable indicators of the numbers of nests (Kadlec and Drury 1968); however, in our census the ratio of gulls counted on photographs to the number of nests in a colony was not reliable. In several of these colonies gull numbers changed considerably in the two days between the initial aerial visual estimate and aerial photographs as a result of egging. Human predation of gull eggs in the Grand Manan archipelago has occurred for many years (Hébert 1989). However, there has been a concerted effort by residents in the Grand Manan Archipelago in the past three years to kill gulls, break up their nests, collect eggs, and shoot them around salmon cages (B. Dalzell, Grand Manan Bird Observatory, pers. comm., 1998). On two of the photographed colonies the number of gulls increased 3.5 times from the original estimate due to loafing gulls and there were no eggs in the nests. On another island, two pairs of herring gulls and several empty nest bowls could be identified in the photograph where nine great black-backed gulls and 361 herring gulls had been counted 3 days previously.

Great black-backed gulls in eastern Canada have increased during the last 70 years and, as in New England (Drury 1973-1974, Erwin 1979, Schauffler 1998), increases in recent decades have apparently come at the expense of herring gulls (Cannell and Maddox 1983, Hébert 1989, Erskine 1992). With the exception of islands within the Wolves Archipelago, great black-backed gull numbers have increased 2.5 times and herring gull numbers have declined by one half, since surveys conducted in 1979 (Diamond *et al.* 1999). Breeding pairs of great black-backed gulls were eliminated on two of the five islands in the Wolves Archipelago in 1996 (Mawhinney and Diamond 1999). The 1998 populations of herring gulls and great black-backed gulls breeding in the Bay of Fundy in New Brunswick were estimated at 5,367 pairs (5,011-7,282: 95% CI) and 1,771 pairs (1,685-1,868: 95% CI) respectively. However, large gulls do not breed until their fourth year and there are, consequently, numerous sub-adult non-breeding birds in gull populations (Coulson *et al.* 1982; Migot 1992; Pons and Migot 1995). Assuming that the age structure of gulls in this region is similar to that of the New England population, the total number of individual gulls in the Bay of Fundy probably exceeded 19,550 (18,780-21,593: 95% CI) in 1998.

Great black-backed gulls are relative newcomers to temperate eastern Canada, their ranges having expanded southward as garbage and fisheries offal have become more abundant (Belant *et al.* 1993; Furness *et al.* 1992; Pons 1992), and they are more predatory than herring gulls. In the southern reaches of its range, the eider now faces a predator that historically was scarce or absent (Boardman 1862, Squires 1952, Erskine 1992). Gull predation of flightless young eider exceeding 90% has been documented in other areas (Mendenhall and Milne 1985), as well as in the Bay of Fundy (Mawhinney and Diamond 1999). Bald Eagles (*Haliaeetus leucocephalus*) breeding on offshore islands are frequently observed depredating eider ducklings in both Maine (B. Allen, Maine Dept. Inland Fisheries and Wildlife, pers comm., 1998) and New Brunswick (N. Wheelwright, Bowdoin College, pers. comm., 1998), and they also have the potential to cause substantial duckling mortality as they continue to increase along the Atlantic coast (Erskine 1992).

Density-dependent mortality of juveniles and adults, as well as condition of females during clutch formation in the spring, have been considered the major factors regulating common eider populations (Milne 1974). Survival of eider ducklings does not apparently regulate common eider populations, but it may potentially limit their growth rate (Mendenhall and Milne 1985). Low annual recruitment over several years has been associated with gradual declines in breeding populations of common eiders elsewhere, just as good production years have been reflected in subsequent population increases (Milne 1974). Although numbers of common eiders breeding in New Brunswick appear stable, the number of ducklings surviving to fledging has declined dramatically. The current levels of recruitment observed for the eider population in the Bay of Fundy are not enough to offset the estimated 13% mortality rate for adult female eiders originating in the Atlantic Coast subpopulation (Krementz *et al.* 1996). Persistently low duckling production of eiders in the Bay of Fundy could result in gradual shifts in the population structure, and ultimately in declines in population size.

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Table 6.1. Summary of breeding pair and brood surveys for the common eider in the Bay of Fundy, 1987-1998.

Date	Area			Total
	Grand Manan Archipelago	Deer Island/ Campobello Island/ Wolves Archipelago	Coastline from St. Stephen to Saint John	
Breeding Pair Survey (Number of adult males)				
May 12, 1987	5237	2039	2573	9849
May 15, 1990	3060	924	2995	6979
May 4, 1995	3092	944	4242	8278
May 14, 1996	4069	1382	4347	9798
May 19, 1998	4030	1488	3250	8768
Brood Survey (Number of ducklings)				
August 4, 1987	1147	173	113	1433
July 31, 1990	323	130	509	962
August 15, 1991	742	239	264	1245
August 8, 1995	165	47	150	362
August 11, 1996	452	89	253	794
August 6, 1998	426	28	36	490

Note: See Fig. 6.1 for designated areas.

Table 6.2. Numbers of common eider ducklings counted during aerial surveys, compared to the number of ducklings counted on boat surveys.

Aerial counts	Boat count	Location of boat count	Ratio (Ducklings counted from the air: ducklings counted from the boat)
13	12	Wolves	1.08:1
8	9	Wolves	0.89:1
15	14	Wolves	1.07:1
198	201	Wolves	0.98:1
234	237	Petit Manan/ Green Island	0.99:1

Table 6.3. Aerial visual estimates of great black-backed gull (GBBG; corrected with ratio established from ground counts; 1.01:1) and herring gull (HG; 0.904:1) breeding pairs on different colonies in the Bay of Fundy, 1998. Numbers in bold indicate total nests counted from the ground (* Probably egged; **Corrected with overall ratio (0.95:1).

	Estimated breeding pairs			Estimated breeding pairs			Estimated breeding pairs	
	GBBG	HG		GBBG	HG		GBBG	HG
Grand Manan			West Pumpkin*	**0**	**11**	**Musquash/St. George/St. Stephen**		
Long-2	8	22	**Subtotal**	202	2975	Manawagonish	268	33
High Duck	9	90	**Campobello**			Gooseberry	119	0
Low Duck	0	44	Thrumb Cap	55	0	Dry Ledge	29	45
Nantucket	0	2	S Spectacle	**7**	**51**	Molly Brown Rock	19	10
Gull Islet	0	25	N Spectacle	2	1	SE Salkeld	122	59
Great Duck	25	525	Hospital-2	**76**	**365**	NW Salkeld	116	14
Cheney	0	2	Tinkers	24	40	New River	**72**	**178**
Gull Rock	94	0	Sandy	**9**	**361**	Douglas	0	3
SW Gull Rock	1	33	The Pup	2	0	Long-1	1	0
Pumpkin Islet	19	0	Spruce-1	0	7	Hog	137	0
N Green	23	101	St. Helena	0	7	E Hog	35	0
S Green	12	55	Casco Bay	6	0	Dicks	39	173
Hay	0	147	Green	**6**	**32**	Dicks Rock	0	88
Kent	10	940	South Wolf	**99**	**173**	Hardwood	3	17
Sheep	1	202	Flatpot	**41**	**426**	Hospital-1	**165**	**116**
Whitehorse Islet	0	39	Spruce	**51**	**49**	Subtotal	1125	736
Outer Wood	0	448	Green Rock	**63**	**80**	**Total Pairs**	1771	5367
Wood	0	232	East Wolf	18	64	**95% CI**	1,685-1,868	5,011-7,282
W Green*	0	57	**Subtotal**	457	1656	**Total Gulls****	**7,519 (7,223-8,305 95% CI)**	

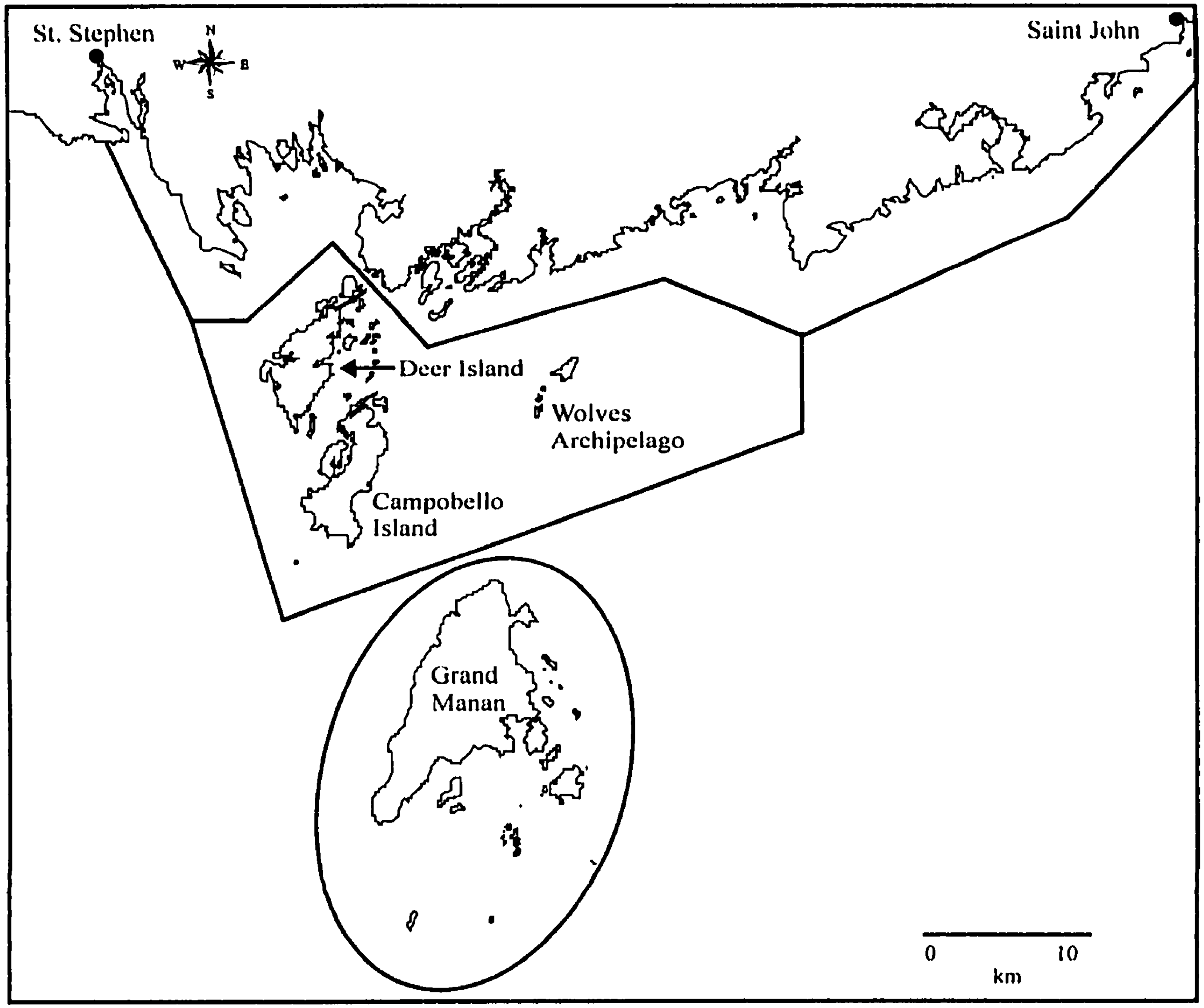

Fig. 6.1. Location of survey zones used for aerial surveys of common eiders adult breeding pairs and ducklings in the Bay of Fundy, New Brunswick.

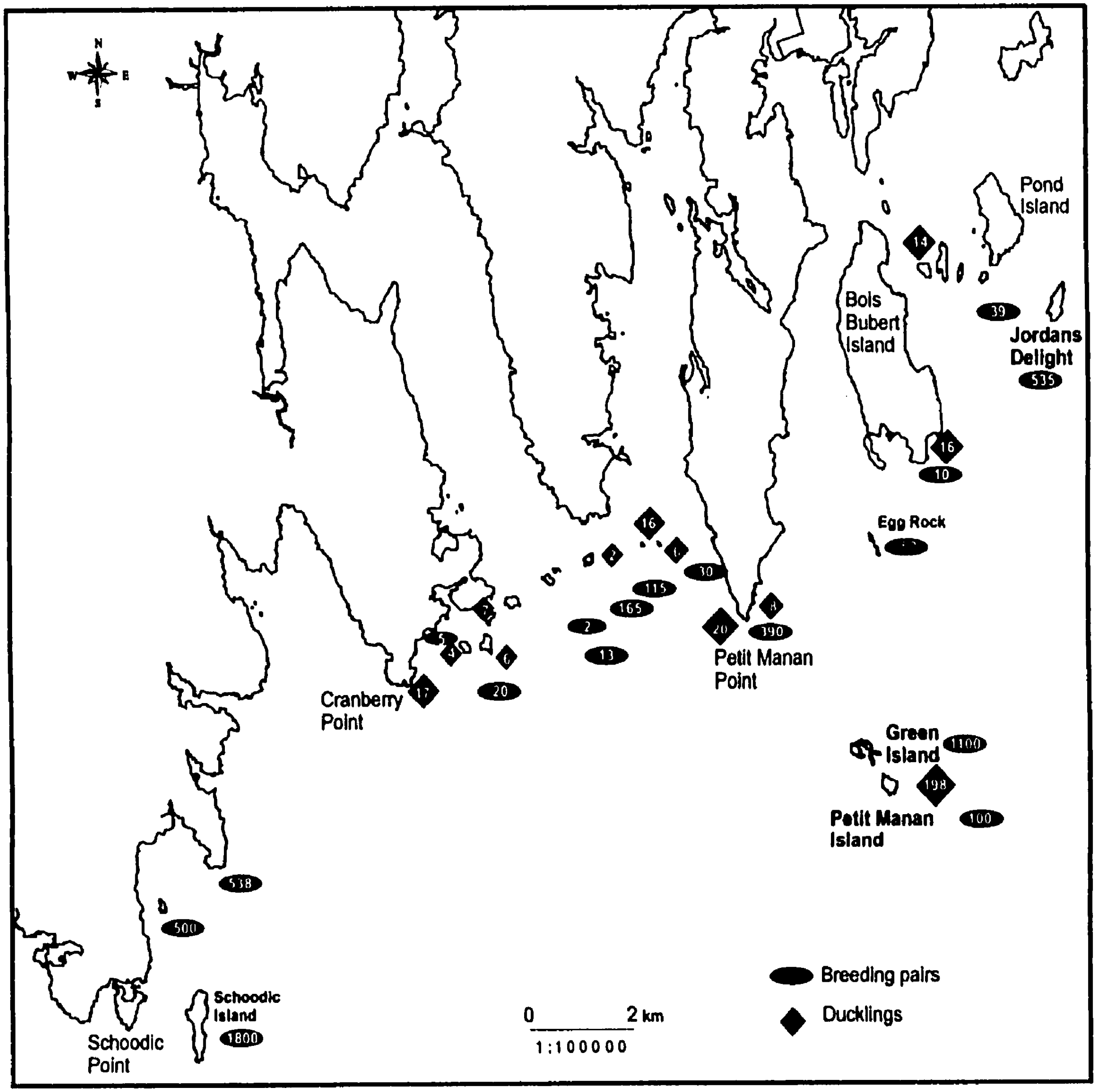

Fig. 6.2. Common eider breeding pairs and ducklings surviving to seven weeks observed between Schoodic Point and Jordan's Delight in the Gulf of Maine during the 1998 breeding season.

Effects of capture and tagging on nest success of common eiders

Chapter 7

Mawhinney, K., and A. W. Diamond. 1999. Effects of capture and tagging on nest success of common eiders. Waterbirds. *Submitted.*

Abstract

Identification of capture and handling procedures that influence nest success of waterfowl captured during incubation has important research and management implications. We evaluated the effects of capture and handling associated with nasal-tagging, and implanting intra-abdominal radio-transmitters, in 326 common eider (*Somateria mollissima*) hens captured during incubation. Nest success of marked hens was lower than that of unmarked hens; and was higher for nasal-tagged hens than for radio-tagged hens. Nest success of common eiders increased during the early stages of incubation and stabilized by the late stages of incubation. Nest success was higher when common eider hens were captured as they flushed from the nest, than when they were captured with a nest trap. Common eiders demonstrated an ability to undergo and recover from surgery with no risk to survival, and implanted transmitters were an effective tool to track and monitor long-distance post-hatch movements. Common eider that were radio-tagged were more readily identifiable when they also possessed nasal tags. We recommend common eider hens not be captured as they flush from the nest until 15 days into incubation. When hens are captured with a nest-trap and radio-tagged, capture and handling should be delayed until 20 days into incubation.

7.1. Introduction

Nest success is an important determinant of recruitment (Johnson *et al.* 1992) and nesting studies which assess the production of breeding waterfowl are common (Greenwood *et al.* 1995, Beauchamp *et al.* 1996). Early studies simply reported nest success as the proportion of nests that eventually hatch eggs (i.e., all nests were treated as being at equal risk). Current studies now report nest success using the Mayfield method, which takes into account the length of time each nest is exposed to predation because not all nests are located at the same time (Mayfield 1975, Johnson 1979). The actual number of eggs that hatch per nest is an important factor in correctly estimating duckling mortality, but few studies have attempted to provide unbiased estimates of the actual number of eggs that hatch per successful nest (Swennen 1983, Flint *et al.* 1995, Flint and Grand 1997).

A successfully hatched nest is only the first step in understanding recruitment. Survival of young to fledging (Johnson *et al.* 1992), philopatry (Anderson *et al.* 1992), age, and adult mortality (Owen and Black 1990) are also important determinants of annual recruitment, and involve repeated observations of identifiable individual adults. The use of nasal-tags increases the number of individuals that can be identified without recapture and has been widely used in waterfowl research (Bartonek and Dane 1964, Greenwood 1977, Lokemoen and Sharp 1985). More recent studies have demonstrated the feasibility of tracking and monitoring long-distance movements of waterfowl with the use of internal (intra-abdominal) radio-transmitters (Korschgen *et al.* 1984, Olsen *et al.* 1992, Petersen *et al.* 1995) without the behavioural changes associated with external attachments (Dwyer 1972, Perry 1981).

A small number of birds die in most telemetry studies (Conroy *et al.* 1989, Migoya and Baldassarre 1995) and investigators simply exclude these deaths from their analyses (Bergan and Smith 1993, Miller *et al.* 1995). Few studies, however, have attempted to quantify the effects on nest success of capture and handling of adult birds captured during incubation. A study examining duckling survival of common eiders (*Somateria mollissima*) (hereafter eiders) (Mawhinney and Diamond 1999) afforded us the opportunity to evaluate the effects of capture and handling associated with nasal-tagging and implanting intra-abdominal radio-transmitters into adult females captured during incubation.

7.2. Methods

All 5 islands of the Wolves Archipelago (44°56'N, 66°44'W) were searched systematically for common eider nests when egg-laying started in late April/early May in 1995, 1996 and 1997, and were visited weekly thereafter throughout the breeding season. Green Island (44°30'N, 68°30'W) was systematically searched every 4 days for eider nests once egg laying started in late April/early May in 1997 and 1998. The eggs within each nest were marked individually with a black felt marker to indicate the nest and number in the laying sequence, and the clutch size was recorded. On the Wolves Archipelago, all eider nests were marked with coloured vinyl flagging. A combination of poor nesting cover and high density of eider nests, made it impossible to flag all eider nests on Green Island.

Incubating females on the Wolves Archipelago were initially captured in 1995, with drop-door nest traps (Weller 1957). However, females were more easily captured as they flushed from the nest, and nest trapping efforts were discontinued for the duration of the study. Females on Green Island were captured with nest traps in 1997 because poor nesting cover made the capture of flushing hens impossible. In 1998, females were captured as they flushed from the nest. Each bird was marked individually with plastic nasal tags (Lokemoen and Sharp 1985) and standard U.S.F.W.S. leg bands and released immediately. The nests of these females were marked with vinyl flagging (or with a different colour of flagging tape on the Wolves Archipelago). Nests were visited regularly throughout the breeding season to monitor presence, nest contents, and evidence of predation. In 1995 and 1996, a sample of hens (50 in each year) was fitted with intra-abdominal radio-transmitters (Model ½ AA, 150 MHz, Advanced Telemetry Systems, Isanti, MN) in addition to being banded and nasal-tagged. Once captured, hens were placed in a handling crate and transported by boat to Flatpot Island, where the operation took place in a small camp. The inhalation anesthetic isoflurane was administered by a vaporizer to induce and maintain anesthesia. Surgical methods for implanting the transmitter followed Olsen *et al.* (1992). After the surgery, hens were banded and nasal-tagged as in 1995, and held until fully recovered. They were returned to a handling crate and transported and released on the shoreline of the island from which they were taken. Length of time between capture and release was 20-30 minutes.

Hatch date of all tagged females was calculated from direct observations of clutch initiation during visits to nests while laying was in progress and/or the eggs of these clutches were candled (Weller 1956). An incubation period of 27 days (Choate 1966, Milne 1974) and an interval of 24 hours between the laying of eggs was used to predict hatching dates. Permanent egg attendance starts with laying of second egg, and is independent of the actual number of eggs in the nest and the final clutch size (Swennen *et al.* 1993). We revisited the nests of nasal-tagged females every second day during hatching to confirm hatch date and number of eggs hatched.

Post-hatch nest evaluations were conducted on the nests of all tagged females and a sample of marked nests on the Wolves Archipelago within 10 days of hatch. A nest was considered successful if ≥ 1 newly hatched membranes were found in or near it (Girard 1939). Nests which showed at least one hatched membrane were considered successful. The number of unhatched eggs, egg caps, shell membranes and depredated eggs (when individual eggs could be identified) in each nest, as well as the number of totally depredated nests (nests with shell fragments from unhatched eggs) were recorded. No distinction was made between infertile and unviable eggs. Clutch size was not determined for depredated nests because individual eggs could not be counted. Clutch size of successful nests was determined by summing the number of unhatched eggs, the number of membranes and the number of depredated eggs.

7.2.1. Statistical analyses

Paired t-tests were used to test within year differences between clutch size in late incubation and the actual number of hatched eggs, and the difference between the actual number of hatched eggs and estimated number of hatched eggs. Nest success was estimated by the Mayfield method (Mayfield 1975, Johnson 1979), assuming that the clutch exposure period was 27 days. Dates of nest abandonment were rarely known so they were estimated by adding the number of days of probable exposure as determined by the modified Mayfield method to the last date the nest was observed to be viable (Klett *et al.* 1986). Probable exposure equaled half of the interval between the last date the nest was viable and the date nest fate was determined or the estimated hatch date, whichever was less. If the interval was > 14 days it was multiplied by 0.4 instead of 0.5 (Johnson 1979). We tested for differences in nest success using a general Chi-square statistic (Sauer and Williams 1989). We estimated separate nest success rates at 0-5, 6-10, 11-15, 16-20, 21-26 days into incubation for the nests of females captured on the Wolves Archipelago to examine the relationship between stage in incubation at which females were captured and subsequent nest success.

7.3. Results

Clutch size late in incubation was higher than the actual number of eggs hatched in each year on the Wolves Archipelago ($t = 5.10$, 91 df, $p < 0.001$ for 1995; $t = 4.47$, 88 df, $p < 0.001$ for 1996; $t = 4.45$, 88 df, $p < 0.001$ for 1997) and Green Island ($t = 3.39$, 23 df, $p < 0.003$ for 1997; $t = 1.92$, 20 df, $p < 0.007$ for 1998) (Table 7.1). Estimates of the number hatched based on shell membranes in the nest bowl was lower than the actual number hatched in each year on the Wolves Archipelago ($t = 3.64$, 87 df, $p < 0.001$ for 1995; $t = 4.04$, 91 df, $p < 0.001$ for 1996; $t = 3.86$, 88 df, $p < 0.001$ for 1997) but did not differ on Green Island ($t = 1.45$, 23 df, $p = 0.16$ for 1997; $t = 0.57$, 20 df, $p < 0.58$ for 1998) (Table 7.1). The number of unhatched eggs ranged from 5 - 8 % (5% in 1995, 5% in 1996, 8% in 1997 for the Wolves Archipelago; and 8% in 1997, 6% in 1998 for Green Island) and accounted for approximately 60% of the difference between clutch size in late incubation and the actual number hatched. The proportion of nests containing unhatched eggs ranged from 12 - 23% (12% in 1995, 15% in 1996, 21% in 1997 for the Wolves Archipelago; and 23% in 1997, 17% in 1998 for Green Island).

Between 1995 and 1997, 392 (176 in 1995, 126 in 1996 and 90 in 1997) adult females breeding on the Wolves Archipelago were captured and nasal-tagged. Of 216 captured during 1995 and 1996, 50 hens were fitted with radio-transmitters. We observed no direct mortalities or abnormal behaviour attributable to the surgery after release. A total of 263 (132 in 1997 and 131 in 1998) adult females breeding on Green Island were captured and nasal-tagged. Nest success of marked hens was lower than that of unmarked hens in 1995 and 1997 on the Wolves Archipelago ($\chi^2_1 = 3.9, p < 0.05$ for 1995; $\chi^2_1 = 4.7, p < 0.05$ for 1997), but did not vary in 1996 ($\chi^2_1 = 0.2, p > 0.05$ for 1996) (Table 7.2). Nest success varied between years on the Wolves Archipelago for unmarked hens ($\chi^2_1 = 12.7, p < 0.005$) but not for marked hens ($\chi^2_2 = 0.5, p > 0.05$). Nest success was lower for unmarked hens in 1996 ($\chi^2_2 = 4.3, p < 0.05$) than unmarked hens in 1995 and 1997, and was similar to that of marked hens between 1995 and 1997 ($\chi^2_3 = 1.2, p > 0.05$) (Table 7.2). Nest success did not differ between unmarked hens in 1995 and 1997 ($\chi^2_1 = 0.7, p > 0.05$). Overall nest success of nasal-tagged females (59.5%, 0.002 SE) from all years on the Wolves Archipelago was greater than that of radio-tagged females (43.7%, 0.002 SE) ($\chi^2_1 = 4.9, p < 0.05$). Nest success increased the later into incubation that of radio-tagged hens were captured and handled on the Wolves Archipelago, and ranged from 80 - 100% for hens captured in the final 6 days (Fig. 7.1). Nest success of nasal-tagged hens increased up to 11 - 15 days and remained stable thereafter, ranging from 70 - 80% to the end of incubation (Fig. 7.1).

Nest success of nasal-tagged hens nest trapped in 1997 did not vary from nest success of nasal-tagged hens captured as they flushed from their nest in 1998 on Green Island ($X^2_1 = 0.05, p > 0.05$, Table 7.2). Nest success of marked hens was higher throughout the incubation period, than for those captured with a nest trap, with the exception of the first 5-day interval (Fig. 7.2). The high nest success observed for these hens was probably unreliable due to small sample size (n = 8). Rate of increase of nest success reached an asymptote at 11-15 days for hens captured as they flushed from the nest, and at 16-20 days for hens that were nest trapped.

7.4. Discussion

The actual number of eggs that hatch per nest is an important factor in correctly estimating duckling mortality. During this study, use of observed clutch size immediately prior to hatching overestimated the initial brood size and caused underestimation of early duckling survival. Unhatched eggs accounted for approximately 60% of the difference between clutch size in late incubation. We likely underestimated the number of unhatched eggs and abandoned nests because both great black-backed and herring gulls in the study areas removed some of these eggs soon after eiders left the nest site. Estimating the number of eggs hatched per nest on the basis of remaining shell membranes underestimated the number of ducklings produced, and caused overestimates of early duckling survival. Therefore, using either measure as an estimate of initial brood size should be done with caution.

Although complete nest destruction or abandonment results in a much larger loss of production, 5 - 8% of all eggs in successful eider nests did not hatch due to either embryonic mortality or infertility. The proportion of inviable eggs was relatively low, while the proportion of successful nests containing eggs that were inviable (12 - 21%) was higher than expected. Swennen (1983) found that only 0.6 - 4.3 % of successful common eider nests in the Netherlands contained eggs that did not hatch.

Success rates for nests of unmarked hens fell well within the range reported for common eider on breeding colonies not experiencing researcher disturbance (Woolaver 1997, Mawhinney *et al.* 1999). However, it would be unwise to assume that nest success measured on these nests represents that of an undisturbed colony. Common eider hens were flushed from their nests during every visit made by researchers during this study, leaving their nests exposed and vulnerable. Annual differences observed in nest success rates reported for the Wolves Archipelago likely reflect activities associated with gull control, and subsequent recolonization, rather than differences in researcher disturbance. In 1996 the eggs of gulls nesting in the area were prevented from hatching (Mawhinney and Diamond 1999), partly to test whether by eliminating the presence of chicks we would reduce the need for gulls to secure food near their nests, thereby reducing predation rates on eider ducklings in the area. However, these gulls remained in the study area (Mawhinney and Diamond 1999) and with no nest to incubate, it appears that their predation on eider clutches was not reduced.

With the exception of eider hens captured in 1996, nest success of marked birds was lower than that of unmarked hens regardless of tagging technique. Nest success of captured females increased to 75-100% in the final 10 days. However, we did observe a slight decline in the rate of increase for all nasal-tagged hens (Fig. 7.1 and 7.2), due to abandonment late in the incubation period. Nest abandonment by females late in the incubation period has been well documented in common eiders (Gross 1938, McAloney 1973, Korschgen 1977, Bustnes and Erikstad 1991). A female at the end of the incubation period, perhaps sensing the near arrival of her own brood, may be receptive to the stimulus provided by the sight and sound of newly hatched broods in the vicinity. At that time, the urge to begin caring for the young may be stronger than the instinct to complete incubation, resulting in the abandonment of the nest (McAloney 1973). Alternatively, capture late in incubation may be more disruptive to birds with nearly depleted nutrient reserves (Korschgen 1977). Several studies have reported incidents in which eiders became so weak late in incubation that they abandoned pipped clutches (Tinbergen 1958, Korschgen 1977, Bustnes and Erikstad 1991).

Overall nest success did not differ on Green Island when hens were captured as they flushed from the nest in 1998, than when hens were captured with a nest-trap in 1997. Closer examination revealed that nest success of hens captured as they flushed from the nest was higher than for those captured with a nest trap, throughout the incubation period, with the exception of the first 5-day interval. Trapping effort was focused more heavily towards the end of incubation in 1997, and therefore, hens captured in the latter stages of incubation were more heavily represented. Hens captured early in incubation were more heavily represented in 1998, and capture efforts were ceased approximately 1 week prior to hatch to reduce disturbance to newly-hatched ducklings.

Whenever possible eider hens should be captured as they flush from nests rather than with nest traps. However, if trapping is the only option available, as was the case on Green Island in 1997, predation and abandonment associated with nest trapping can be reduced by using methoxyflurane or propofol anesthesia (Rotella and Ratti 1990, Machin and Caulkett 1997). Propofol may be preferable due to a smoother recovery from anesthesia and lower human health risks (Machin and Caulkett 1997). Common eiders demonstrated an ability to undergo and recover from surgery with no risk to survival, and implanted transmitters were an effective tool to track and monitor post-hatch movements of hens out of the study area (Mawhinney and Diamond unpublished). Nest success was higher for nasal-tagged hens than for radio-tagged hens throughout incubation. Nasal-tagged hens were frequently observed and were extremely effective in assisting us with the identification of females throughout the brood-rearing period in both study areas and in all years.

The use of nasal-tags on adult waterfowl has become an important tool in waterfowl research (Bartonek and Dane 1964, Greenwood 1977, Greenwood and Sargeant 1973, Lokemoen and Sharp 1985). However, 18 (5%) of 326 nasal tagged eider hens on the Wolves Archipelago drowned as a result of their nasal-tags becoming entangled in the nets of fishing weirs. Weirs are permanent net and pole structures designed to fish for herring (*Clupea harengus*) during late summer along the coastline in the Bay of Fundy. This type of fishery does not exist elsewhere in the breeding range of common eiders, and death caused by drowning has not been reported elsewhere. Radio tagging may be a more suitable technique to identify common eiders for research conducted in the Bay of Fundy, especially when conducting survival analyses. Patagial tags are not a viable alternative for common eiders because they affect a female's ability to accumulate body reserves before breeding by decreasing feeding time, increasing preening activity, and increasing energy costs of diving (Bustnes and Erikstad 1990).

Given the high mortality rates experienced by common eider ducklings in the Bay of Fundy (Mawhinney and Diamond 1999, Mawhinney *et al.* 1999) and low recruitment rates in general (McAloney 1973, Mendenhall and Milne 1985, Swennen 1989), every attempt should be made to decrease losses associated with capture and handling activities. The probability of nest survival increases the later into incubation that females are captured and handled for all tagging techniques. Therefore, we recommend that nasal-tagging common eider hens captured as they flush from the nest, be delayed until 15 days into incubation. When hens are to be captured with a nest trap and radio-tagged, capture and handling should be delayed until 20 days into incubation.

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Table 7.1. Clutch size in late incubation, actual and estimated number of eggs hatched, and number of unhatched eggs from common eider nests on the Wolves Archipelago, New Brunswick, 1995-1997 and Green Island, Maine, 1997-1998.

	Wolves Archipelago, New Brunswick									Green Island, Maine					
	1995			1996			1997			1997			1998		
Variable	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n
Clutch size in late incubation[a]	4.2	0.04	591	4.1	0.1	463	4.0	0.04	687	4.1	0.1	125	4.6	0.1	143
No. of eggs hatched[b]	3.8	0.1	92	3.8	0.1	89	3.8	0.1	489	4.0	0.3	24	3.9	0.2	21
Estimated no. hatched[c]	3.5	0.05	380	3.6	0.1	276	3.4	0.06	467	3.6	0.1	94	4.2	0.1	108
No. of unhatched eggs[d]	0.2	0.03	380	0.2	0.2	276	0.3	0.03	467	0.3	0.5	94	0.3	0.06	108

[a] Clutch size on nest visit prior to when hatched or hatching eggs were found.

[b] No. of ducklings hatched for nests visited on the day of hatching.

[c] No. of hatch shell membranes present on first post-hatch visit.

[d] No. of unhatched eggs found in nest during visit on hatch date or first post hatch visit.

Table 7.2. Fate of common eider nests on the Wolves Archipelago, New Brunswick, 1995-1997 and Green Island, Maine, 1997-1998.

	Wolves Archipelago, New Brunswick						Green Island, Maine	
	1995		1996		1997		1997	1998
	Marked hens	Unmarked hens	Marked hens	Unmarked hens	Marked hens	Unmarked hens	Marked hens	Marked hens
Nest Success (%)	56.4	68.3	50.3	53.7	54.8	73.1	63	61.2
SE	0.002	0.002	0.004	0.002	0.005	0.001	0.003	0.003
n	189	343	92	321	58	516	94	108
Depredated Nests	29	62	16	87	14	63	23	30
Abandoned Nests	32	20	15	19	4	25	8	5

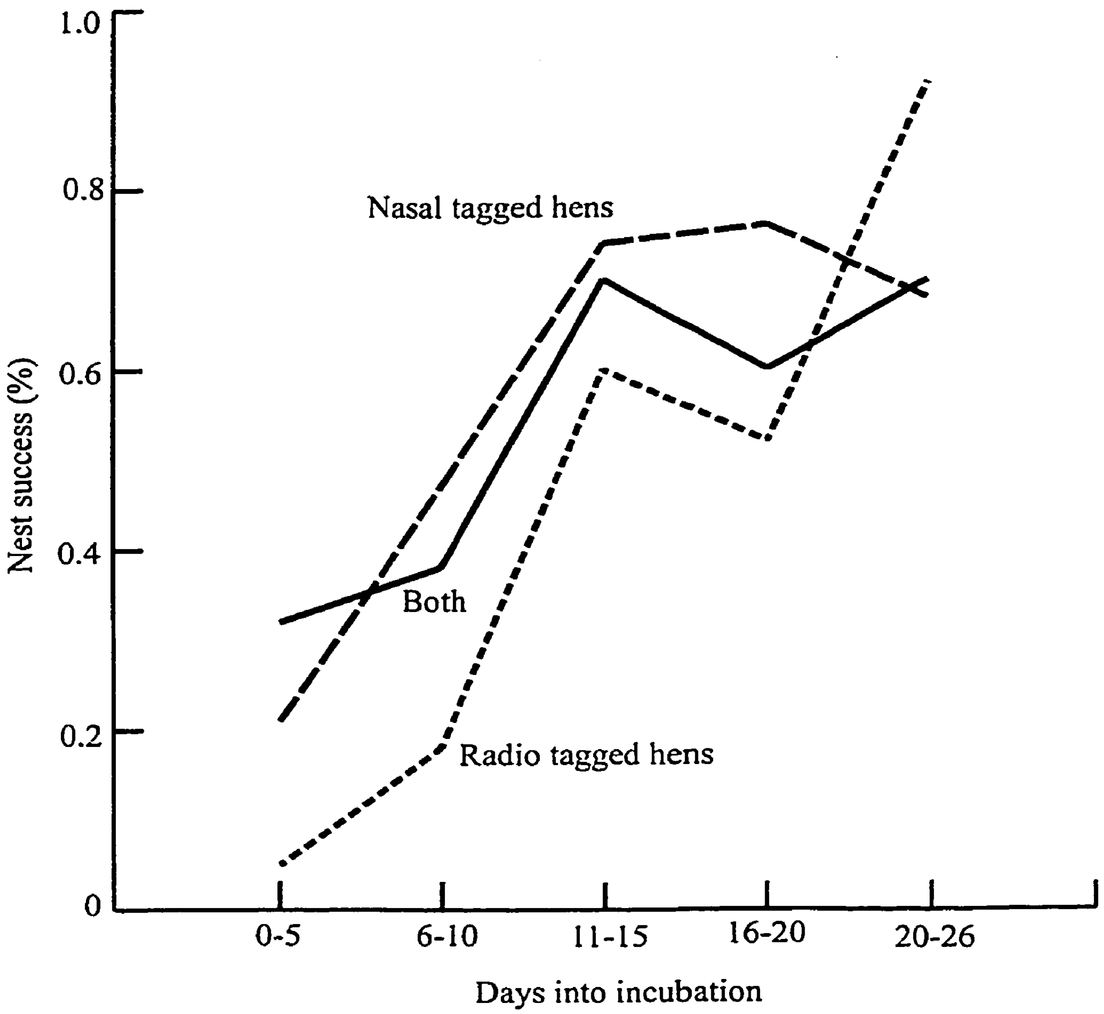

Fig. 7.1. Nest success (%) of common eiders on the Wolves Archipelago, New Brunswick, 1995-1997, calculated by estimating separate success rates for females captured as they flushed from the nest at 0-5, 6-10, 11-15, 16-20, 21-26 days into incubation.

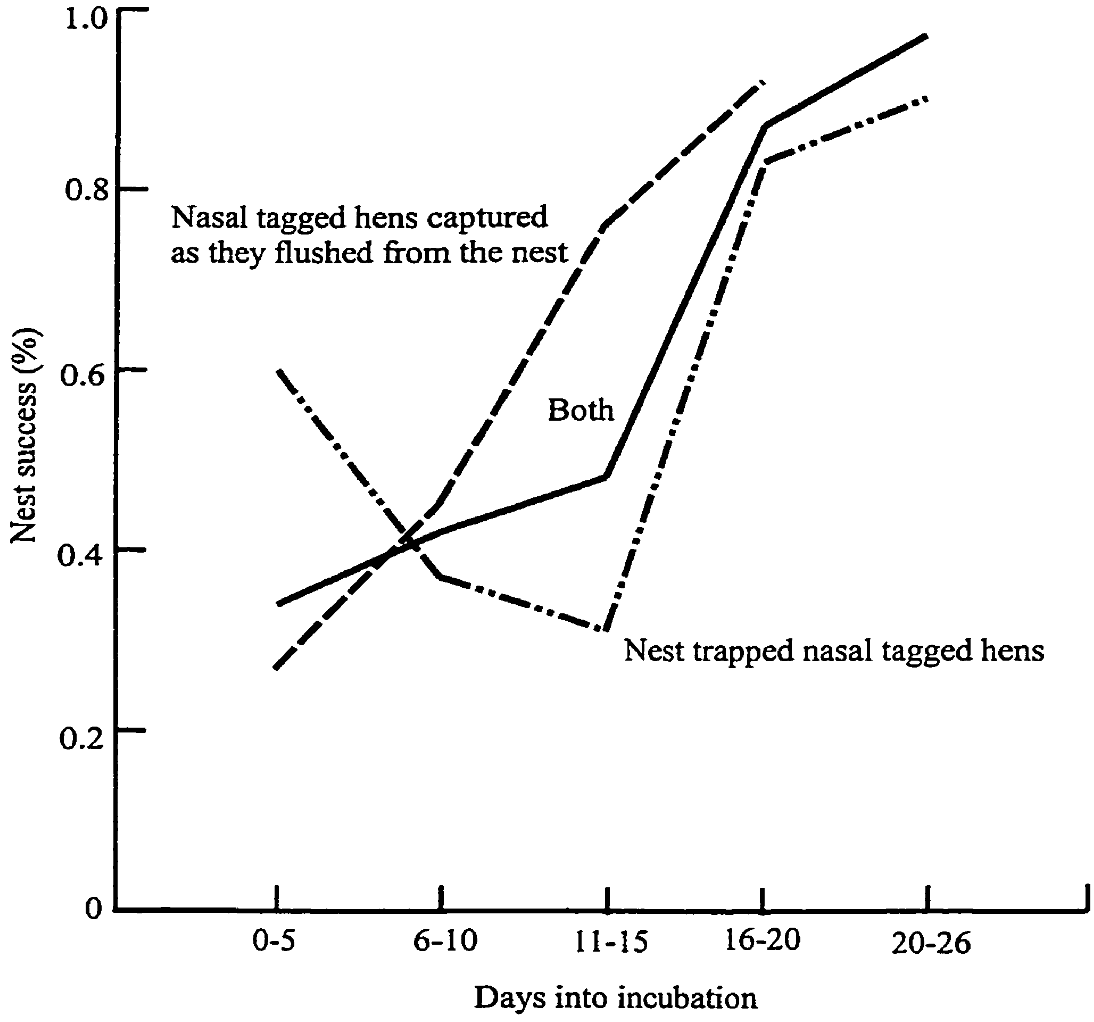

Fig. 7.2. Nest success (%) of common eiders on Green Island, Maine, 1997-1998, calculated by estimating separate success rates for females captured at 0-5, 6-10, 11-15, 16-20, 21-26 days into incubation.

General Discussion

Chapter 8

8.1. Overview of findings

Predation by great black-backed gulls on eider ducklings precluded the study of their brood ecology on the Wolves Archipelago in the Bay of Fundy. I expanded the study to include a gull-free, two-island archipelago within the Petit Manan Wildlife Refuge, a National Wildlife Refuge in the Gulf of Maine, USA. In addition to allowing me to study female condition and brood ecology of common eiders in the Gulf of Maine, I was able to assess the impact of gulls on eider duckling survival in relation to various levels of gull control, and provide a broader perspective of eider recruitment in the Gulf of Maine.

8.1.1. The effect of female condition on clutch size, incubation and crèche attendance in common eiders

I examined the relationship between female condition and clutch size, incubation and crèche attendance in common eiders. My results did not support the "incubation-cost hypothesis" that clutch size is determined by the interaction between the allocation of body reserves to egg production, incubation and care of chicks. I provided evidence which supports the "egg-production hypothesis" that clutch size is limited by a hen's ability to allocate nutrient reserves to egg laying and argue that clutch size and the likelihood that females tend their own brood are both determined by pre-laying body condition. My results did not support the predictions of the *alternative reproductive strategy*, which states that post-hatch brood amalgamation is maintained in a population as a mixed evolutionarily stable strategy. I suggest that the *age or experience* hypothesis, which predicts that young females abandon their young to older females, is correlated with the *energetic stress* hypothesis, which predicts that females abandon their brood because of depleted energy reserves.

Clutch size of common eider hens in the Gulf of Maine was related to body condition at clutch initiation and the cost of incubation did not increase with clutch size. Body condition at clutch initiation was strongly correlated with within-season variation in clutch size and laying date. Females tending a crèche were in better condition than abandoning females regardless of the point at which they were captured in the incubation period. Whether a female eider abandoned her nest/ducklings was a state-dependent decision related to her nutrient reserves at the beginning of nest initiation. Females who cared for ducklings lost only 32% of their pre-incubation body reserves at the time of hatch, where females which abandoned their clutches and ducklings lost 35% and 37%, respectively. 'Aunties' were females in good condition that hatched and lost their own ducklings or their clutch early in incubation such that they were in good condition when ducklings in the colony hatched.

8.1.2. Survival of common eider ducklings in the southern Bay of Fundy and the northern Gulf of Maine.

The great black-backed gull constitutes 25% of the large gull population in the southern Bay of Fundy and 35% in the Gulf of Maine and is becoming increasingly important in relation to the numbers of other species breeding in these areas. I assessed the impact of gull predation on eider duckling survival in relation to various levels of gull control in the southern Bay of Fundy and the northern Gulf of Maine. When gulls were controlled, through a combination of culling and reduced gull production on the Wolves Archipelago, the daily survival rate of radio-tagged ducklings did not differ from that of radio-tagged ducklings when gulls were not controlled. The daily survival rate of ducklings was considerably higher on Petit Manan/Green Island where total gull control through the elimination of breeding pairs was instituted. The overall number of ducklings surviving to fledging was considerably higher in the Petit Manan/Green Island Archipelago, 21% of the breeding pairs in both 1997 and 1998, than on the Wolves Archipelago in 1995, 1996 and 1997 (<5% of the breeding pairs in all years) and represented an important source of potential recruits in this region. The breeding population of common eiders in the southern Bay of Fundy has remained stable over the last decade, ranging from 8,000 to 10,000 breeding pairs. However, the number of ducklings surviving to fledging in the Bay of Fundy decreased from > 14% of the adult breeding population prior to 1991 to < 10% between 1995 and 1998.

8.2. Future Research

8.2.1. Crèching behaviour

In common eiders, predation by gulls is an extremely important factor in duckling mortality (Mendenhall and Milne 1985, Ahlund and Gotmark 1989, Hario and Selin 1989), and any mechanism that reduced mortality from predation would be selectively advantageous. Crèching behaviour has been suggested to be a strategy adopted by eiders in areas with high predation (Munro and Bedard 1977a, Munro and Bedard 1977b). In all three years on the Wolves Archipelago, common eiders did not exhibit a strong tendency to crèche, as broods ranged in size from 1-8 ducklings with only one or two tenders. In Petit Manan National Wildlife Refuge large crèches of up to 75 ducklings and 12-45 tenders were observed consistently. Perhaps there is a threshold of predation above which crèching behaviour breaks down, or perhaps ducklings in the Wolves Archipelago do not survive long enough to form crèches. Regardless, the lack of crèching on the Wolves Archipelago likely exacerbated the lower survival rates of eider ducklings due to great black-backed gulls' predation (Mawhinney and Diamond 1999). Munro and Bedard (1977b) and Minot (1980) found more effective protection of ducklings in eider crèches when the number of brood-tending females increased.

Alternatively, the lack of crèching behaviour on the Wolves Archipelago may reflect a reduced opportunity caused by a lack of females without young on the brood-rearing areas. Females whose ducklings were depredated within days of hatch (i.e., without parental duties) on the Wolves Archipelago left the breeding colony and undertook post-hatch movements to the Grand Manan Archipelago and Passamaquoddy Bay (unpublished data), whereas brood-caring females remained within the archipelago until their ducklings fledged. In contrast, females without parental duties on Green Island, moved similar distances,, to that of females with ducklings from the nesting colony to the feeding areas. Minot (1976) found that rockweed-covered shorelines in the Grand Manan Archipelago were important for both the rearing of eider broods and the physical recovery of post-nesting females independent of young. Gorman and Milne (1977), however, found that females left crèches in the Ythan estuary (Scotland) after only four days because the food of females was spatially separated from that of ducklings. Bustnes (1996) found that feeding habitat used and feeding mode were similar between females without young and brood-caring females. Schmutz *et al.* (1982), however, found that duckling feeding areas (shallow intertidal) are disjunct from the subtidal mussel beds used by adults. Although I did not quantify differences in feeding mode between brood-caring females and females without young, females without parental duties on Green Island fed further offshore and fed by diving in the subtidal zone, whereas female with young fed with their ducklings by dabbling in the intertidal zone. Shoreline habitats used by these females may be able to sustain the whole population of the colony. Shoreline habitats used by females without young on the Petit Manan Archipelago also supported a large population of moulting males (~ 5000) throughout the breeding season (unpublished data).

Long-distance post-hatch movements by females without young on the Wolves Archipelago may have allowed these females to avoid competition for food that may occur in the crowded brood-rearing areas closer to the nesting colony on the Wolves Archipelago. Alternatively, it may be impossible for females with young to reach good feeding areas, forcing them to use suboptimal habitats. A study examining the post-hatch recovery rates of body condition and digestive organs of females with and without young may reveal whether females with young are limited to feeding in suboptimal habitats suggesting a habitat influence upon crèche formation as channelled through the implied segregation of females adult and duckling food resources. Changes in feeding activity during the incubation and post-hatch period are correlated with changes in body condition (Ankney and MacInnes 1978) and digestive organ size in arctic-nesting geese

(Ankney 1977).

8.2.2. Population dynamics

Elsewhere, increases in eider populations are not steady, but a stepped trend reflecting a group of years with high recruitment separated by long periods of stability (Coulson 1984, Baillie and Milne 1982). In these studies, recruitment varied more than adult mortality, and periods of population increase were associated with increased recruitment rather than with below average adult mortality. This suggests that adult survival regulates the size of the adult population, but factors responsible for duckling survival up to recruitment are the main cause of changes in population size. Body condition of females in the spring should be considered a major factor contributing to the regulation of common eider populations. In addition to producing a clutch, females incubate without feeding and must have enough energy reserves to ensure the care of their young. Evidence of extensive non-breeding by eiders in some years has been related to poor condition (Coulson 1984) suggesting that females appear to reduce the risk of death caused by the stress of breeding by avoiding nesting altogether in some years.

Nutrient reserves acquired by hens prior to the breeding season depend on conditions encountered on the wintering grounds. Therefore, we need to identify and protect critical winter habitats and develop a better understanding of male eiders, especially given the potential importance of their contribution to female's food intake prior to laying. Few studies have attempted to gather even basic information on the biology of male eiders. It is assumed that patterns of population change in females apply to adults as a whole (Coulson 1984). Likewise, the survival rates and recruitment of drakes must be similar to those of females since sex-ratio of ducklings is close to equality (Shkyarevick and Nikulen 1979).

The current levels of ducklings recruited to the fall flight in the eider population in the Bay of Fundy are not enough to offset the 13% mortality rate estimated for adult females of the Atlantic Coast subpopulation in the early 1980s (Krementz *et al.* 1996), and band recoveries indicate that the survival rate estimates have declined from 90% to 72% between 1989 and 1990 (R. Milton, Nova Scotia Dept. Natural Resources, unpublished data, 1998). Although numbers of breeding pairs are unchanged since the late 1980's (at ca. 8,500), the number of ducklings fledging (i.e., recruiting to the fall flight) is now only 45% of what it was 10 years ago, and ducklings produced in the Grand Manan Archipelago contribute most potential recruits (44-87%) to the eider population in the Bay of Fundy. We still do not know either the juvenile survival rate, or the age of first breeding, of Bay of Fundy eiders; yet these are critical components of waterfowl population dynamics (Johnson *et al.* 1992).

8.2.3. Management

The harvest of common eiders (*Somateria mollissima dresseri*) in the Atlantic Flyway rose seven-fold between the 1960's and 1980's (Krohn *et al.* 1992). Furthermore, increasing human pressures such as aquaculture and residential, recreational and industrial development (e.g., rockweed harvesting) in coastal habitats, potentially threaten eider populations. In both Canada and the United States, planning has begun to address the issue of apparent declines in several populations of sea ducks. All syntheses of information have demonstrated the lack of basic information on biology needed to support current and future management decisions, and there is a general consensus that hunting mortality of sea ducks is nearly completely additive to natural mortality (rather than complementary as in most waterfowl hunting) (Caithamer *et al.* 1998). Current hunting regulations are old and allow generous harvest compared to dabbling ducks, yet seaducks have a lower tolerance to harvest pressure because their populations and reproductive potential are lower.

The provincial government of Nova Scotia has recently eliminated sea ducks from the regular duck season, by reducing bag limits and season length in 1998 (Nova Scotia Department of Natural Resources); and similar changes have been proposed in the

United States for 1999 (B. Allen, Maine Dept. Inland Fisheries an Wildlife, pers. comm., 1998). It has been suggested that the subspecies of common eider breeding along the Atlantic coast be managed as one unit because band recoveries from hunters reveal that groups that nest in different geographic areas use the same wintering grounds. However, band returns from breeding colonies indicate that there is no interchange between eiders breeding in the Gulf of St. Lawrence (Reed and Erskine 1986), Maine (Wakeley and Mendall 1976), and New Brunswick and Nova Scotia (Mawhinney *et al.* 1997) and Newfoundland. Given that the status and management conditions for individual groups on the breeding grounds can change rapidly, detailed information on the genetic structure and demographics from these breeding regions is needed. Molecular genetic data may be used to infer levels of gene flow and movements among wintering areas, breeding areas, or flyways and to identify the breeding areas of birds harvested on winter ranges. This would allow wildlife managers to adjust harvest rates, conservation plans, and habitat protection measures for common eiders in the Atlantic Flyway.

Hypotheses put forward to explain crèching behaviour for brood-caring females include increased reproductive success of adoptive parents, adopted young and/or genetic parents. Extremely high nesting philopatry of females would lead to close relationships among females nesting in a colony. Lower-than-expected nesting philopatry among the breeding colonies in New Brunswick, as revealed by banding recaptures, suggests that females may not be as closely related as in breeding colonies in Nova Scotia and Maine (Mawhinney *et al.* 1997). Genetic studies would clarify this situation by showing whether females nesting at colonies where females exhibit lower nesting philopatry are less closely related than are females at colonies where females are highly philopatric. If so, the kin selection explanation for crèching behaviour is weakened. This in turn would strengthen the need to find other adaptive explanations for this behaviour.

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APPENDICES

Appendix I

Sex determination of great black-backed gulls using morphometric characters

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Mawhinney, K., and A. W. Diamond. 1999. Sex determination of great black-backed gulls using morphometric characters. Journal of Field Ornithology 70: 206-210.

Abstract

We evaluated sexual size dimorphism of great black-backed gulls (*Larus marinus*) from a breeding colony in the Bay of Fundy and provide a reliable method for predicting the sex of measured individuals. Males were significantly larger than females in all body measurements. A predictive function using only three linear measurements (head length, bill depth and wing length) was more accurate than any single linear measure and correctly sexed 99-100% of the individuals.

I.I. Introduction

In ecological and behavioral studies, it is often important to know the sex of individuals. In sexually monomorphic species such as Larids, researchers have developed predictive models based on the relationship between body size and sex for samples of known individuals (Fox *et al.* 1981, Hanners and Patton 1985, Bosch 1996). Discriminant functions derived from morphometric data are commonly used. However, these functions can be applied only to the populations from which they were derived because geographic variation within a species (Threlfall and Jewer 1978, Coulson *et al.* 1983, Evans *et al.* 1993) may limit a function's generality.

Great black-backed bulls (*Larus marinus*) have expanded their range and numbers along the eastern coast of North America since the early 1920s (Drury 1973, 1974) and have become quite common. However, little is known about their ecology in this region, and no studies have investigated sexual size dimorphism and geographic variation. A gull control program in the Bay of Fundy provided a large sample of great black-backed gulls (Mawhinney and Diamond unpubl. data) and we used the opportunity to gather mophological data on the specimens. The objectives of this paper were to: 1) quantify sexual size dimorphism in great black-backed gulls; 2) and offer a reliable method for determining the sex of great black-backed gulls.

I.II. Study Area

Spruce and Flatpot Island are two islands within the Wolves Archipelago (44°56'N, 66°44'W), 12 km offshore from Beaver Harbour, New Brunswick, Canada. The dominant vegetation on the islands is balsam fir (*Abies balsamea*) and spruce (*Picea* spp.). Breeding seabirds on the two islands include great black-backed gulls, herring gulls (*Larus argentatus*), common eiders (*Somateria mollissima*) and black guillemots (*Cepphus grylle*).

I.III. Methods

In mid-April to early May, great black-backed gulls were removed from Spruce and Flatpot Island in New Brunswick in 1996 (Canadian Wildlife Service Scientific Kill Permit No. SK196) through a combination of shooting and nest trapping. Gulls captured on the nest (sea bird traps, Mills and Ryder 1979) were killed by cervical dislocation. Each bird was weighed to the nearest 25 g with a spring balance and six measures of structural size were recorded: (1) head and bill (HL), the maximum distance from the bill tip to the posterior extremity of the occipital process; (2) bill length (BL), from the bill tip to the posterior extremity of the lateral side of the bill; (3) culmen (C), from the bill tip to the posterior extremity of the culmen; (4) bill depth (BD), vertical height of the bill with the mandibles closed, from the gonys; (5) wing length (WL), distance from the wrist to the tip of the wing with the wing flattened and flexed at the wrist; (6) tarsus length (TL), from the pit at the posterior junction of the tibiotarsus and the tarsometatarsus to the anterior distal end of the tibiotarsus. All measurements were taken to the nearest 1 mm with callipers except wing length, which was measured to the nearest mm with a flat ruler. All birds were sexed by dissection.

Morphometric analyses were performed using $\log_{10}$ transformed data. Multivariate analyses of variance (MANOVA) were used to determine whether overall external morphology varied with sex (SAS Institute 1990) and discriminant function analyses (DFA) were used to explore the nature of this variation. Gulls were analysed with a stepwise DFA of transformed morphometric measurements, entering at each step the measurement that added the most separation between the two sexes (Bosch 1996). Results were considered to be non-significant at $\alpha < 0.05$. The data of the discriminant functions were validated using a jackknife statistical procedure (also called Leave-one-out; Lachenbruch and Mickey 1968) in which each individual was classified using a function derived from the total sample less the individual being classified (e.g., Chardine and Morris 1989, Amat *et al.* 1993). This method produces an unbiased estimate of the success rate of the discriminant functions (Seber 1984).

I.IV. Results

Male gulls were larger than females in all body measurements in both breeding populations ($p < 0.001$, Table I.I). Head length was the most useful single measurement in discriminating between sexes, correctly identifying 97% of females and 99% of males (Table I.II). Stepwise DFA found that the combined function using head length, bill depth and wing length correctly identified the sex of 99% of all females and 100% of all males. The resulting function was:

Equation 1: $D_1 = 73.46\log_{10}HL + 18.64\log_{10}BD + 32.97\log_{10}WL - 3.31\log_{10}B2 - 233.51$ ($p = 0.001$, $r^2 = 0.91$);

where values of $D_1 < 0$ identified females and values of $D_1 > 0$ identified males. Because head length and bill depth are common measurements recorded for gulls we derived a function based on these measurements. The resulting function was:

Equation 2: $D_2 = 82.69\log_{10}HL + 18.03\log_{10}BD - 203.06$ ($p = 0.001$, $r^2 = 0.89$).

This function had slightly less discriminatory power but was able to correctly classify 97% of the jackknifed classifications.

I.V. Discussion

As in other gull species (Monaghan *et al.* 1983, Evans *et al.* 1993, Bosch 1996) male great black-backed gulls were larger than females. The predictive function, using three linear measurements relatively easy to record in the field, was more accurate than any single linear measure. Despite the relative ability of some linear measurements (bill lengths and tarsus) to predict sex accurately, some were not selected in the stepwise DFA because their inclusion in the function did not improve its accuracy. The absence of some of the more accurate measurements (e.g., bill lengths) may be explained by the presence in the function of another measurement which was both more accurate and closely correlated with bill lengths (i.e., head length).

Wing length is the most difficult of the three measurements to take on adult great black-backed gulls in the field. Therefore, a function requiring only the two important head measurements was determined (Table I.II). While this function had slightly less discriminatory power, it was able to classify correctly 100% of the jackknifed classifications. The power of head length and bill depth to discriminate sex agrees with studies of other gull species (Fox *et al.* 1981, Hanners and Patton 1985, Bosch 1996). However, it should be used with caution as bill depth can vary with age (Coulson *et al.* 1981). To improve the degree of accuracy, the combined function using three measurements should be used.

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Table I.I. Means (± SD) of linear measurements (mm) taken from adult great black-backed gulls collected from their breeding territory on the Wolves Archipelago, New Brunswick, 1996.

	New Brunswick		MANOVA	
	Females	Males		
Measurement	(n = 108)	(n = 78)	F	*p*
Head length	136.4±3.4	149.2±3.6	610.788	<0.001
Bill length1	90.2±5.1	98.9±4.9	121.492	<0.001
Culmen	61.3±3.5	67.8±3.6	144.02	<0.001
Bill depth	24.1±1.0	26.5±1.6	167.076	<0.001
Wing length	468.4±1.4	495.9±1.3	188.037	<0.001
Tarsus length	77.2±3.1	82.7±4.3	96.26	<0.001

Table I.II. Accuracy of sexing great black-backed gulls in New Brunswick by discriminant analysis using single measurements or combined functions.

Variable	r^2	Jackknifed classifications (n = 186) Females	 Males
Head length (HL)	0.88	97% (105/108)	99% (77/78)
Bill length1 (B1)	0.63	87% (94/108)	86% (67/78)
Culmen (C)	0.66	87% (94/108)	83% (65/78)
Bill depth (BD)	0.69	94% (101/108)	85% (66/78)
Wing length (WL)	0.71	82% (89/108)	90% (70/78)
Tarsus length (TL)	0.59	83% (90/108)	88% (68/78)
$D_1 = 70.26\log_{10}HL+18.53\log_{10}BD+31.91\log_{10}WL-230.66$	0.91	99% (107/108)	100% (78/78)
$D_2 = 82.69\log_{10}HL+18.03\log_{10}BD-203.06$	0.89	97% (105/108)	97% (76/78)

Appendix II

The use of energy, fat and protein reserves by breeding great black-backed gulls

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Mawhinney, K., A. W. Diamond, and F. P. Kehoe. 1999. The use of energy, fat and protein reserves by breeding great black-backed gulls. Canadian Journal of Zoology. *In press.*

Abstract

Changes in weight (adjusted for body size) and nutrient reserves were examined in adult male and female great black-backed gulls from arrival at the colony to one week prior to the fledging of young. During the pre-laying period, males lost approximately as much of their pre-breeding fat reserves as females gain in weight, suggesting that males contributed substantial energy to the reproductive investment of the pair. We did not analyze pre-breeding females for fat or protein, but based on the weight fat correlation, pre-breeding females likely put on fat which was allocated to egg formation. However, their overall loss in weight was equal only to the accumulation prior to laying, suggesting that increased body reserves serve breeding directly as capital costs for clutch formation. In contrast, males did not regain pre-breeding weights until pre-fledging, suggesting that costs associated with pre-breeding activity by males were larger than those for females. Once the clutch was completed, both sexes carried comparable reserves and neither sex fully regained to pre-breeding levels. Female weights at the end of the chick-rearing period were lower than those during or before incubation, while males had recovered to their pre-breeding weights (adjusted for body size) by this time.

II.I. Introduction

Egg production has been shown to make considerable nutritional and energetic demands in gulls (*Larus* spp.) despite their comparatively large body size (Ricklefs 1974, Robbins 1981, Houston *et al.* 1983, Salzer and Larkin 1990), and in most species, females bear the heavier energetic cost of reproduction (O'Connor 1980, Houston *et al.* 1983, Norstrom *et al.* 1986, Pierotti and Annett 1990, Hario *et al.* 1991). In general females, because they produce the clutch of eggs, have higher nutrient demands and costs than males that invest only their sperm. However, for gulls parental investment includes both the cost of gamete production and the cost of parental care. There is growing evidence that males contribute substantially to parental care in several larid species (Burger and Beer 1975, Burger 1981, Southern 1981, Butler and Janes-Butler 1983). The contribution that males make to parental care should be reflected in changes in nutrient reserves during the breeding season.

Burger (1987) found support for selection favouring equalized parental investment in herring gulls (*Larus argentatus*) during the entire breeding season in terms of behaviour activities that directly or indirectly affected the reproductive success during the entire breeding season. The pre-laying investment of males in this species involved chiefly territorial behaviour and courtship feeding, which can provide up to 67% of the minimum energy requirements of female herring gulls (Norstrom *et al.* 1986). Hario *et al.* (1991) found that despite considerable variation in lipid reserves between sexes during the period from colony occupation to laying, male and female herring gulls were energetically equivalent (i.e., carried similar fat and protein reserves) by the end of incubation. Houston *et al.* (1983) found that lipid stores did not differ between non-breeding and laying lesser black-backed gulls (*L. fuscus*), whereas in herring gulls the loss of fat reserves during laying was larger than the accumulation prior to laying (Hario *et al.* 1991). Houston *et al.* (1983) also found that female lesser black-backed gulls lost a significant proportion of stored proteins during the early stage of clutch formation, whereas Hario *et al.* (1991) and Bolton (1991) did not find any difference in protein between sexes in herring gulls and lesser black-backed gulls, respectively.

Butler and Janes-Butler (1983) suggested that parental investment by the sexes was equal despite qualitative and quantitative differences in behaviour of great black-backed gulls during the pre- and post-hatch periods. Following clutch completion, female great black-backed gulls (*L. marinus*) invest more time in both territorial attendance and incubation, while males engage in more agonistic behaviour before chicks hatch; during the post-hatch period, there were no sexual differences in territorial attendance, brooding, or frequency of chick feedings(Butler and Janes-Butler 1983).

We investigated differences in energy reserves between male and female great black-backed gulls nesting on the Wolves Archipelago in the Bay of Fundy, New Brunswick, Canada, where gulls on two islands were culled to reduce interspecific predation on eider (*Somateria mollissima*) ducklings in 1996 (Mawhinney and Diamond 1999). This provided us with the opportunity to examine weight change and size of endogenous nutrient reserves in male and female great black-backed gulls during the period from colony occupation to one week prior to the fledging of young. The objectives of the study were to: (i) examine how energy reserves changed according to breeding phase; (ii) evaluate male and female costs in terms of their use of nutrient reserves, and; (iii) test whether the pattern of nutrient use in the two sexes supports Burger's (1987) hypothesis of equal parental investment.

II.II. Methods

From mid-April to early May 1996, great black-backed gulls were collected from Spruce and Flatpot Islands (44°56'N, 66°44'W) through a combination of shooting (n = 119) and nest trapping (n = 126) (Canadian Wildlife Service Scientific Kill Permit No. SK196). Gulls captured on the nest (sea bird traps, Mills and Ryder 1979) were killed by cervical dislocation. Each bird was weighed to the nearest 25 g with a spring balance and three measures of structural size were recorded: (1) head and bill, the maximum distance from the bill tip to the posterior extremity of the occipital process; (2) bill length, from the bill tip to the posterior extremity of the lateral side of the bill; (3) wing length, distance from the wrist to the tip of the wing with the wing flattened and flexed at the wrist. All measurements were taken to the nearest 1 mm with callipers except wing length, which was measured with a flat stopped ruler. All birds were sexed by dissection and the oviducts of females were examined for follicle development. Gastro-intestinal tracts were removed to examine parasite load (M. Burt, University of New Brunswick, unpublished data, 1998) and carcasses were frozen for subsequent analysis.

Of 245 great black-backed gulls collected, the timing of laying and incubation start were known for 109 females and 69 males. Each gull was assigned to one of five periods of the breeding cycle. Pre-breeding: birds collected on the staging area 1 to 3 weeks before the first eggs were laid in the colony. Laying start: birds taken at nests with one egg or females having one developing ovum in the oviduct but no post-ovulatory follicles. Laying end/incubation start: birds taken at nests with females either having the third egg in the oviduct or incubating a full clutch of three for the 1st or 4th days; males were categorized according to the category of their mate. Incubation: birds incubating from > 4 days after laying to the end of incubation at 28 days. Pre-fledging: birds collected from nests with chicks one week prior to fledging.

A sub-sample of the whole carcasses (excluding gastrointestinal tracts) of gulls were thawed and ground with a blender (Whirling^R, model 7005), then oven-dried to constant weight at 80°C (Kerr *et al.* 1982). The dry homogenate was weighed and then ground to a powder in an electric coffee grinder (Moulinex^R, model 505). Lipid (hereafter fat) was removed from an 8-10 g sub-sample of powdered homogenate, using petroleum ether in a modified Soxhlet apparatus for 8 hours (Dobush *et al.* 1985). The weight of the lean dry sample was subtracted from the dry weight of the original sample to obtain the weight of fat in the sample. Each lean dry sample was transferred to an ashing crucible and placed in a furnace at 550°C for 8 hours. The remaining ash was weighed and divided by the weight of the lean dry sample to obtain the percent of ash in each sample. Total body fat was determined by multiplying the dried body weight of a gull by the proportion of fat in the subsample of homogenate. Total body ash was determined by multiplying the proportion of ash in the sample by the lean dry body weight of a gull. Ash-free lean dry weight (a measure of protein content) was calculated as the dry carcass weight minus total body fat and total body ash.

Total body weight, fat and protein were corrected for structural size using the first principal component (PC1) scores from an analysis of the correlation matrix of log-transformed morphological variables (head, bill, wing) (Alisauskas and Ankney 1987, Hanson *et al.* 1990). Body weight, fat and protein were adjusted for variation in structural size by two techniques. The simplest method was to include PC1 scores (Rising and Somers 1989, Freedman and Jackson 1990) as a covariate in the statistical model. The other method involved regressing weight, fat and protein on the PC1 score and using the residuals for each bird to calculate a new value, Y_i, which is corrected for body size. The equation is as follows: corrected body weight = residual + mean body weight, or $Y_i = Y_{obs} - ((a + b(PC1)) + Y_{obs})$ (Alisauskas and Ankney 1987, Hanson *et al.* 1990). This technique was used for the purposes of examining the changes in weight, fat and protein during the different breeding phases in Fig. II.I and II.II. Hereafter, weight, fat and protein will refer to these indices corrected for structural size. Analyses of variance (ANOVA) were used to determine if weight, fat and protein differed between breeding phases for each sex, or between sex, within each breeding phase.

To examine the relationship between weight, fat and protein during incubation, analysis of covariance (ANCOVA, SYSTAT, Wilkinson 1988) was performed to test for the independent effects of size (PC1), time (days into incubation) and sex. ANCOVA procedures were based on type III sums of squares. This procedure tests for the effect of an independent variable in the model on the dependent variable by adjusting for the effects of all other independent variables (SAS Institute Inc. 1990). Higher order interactions were excluded from the statistical model if they were non-significant and had no biological importance.

II.III. Results

PC1 accounted for 75% of the variation in gull morphology and was characterized by the following eigenvectors: head and bill 0.93; bill 0.85; wing 0.81. Weight was correlated with fat in both sexes (males: $r_s = 0.63, p < 0.001$, n = 55; females: $r_s = 0.65, p < 0.001$, n = 83). Weight correlated significantly with protein in females ($r_s = 0.61, p < 0.001$, n = 83), but not in males ($r_s = 0.20, p < 0.14$, n = 55). Weight and protein varied with body size and sex, but not with time, during incubation (Table II.I and II.II). The amount of variation explained by the weight x time relationship ($p = 0.06$) was only 0.02. Both weight and protein increased with body size ($p < 0.001$ in both cases, $r^2 = 0.63$ and 0.68 respectively). Fat did not vary with body size, sex or time during incubation ($p > 0.05$ in all cases). Budget constraints limited the number of carcasses analyzed for fat and protein content and unfortunately carcasses from the pre-breeding and pre-fledging phases were not analyzed.

In females, all three condition indices varied between breeding phases (weight: F = 13.40, $p < 0.001$, n = 109; fat: F = 4.85, $p < 0.002$, n=83; protein: F = 2.44, $p < 0.05$, n = 83). Weight and fat followed the same general pattern, increasing from pre-breeding to clutch initiation followed by a decline in each successive phase of the breeding cycle (Fig. II.I and II.II). Protein also declined following clutch initiation but began to increase during incubation (Fig. II.II). In males, both weight and fat varied during the breeding phases (weight: F = 5.86, $p < 0.001$, n = 169; fat: F = 9.67, $p < 0.001$, n = 55). Weights declined during early laying, remained stable thoughout the late stages of laying and incubation, and increased by pre-fledging (Fig. II.I). Pre-breeding season declines in fat continued through the late stages of laying but began to recover by incubation (Fig. II.II). Protein did not vary during the breeding season in males (F = 0.60, $p = 0.62$, n = 55) (Fig. II.II). Weights were significantly lower during incubation than in the pre-breeding season in males (F = 10.94, p = 0.003), but not in females (F = 2.54, p = 0.12). Pre-fledging weights ($\bar{x}$ = 1.69 kg ± 0.08 SD, n = 6) were significantly lower than pre-breeding season weights ($\bar{x}$ = 1.59 kg ± 0.11 SD, n = 12) (F = 3.45, p = 0.03) in females, but not in males ($\bar{x}$ = 1.81 kg ± 0.17 SD, n = 20) (F = 0.84, p = 0.37).

Pre-breeding weights did not differ between male and female gulls (Table II.III). Weight (Fig. II.I), fat and protein (Fig. II.II) were higher in female gulls at the beginning of laying, but did not differ between sexes by the end of Laying (Table II.III). During incubation, weight and protein were higher in males, but fat did not differ between the sexes. Weights of males were significantly higher than females in the pre-fledging period (Table II.III).

III.IV. Discussion

Fluctuations in overall weight can be a reliable indicator of changes in fat reserves in many birds (McEwan and Whitehead 1984, Johnson *et al.* 1985). In general, fat accounts for the greatest variation in body mass (Witter and Cuthill 1993). Fluctuations in weight reflected changes in both fat and protein reserves in female great black-backed gulls, but only of fat in males. The importance of protein for egg production in females has been demonstrated in a wide range of species, such as red-billed quelea (*Quelea quelea*) (Jones and Ward 1976), lesser snow goose (*Chen caerulescens caerulescens*) (Ankney and MacInnes 1978) and lesser black-backed gulls (Houston *et al.* 1983). The prime source for endogenous protein is the pectoral muscle (Blem 1990). In all these species, there was a decline in pectoral muscle protein associated with egg formation, and potential clutch size has been shown to be positively correlated with flight muscle condition in pre-laying female lesser black-backed gulls (Houston *et al.* 1983).

Great black-backed gull weights varied considerably during the breeding season, and males and females appeared to have distinct patterns of mass variation. There have been no studies on pre-breeding activities in great black-backed gulls, but in other gulls, male are more active in territorial defense than females, and they also feed the female frequently prior to egg laying (Burger 1987, Niebuhr 1981, Tasker and Mills 1981). Decreased fat and weight in male great black-backed gulls in the pre-breeding period is presumably due to higher "up-front" investment in territorial defense, courtship and feeding (Burger 1987, Norstrom *et al.* 1986), suggesting that males contribute substantially to female fattening, and by doing so they invest directly in the clutch. Male great black-backed gulls lost approximately as much of their pre-breeding fat reserves as females gained in weight during the pre-laying period. We did not analyze pre-breeding females for fat or protein, but based on the weight-fat correlation, pre-breeding females likely put on fat which was clearly allocated weight to egg formation. However, their overall loss in weight was equal only to the accumulation prior to laying (Fig. II.I), suggesting that increased body reserves serve breeding directly as capital costs for clutch formation. Thus the initial heavy investment of energy reserves by females in clutch formation is only apparent. In contrast, males did not regain their pre-breeding weights until pre-fledging, suggesting that costs associated with pre-breeding activity by males were larger than those for females.

In contrast to what has been observed in herring gulls (Hario *et al.* 1991), we found that female great black-backed gulls lost a significant proportion of stored proteins during laying. Hario *et al.* (1991) suggested that herring gulls did not deplete endogenous protein because most of the protein required for clutch formation came from protein-rich exogenous food sources. Great black-backed gulls on the Wolves Archipelago feed largely on low protein anthropogenic food sources in the early stages of breeding (Gilliland 1990), and therefore, must depend on endogenous protein for clutch formation. Protein remained unchanged in males throughout the breeding season; extensive depletion of endogenous protein might reduce the mass of flight muscles (Blem 1990) and would clearly be maladaptive for males during this phase as they are more active in territorial defense than females (Butler and Janes-Butler 1983).

Once the clutch was completed both sexes were nutritionally equivalent and neither sex replenished endogenous reserves during incubation. Lower weights of incubating females were related to differences in protein rather than fat. Fat reserves in males did show some recovery (though not statistically significant) during incubation; by contrast, female weights declined over the remainder of the breeding season, although there was no change within the incubation period when it was considered separately. However, the recovery of protein from the losses associated with clutch formation masked further declines in fat during this period (Fig. II.II). Sexual differences in energy expenditure of great black-backed gulls during incubation may reflect qualitative and quantitative differences in behaviour (Butler and Janes-Butler 1983). Butler and Janes-Butler (1983) found that female great black-backed gulls invested more time in territorial attendance and incubation, while males engaged in more agonistic behaviour before chick hatching. Burger (1987) showed equitability in herring gulls during incubation, allowing both sexes to replenish their endogenous stores during incubation (Hario *et al.* 1991).

Females weighed less at the end of the chick-rearing period than during incubation and pre-breeding weights, while males had recovered to their pre-breeding weights. Butler and Janes-Butler (1983) found no sexual differences in territorial attendance, brooding, or frequency of chick feedings during the first 20 days post-hatch in great black-backed gulls. Burger (1981), however, reported that although both sexes of herring gulls contribute equal investment early in the post-hatch period, sexual differences in investment patterns developed as chicks grew older. Sexual differences in spiteful and altruistic behaviour have been observed in both herring and western gulls (*L. occidentalis*) (Pierotti 1981). Male western gulls not only are responsible for the bulk of territorial defense, but also feed chicks more often than do females (Pierotti 1981). Our results suggest that the females' costs by the end of chick rearing are greater than those of males. This pattern of mass loss could arise if there were exceptionally high energy demands on the female during brooding. A loss of energy reserves related to differing reproductive roles after hatching has been observed in female arctic skuas (*Stercorarius parasiticus*) (Phillips and Furness 1997).

Our results differ from Burger's (1987) conclusion of equal parental investment by the sexes of herring gulls during the breeding season in that male and female great black-backed gulls in the Bay of Fundy are not energetic equivalents at the end of the breeding season. However, the relative significance of male and female contributions in terms of parental investment may be equal in terms of their overall contribution to the breeding period. Periods of physiological decline and recovery of each sex may vary during the different breeding phases in such a way that the overall reproductive success of the breeding pair is ensured.

Female body condition in birds is thought to be an important determinant of reproductive success, with females in better condition laying earlier and producing more, better quality, or larger eggs (Houston *et al.* 1983, Järvinen and Ylimaunu 1986, Meathrel and Ryder 1987, Bolton *et al.* 1993, Viñuela 1997). Females should therefore maximize energy or protein reserves prior to egg laying (Bolton *et al.* 1993). Early in the breeding season, food for great black-backed gulls on the Wolves Archipelago is limited to low quality resources of intertidal prey and human refuse (Gilliland 1990). Loss of energy reserves through courtship feeding by males may ensure that females attain the energy reserves necessary to ensure a successful clutch. Females of many seabird species that do not attain a threshold mass often do not attempt to breed (Shaw 1986, Weimerskirch 1992).

Parental quality is important in determining chick survival, especially for a species with a comparatively long fledging period in which the young are fed by both parents (Bolton 1991). At the beginning of incubation and chick rearing, female energy reserves with respect to weight are equal to pre-breeding levels, allowing her to take on more territorial attendance and incubation than males during the incubation period

(Butler and Janes-Butler 1983), thus ensuring that the clutch will hatch successfully. The recovery of energy reserves in females is presumably delayed until after the chicks have fledged, when protein-rich herring (*Clupea harengus*) stocks in the study area are high. Herring is the major prey item for gulls during the later half of chick rearing (Gilliland 1990) and stocks remain in the study area until well into the fall (Stephenson *et al.* 1993).

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Table II.I Analysis of covariance among factors affecting body weight of great black-backed gulls during incubation on the Wolves Archipelago, 1996.

	Dependent variable = Weight		
Source of variation	df	F	*p*
Date	1	3.6	0.06
Sex	1	43.53	0.001
Body size (PC1)	1	18.83	0.001

Table II.II. Analysis of covariance among factors affecting protein of great black-backed gulls during incubation on the Wolves Archipelago, 1996.

	Dependent variable = Protein		
Source of variation	df	F	*p*
Date	1	0.29	0.59
Sex	1	34.95	0.001
Body size (PC1)	1	7.98	0.006

Table II.III. Differences between male and female great black-backed gulls in weight, fat and protein (corrected for differences in structural size, PC1) during different breeding phases on the Wolves Archipelago, 1996 (significant differences in boldface).

	Weight			Fat			Protein		
	n	F	*p*	n	F	*p*	n	F	*p*
Pre-breeding	21	1.82	0.19	-	-	-	-	-	-
Laying start	16	24.45	**0.001**	12	7.82	**0.02**	12	6.4	**0.03**
Laying end/ Incubation start	26	0	0.96	21	1.74	0.2	21	0.7	0.42
Incubation	98	8.92	**0.004**	92	1.62	0.21	92	8.3	**0.005**
Pre-fledging	21	20.05	**0.001**	-	-	-	-	-	-

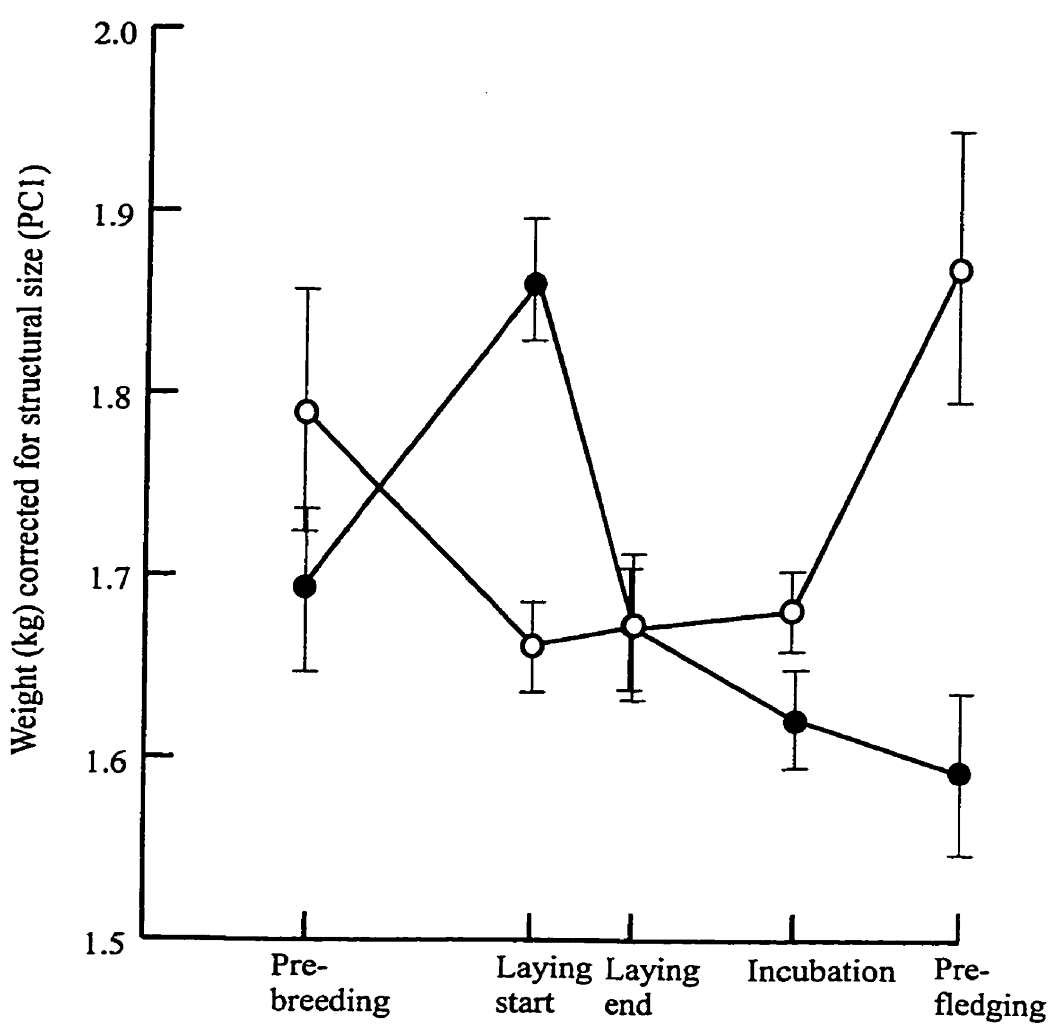

Fig. II.I. Changes in weight (kg) corrected for structural size (PC1) in male (open circles) and female (closed circles) great black-backed gulls during the different breeding phases. Mean ± 1 SE.

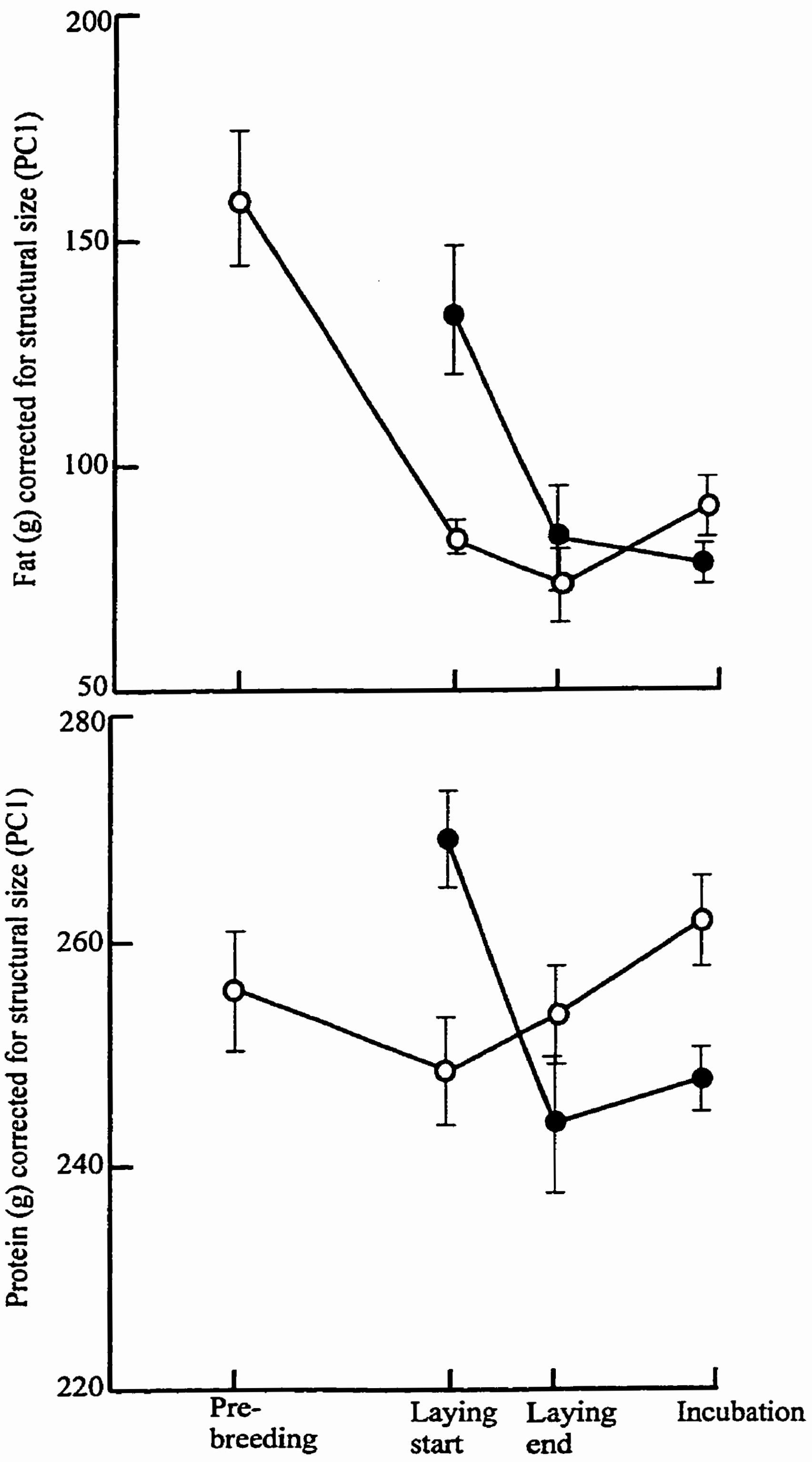

Fig. II.II. Changes in fat (g) and protein (g) (corrected for structural size, PC1) in male (open circles) and female (closed circles) great black-backed gulls during the different breeding phases. Mean ± 1 SE.