HABITAT USE BY BREEDING AND MOLTING RED-BREASTED MERGANSERS IN THE GULF OF ST. LAWRENCE

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- For Owen Fraser and Rodger Titman -

Your passion for discovering and learning about nature
has had a significant influence on my life’s path.

ABSTRACT

The choice of habitat plays an important role on the population dynamics of ducks (Anatinae). However, little is known of the patterns of habitat use by nearctic Red-breasted Mergansers (*Mergus serrator*). From 2002 to 2006, I studied habitat use and selection by breeding and molting Red-breasted Mergansers in the Gulf of St. Lawrence, Canada, by measuring macro- and microhabitat and obtaining radio telemetry, time-activity, and stomach content information. My objectives were to examine 1) nest-site selection, 2) brood habitat selection, and 3) habitat use by flightless male mergansers.

Concealment was the most important feature for nest placement by Red-breasted Mergansers on Tern Islands at Kouchibouguac National Park, New Brunswick. Over 95% of nests were in dense stands of marram grass (*Ammophila breviligulata*), and overhead concealment, vegetation density, and vegetation height at nests were greater than that at random sites. Microhabitat at successful nests was similar to that at unsuccessful nests. Radio-marked broods originating from Tern Islands moved large distances (>3 km) to rearing habitat and remained highly mobile throughout the rearing period ($\bar{x}$ = 1.0 km day^{-1}). Broods selected shallow waters (<75 cm) over continental estuarine intertidal flats and in tidal streams, and avoided tidal rivers and marine habitats. Age class I broods (≤10 days post-nest exodus) selected continental estuarine intertidal, tidal stream, and saltmarsh habitats, whereas older broods often used estuarine subtidal wetlands.

By the early brood-rearing period, most male Red-breasted Mergansers had migrated from Kouchibouguac National Park to molting sites. At Anticosti Island, Québec, I estimated that males were flightless for 30-33 days between late

July and early September. Flightless males used clear, shallow waters (≤12 m) near shore (<850 m) in coastal bays with a sand-rock substrate and stands of submergent algae. Foraging flocks were generally restricted to intertidal and shallow subtidal areas (<4 m), whereas nonforaging flocks often used deeper subtidal sites. These observations were consistent with analyses of stomach contents, which indicated that males fed on small, inshore fish, particularly grubby (*Myoxocephalus aenaeus*) and sandlance (*Ammodytes* spp.).

My thesis identifies factors influencing the distribution of breeding and molting Red-breasted Mergansers in the Gulf of St. Lawrence, and prioritizes future research that will provide additional insight into habitat selection and its implication on survival of this species.

RÉSUMÉ

La sélection des habitats joue un rôle important dans la dynamique des populations de canards (Anatinae), mais reste méconnue chez le Harle huppé (*Mergus serrator*). De 2002 à 2006, j'ai étudié l'utilisation et la sélection des habitats par le Harle huppé pendant les périodes de reproduction et de mue dans le Golfe du St-Laurent au Canada. Pour ce faire, j'ai recueilli de l'information sur les paramètres d'habitats, les déplacements des couvées, la fréquence des comportements, ainsi que le contenu des estomacs. Les objectifs de mon étude étaient d'examiner 1) la sélection des sites de nidification, 2) la sélection des habitats par les couvées, et 3) l'utilisation des habitats par les mâles pendant la période de mue des ailes.

Le camouflage des nids était le facteur le plus important pour le choix de l'emplacement des nids par les Harles huppés sur les Îles aux Sternes au Nouveau-Brunswick (Parc national du Canada Kouchibouguac). Plus de 95% des nids étaitent aménagés dans de denses parcelles d'ammophile à ligule (*Ammophila breviligulata*). Le couvert végétal au dessus du nid, la densité, ainsi que la hauteur de la végétation, étaient plus grands aux sites de nidification comparativement aux sites aléatoires. Le microhabitat caractérisant les nids qui ont eu du succès était similaire à celui des nids où l'éclosion des oeufs a échoué. Les couvées, qui ont étées suivies à l'aide d'émetteurs radio-télémetriques, ont parcouru de grandes distances (>3 km) à partir des Îles aux Sternes et ont continué de se déplacer pendant la période de d'élevage ($\bar{x}$ = 1.0 km jour^{-1}). Les couvées ont préféré les eaux peu profondes (<75 cm) dans les zones intertidales continentales de l’estuaire et les ruisseaux; elles ont évité les habitats riverains et marins. Les couvées de la classe d'âge I (≤10 jours après avoir quitté le nid) ont sélectionné les zones intertidales continentales de l’estuaire, les ruisseaux, et les marais salés. Les couvées plus agées utilisaient d'avantage les habitats subtidaux de l’estuaire.

Au début de la période d'élevage des couvées, la plupart des mâles Harles huppés avaient quitté Kouchibouguac pour se rendre aux sites de mue. Sur l'Île d'Anticosti, Québec, j'ai estimé que les mâles en mues étaient incapables de voler pour une période de 30-33 jours entre la fin de juillet et le début de septembre. Les mâles incapables de voler fréquentaient les baies côtières ayant un substrat sablonneux à rocheux ainsi que les parcelles d'algues submergées. Ils utilisaient des eaux claires et peu profondes (≤12 m), et restaient près de la rive (<850 m). Les groupes d’harles qui se nourissaient étaient généralement confinés dans les zones de marées intertidales et subtidales peu profondes (<4 m). Les groupes d'harles qui ne se nourrissaient pas, quant à eux, utilisaient le plus souvent les zones subtidales plus profondes. Ces observations ont été appuyées par les analyses des contenus d'estomacs, qui ont indiquées que les mâles se nourrissaient de petits poissons de rivage, comme le chaboisseau bronzé (*Myoxocephalus aenaeus*) et le lançon (*Ammodytes* spp.).

Ma recherche contribue à la compréhension des facteurs influenceant la distribution des Harles huppés pendant les périodes de reproduction et de mue dans le Golfe du St-Laurent, et identifie les priorités de recherche pour mieux comprendre la sélection des habitats et la survie de l’espèce.

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PREFACE

The format of this dissertation is manuscript-based and follows the style of *The Condor* in accordance with thesis guidelines of McGill University. I present six chapters and five appendices. Chapters 2 to 5 address my main study objectives. Chapter 2 is co-authored by S. R. Craik and R. D. Titman, and was published in *Waterbirds*[a]. Chapter three is co-authored by S. R. Craik and R. D. Titman, and was published in *The Wilson Journal of Ornithology*[b]. Chapter four is co-authored by S. R. Craik, J.-P. L. Savard, and R. D. Titman, and was published in *The Condor*[c]. Chapter five is co-authored by S. R. Craik (primary author), J.-P. L. Savard, M. J. Richardson, and R. D. Titman, and was submitted to *The Condor* in June 2009. Appendix I is presented as a short manuscript because it is a study that provides additional information on the nesting ecology of Red-breasted Mergansers (*Mergus serrator*) at Kouchibouguac National Park, and supports a conclusion of Chapter 2 that merganser nest-site placement at this site is adaptive.

[a] Craik, S. R., and R. D. Titman. 2009. Nesting ecology of Red-breasted Mergansers in a Common Tern colony in eastern New Brunswick. Waterbirds 32:282-292.

[b] Craik, S. R., and R. D. Titman. 2008. Movements and habitat use by Red-breasted Merganser broods in eastern New Brunswick. Wilson Journal of Ornithology 120:743-754.

[c] Craik, S. R., J.-P. L. Savard, and R. D. Titman 2009. Wing and body molts of male Red-breasted Mergansers in the Gulf of St. Lawrence, Canada. Condor 111:71-80.

CONTRIBUTIONS OF AUTHORS

I was responsible for developing the research questions and experimental designs, undertaking data collection and analyses, and preparing all manuscripts. Rodger Titman helped develop several research questions, provided research supervision, assisted with data collection at Kouchibouguac National Park and Anticosti Island, and reviewed all manuscripts. Jean-Pierre Savard helped develop several research questions, provided research supervision, and reviewed manuscripts regarding molting birds (Chapters 4 and 5). Michael Richardson provided expertise on the ecology of merganser prey and reviewed Chapter 5.

CHAPTER 1

INTRODUCTION

LITERATURE REVIEW

THE HABITAT CONCEPT

The conspicuous nature of birds (Aves) has permitted ornithologists to gather a great deal of information on the association of birds with their habitats (Cody 1985, Jones 2001). Habitat is the collection of biological and physical characteristics that produce occupancy (Hall et al. 1997), and is therefore responsible for shaping life-history characteristics and ecological strategies that underlie fitness (Southwood 1977). Definitions of habitat, however, vary with the spatial scale of observation, which occurs along a continuum (Fig. 1). Macrohabitat constitutes broad geographic and landscape-level features, whereas microhabitat includes specific, immediate features of the local environment (Johnson 1980). Regardless of scale, habitat use refers to the way in which an individual or species uses habitat to meet its life-history needs (e.g., survival and reproduction). The study of habitat use is important for identifying factors influencing avian distribution, abundance, and population dynamics (Hutto 1985, Johnson et al. 1992), and for providing insight into community ecology (Wiens 1983) and the process of speciation (Lack 1940).

The earliest efforts to study avian-habitat use relationships focused on a general description of habitats at collection sites (see Block and Brennan 1993). Joseph Grinnell (e.g., Grinnell 1904) was largely responsible for redirecting the study of avian habitats in a qualitative natural history era that involved hypothesis testing of evolutionary relationships, particularly those dealing with predicting the presence/absence and abundance of birds (Lack 1933, Leopold 1933). G. Evelyn Hutchinson and Robert MacArthur were prominent in establishing the contemporary era of avian habitat ecology. They showed that a species' distribution is a function of a suite of biotic and abiotic factors acting synergistically (MacArthur 1958), and that it could be interpreted quantitatively with correlative models (MacArthur and Pianka 1966). Habitat correlation, however, must not be construed as habitat selection or preference (Hall et al. 1997, Jones 2001). Habitat selection occurs when a habitat is used disproportionately to its availability, while preference implies choice of a habitat when offered on an equal basis with others (Johnson 1980, Cody 1985). Habitat selection and preference have evolved through increased survival and fitness in response to the differential use of habitats (Hildén 1965, Clark and Shutler 1999).

MECHANISMS OF HABITAT SELECTION

Habitat cues. The process of habitat selection includes an innate reaction to environmental stimuli (ultimate and proximate factors; Hildén 1965). Ultimate factors are tied directly to survival and reproduction, and include 1) food and water, 2) requirements set by structural and functional characteristics of the species, and 3) shelter from predators and adverse weather (Hildén 1965, Huey 1991, Buler et al. 2007). Proximate stimuli need not be related directly to fitness, but when present in adequate abundance, help elicit a settling response (Block and Brennan 1993). Proximate factors may include landscape and physiognomic characteristics (Deppe and Rotenberry 2008) or the availability of features necessary to fulfill life-history requirements (e.g., nests and feeding sites; Orians and Wittenberger 1991). The settling response also may be stimulated by the presence of conspecifics (Nocera et al. 2009) or by the presence/absence of other species, including predators (Erwin 1979, Cresswell 2008).

Imprinting and learning. Habitat preferences may be imprinted or learned (Hildén 1965). Stimuli experienced in natal habitat are often included in habitats selected later on (e.g., following dispersal; Slagsvold and Wiebe 2007), because lower fitness may be associated with unfamiliar conditions (Davis and Stamps 2004). For example, some individuals seek interspecific associations that were imprinted at natal sites (e.g., nesting with larids; Koskimies 1957). Fidelity to habitats or areas where fitness was previously high suggests that experience influences the selection process (Clark and Shutler 1999). Conversely, dispersal may reflect an attraction to more suitable areas, particularly if fitness at the previous site was low (Sonerud 1985).

Spatial and temporal scales. The environmental cues at a single spatial scale are unlikely to ensure all the requisites for survival and reproduction (Hutto 1985). Accordingly, a hierarchical series of decisions is made (Orians and Wittenberger 1991, Graf et al. 1995). An individual first chooses a geographic range [Johnson's (1980) first-order selection, but see Hutto 1985] and then makes decisions regarding the selection of a home range (second order), the selection of sites within the home range (third order), and finally the selection of resources at the site (e.g., food items; fourth order). The factors influencing selection, however, may vary between scales (Mueller et al. 2009). For example, macrohabitat characteristics provide information on food resource levels, whereas certain microhabitat features are selected because they provide cover from predators (Orians and Wittenberger 1991). Ornithologists have become increasingly aware of the importance of considering relevant spatial scales while studying habitat selection (Thompson and McGarigal 2002, Deppe and Rotenberry 2008).

For birds that undergo migratory movements, spatial and temporal variation in environmental conditions, as well as temporal shifts in physiological and ecological requirements, influence patterns of habitat use (Dingle and Drake 2007). Breeding birds, for example, are constrained by nesting requirements (Orians and Wittenberger 1991), whereas habitat use throughout the nonbreeding period is influenced primarily by the abundance and distribution of food resources (Hutto 1985, Buler et al. 2007).

Inter- and intraspecific competition. The balance between inter- and intraspecific competition plays an important role in shaping patterns of habitat selection (Svärdson 1949). Since ecologically similar species may preclude potential competitors from using resources (Maurer 1984), differential habitat selection allows closely related species to minimize competition for resources (Root 1967, Rosenzweig 1981). Intraspecific interactions, however, cause individuals to generalize their habitat requirements and expand what they use because habitat conditions are affected by population density (Fretwell and Lucas 1970). Habitats of greater suitability (e.g., relatively high λ) are used first, whereas less optimal areas are only colonized with greater population size (Pulliam and Danielson 1991).

APPLICATION OF THE HABITAT CONCEPT

Avian habitat selection theory is tested empirically by comparing 1) used and unused habitats or 2) used and available habitats (Litvaitis et al. 1994, Jones 2001). Comparing microhabitat features at used sites with those at random, unused locations is particularly relevant for examining patterns of nest-site selection (e.g., Lusk et al. 2006), and the application of multivariate statistics can help interpret those features related to a nest (James and McCullough 1990). Comparing the composition of used habitats with that of available habitats (Johnson 1980) is useful for identifying whether particular habitat types are selected or avoided (e.g., Granfors and Flake 1999). Radio telemetry allows researchers to examine variation in use and availability of habitats between birds, and thus provides information on individual selection strategies (Thomas and Taylor 2006). Remote sensing and geographical information systems (GIS) are powerful tools in avian use-versus-availability studies (Samuel and Fuller 1994); habitat types are delineated from high resolution imagery (e.g., aerial photographs), and use and availabilities are calculated from habitat maps using GIS software (Breininger et al. 1995).

For waterbirds and other observable species, time-activity budgets help assess habitat requirements because choice of habitat influences the amount of time spent in various activities (Paulus 1988). Accordingly, understanding factors influencing time-activity budgets can provide information on the habitat features associated with particular activities, such as feeding and resting. Habitat distribution of foraging individuals also can be interpreted by understanding the habitat requirements and other ecological strategies of their important food items

(Springer et al. 1996). Thus, complementing traditional habitat use-versus-nonuse or habitat use-versus-availability studies with time-activity budgets and diet information is particularly useful for understanding patterns of habitat use by some species.

HABITAT REQUIREMENTS OF BREEDING DUCKS (ANATINAE)

Population dynamics are a function of vital rates associated with the various breeding and nonbreeding stages of the annual cycle (Johnson et al. 1992, Nichols and Hines 2002). Variation in breeding season parameters, especially nest success and duckling survival, is important to waterfowl population growth (Hoekman et al. 2002), but sensitive to conditions at breeding sites, including habitat use and availability (Arnold et al. 2007). Thus, information on patterns of nest-site- and brood habitat selection reflects strategies to help ensure nest and brood success, and is useful for identifying factors that may affect juvenile recruitment (Afton and Paulus 1992) and population change (Johnson et al. 1992).

Nest-site selection. Predation is an important component of waterfowl population biology, since it is often responsible for most of the nest losses (>75%; Greenwood et al. 1995, Flint and Grand 1996). Accordingly, Anatinae have adopted patterns of nest-site selection that minimize predation pressure (Clark and Shutler 1999). Success of nests on the mainland is generally lower than that on islands without mammalian predators (Giroux 1981b) and isolated from gulls (*Larus* spp.), which may prey on eggs of Anatinae (Götmark 1989). Colonial nesting and associated breeding synchrony lower predation risk to each nest and minimize the period when eggs are available to predators (Wittenberger and Hunt

1985). Some colonial ducks breed among colonies of larger waterfowl (geese; Robertson 1995) or with larids (Kellett and Alisauskas 1997), since these birds defend nesting areas from potential egg predators (Young and Titman 1986). Microhabitat features, especially tall and dense vegetation, may also impede predator detection and accessibility to nests (Sugden and Beyersbergen 1987). Nest success in dense cover is often greater than that in lighter cover (Klett et al. 1988, Durham and Afton 2003, but see Brua 1999), regardless of the composition of plant species (Baldassarre and Bolen 2006). Nest success may increase with greater distance from water and other edges (Traylor et al. 2004) because some predators search the edges (Larivière 2003).

Nest-site choices have implications for reducing nest abandonment, which may be high in dense breeding situations (>10% of nests; Duebbert et al. 1983) or where nest parasitism is common (Andersson and Eriksson 1982). Dense vegetation and greater distance from edges screen nests and attending females from conspecifics and parasitic females (Giroux 1981a, Lokemoen et al. 1984). Also, nests placed near water may be at risk of flooding, particularly where they are poorly elevated (Johnson et al. 1992).

Patterns of nest-site selection reflect long-term optima (Southwood 1977). However, these patterns may not always indicate optimal choice(s) if individuals are kept from using the most suitable habitats (Pulliam and Danielson 1991). Processes underlying patterns of use are generally more subtle than the latter (Clark and Shutler 1999), but some processes can be identified by interpreting differences in habitat between successful and failed nests (e.g., level of concealment; Traylor et al. 2004). Accordingly, Clark and Shutler (1999) encouraged waterfowl biologists to examine processes of nest-site selection by comparing relevant features at successful nests with those at unsuccessful nests.

Brood habitat selection. Following hatching, females must guide ducklings to suitable habitats throughout the brood-rearing period. Young Anatinae grow at an exponential rate (Lightbody 1985), and require substantial protein input from their diet (~20%; Scott et al. 1959) accomplished by feeding over extended periods (>50% of diurnal period; Sedinger 1992). Brood-rearing females must also spend a considerable amount of time foraging, partially because of the energetic and nutrient demands associated with nesting (Alisauskas and Ankney 1992), and they must devote attention to brooding ducklings and protecting them from predators (Afton and Paulus 1992). Suitable brood-rearing habitats should therefore include an abundance of available food sources (Talent et al. 1982) and safe loafing sites (Mauser et al. 1994). Factors associated with increased food availability, such as water permanence (Mauser et al. 1994), wetland size (Pöysä and Virtanen 1994), vegetation dispersion (Murkin et al. 1982), and water chemistry (Haszard and Clark 2007) help elicit a settling response by broods (Sedinger 1992). Also, emergent vegetation and open water provide routes of escape from predation (Beard 1964), an important component of duckling mortality (Johnson et al. 1992).

Brood movements from nests to initial rearing sites (primary movements) and subsequent movements to alternate areas (secondary movements) indicate that broods often select among available habitats (e.g., those that are accessible; Granfors and Flake 1999). Extensive primary movements may reflect unsuitable brood-rearing conditions adjacent to nest sites (Sayler and Willms 1997). For example, island-nesting Anatinae may lead their broods to continental rearing sites (Donehower and Bird 2008), particularly if predatory gulls are associated with the islands (Braun et al. 1980). Likewise, secondary movements may be associated with duckling predation (Chouinard and Arnold 2007), or they can be related to food densities (Talent et al. 1982) or dispersion of emergent vegetation (Keith 1961), although large brood home ranges may result in higher duckling mortality (Hill et al. 1987). Movements and patterns of habitat use may vary with brood age, which can result from varying nutritional and behavioral requirements of ducklings (Beard 1964, Gammonley 1990).

HABITAT REQUIREMENTS OF MOLTING DUCKS

Flightless males. Prior to the brood-rearing period, male Anatinae generally leave their mates and gather together for the wing molt (Hohman et al. 1992). If requirements for a successful wing molt are not met near breeding sites (e.g., competition with broods for resources), males undergo a 'molt migration' to more suitable areas, which often results in concentrations of thousands (Salomonsen 1968). Wing molt involves a synchronous replacement of flight feathers and an associated 20-35-day period of flightlessness (Hohman et al. 1992). While flightless, male Anatinae also molt body feathers (Wishart 1985, Howell et al. 2003). Since feather replacement involves increased protein synthesis and associated metabolic changes (King 1980, Murphy and King 1992), the energetic and nutrient demands associated with molt are relatively high during the flightless period (Thompson and Drobney 1995). In addition, the sulfur-rich amino acids typical of feather protein may be scarce in the environment (Hanson 1962), and waterfowl may be inefficient at converting dietary protein into feathers (Hohman et al. 1992). This suggests that some flightless Anatinae are nutritionally stressed and forced to catabolize body tissue (Hanson 1962, but see Ankney 1979).

Energetic and nutrient demands for feather replacement are met through diet obtained at molting habitats (Fox et al. 2008) or from mobilization of endogenous reserves, which may allow birds to reduce feeding intensity while flightless (Moorman et al. 1993). Also, energy reserves necessary for fall migration may need to be obtained during wing molt (Thompson and Drobney 1996). Flightless waterfowl, however, are constrained to a local food supply and are potentially vulnerable to predators, so they must select habitats that minimize risks to their survival (Fox and Kahlert 2000) and provide adequate food resources to meet energetic and nutrient demands (Einarsson and Gardarsson 2004). Shallow wetlands are important for foraging, but they are often at a high risk to predation (Moorman et al. 1993). Individuals benefit by using cover or offshore areas with open water between feeding periods (Panek and Majewski 1990, Fox and Mitchell 1997). Accordingly, differences in patterns of habitat use between foraging and nonforaging birds may reflect strategies to maximize the efficiency of energy and nutrient intake and minimize exposure to predation (Reed and Flint 2007).

PROBLEM STATEMENT

STATUS OF NEARCTIC SEA DUCKS (MERGINI)

Population declines are known for at least 10 of the 15 species of nearctic sea ducks (Sea Duck Joint Venture 2007). Eastern populations of Harlequin Duck

(*Histrionicus histrionicus*) and Barrow's Goldeneye (*Bucephala islandica*) are of special concern in Canada, and Spectacled (*Somateria fischeri*) and Steller's (*Polysticta stelleri*) eiders are threatened in the United States (Sea Duck Joint Venture Management Board 2008). Nevertheless, sea ducks remain the least understood group of waterfowl in North America, and factors affecting population dynamics are largely unknown for most species. There is an urgent need to understand vital rates and their correlates throughout the annual cycle, including habitat use and selection during breeding and molting (Sea Duck Joint Venture Management Board 2008).

RED-BREASTED MERGANSER (*MERGUS SERRATOR*)

Distribution and status. The Red-breasted Merganser is a medium-sized piscivorous sea duck with a holarctic distribution (Titman 2005), associated with brackish and salt waters and large freshwater wetlands (Titman 1999). In North America, the Red-breasted Merganser breeds from the Aleutian Islands eastward to Newfoundland and from the Arctic coast of the Yukon south to the Great Lakes (Titman 1999). Patterns of habitat use during breeding and the postreproductive wing molt are not well understood, partially because of the species' apparently stable continental population size (Sea Duck Joint Venture 2007), low importance as a game bird (Richkus et al. 2008), and remote distribution (Titman 2005). However, lack of differentiation between Red-breasted and Common (*Mergus merganser*) mergansers and goldeneyes (*Bucephala* spp.) during population surveys prohibits reliable range-wide evaluations (Robert and Savard 2006), and there is recent indication that some breeding populations of Red-breasted

Merganser may be declining, including those in eastern Canada (Canadian Wildlife Service Waterfowl Committee 2005, Craik 2007).

Mergansers in the Gulf of St. Lawrence. The Gulf of St. Lawrence approaches the southeastern breeding limit for the Red-breasted Merganser in North America, yet it provides several important coastal breeding areas (Titman 1999). Over 5000 Red-breasted Mergansers breed in the gulf region of the Canadian Maritime Provinces (Titman 1999), and breeding evidence is most common along the eastern shorelines of New Brunswick, northwestern coast of Prince Edward Island, and along Cape Breton Island in Nova Scotia (Erskine 1992). Erskine (1992) indicated that many of these birds likely nest colonially in association with larids on barrier islands (Young and Titman 1986). Patterns of nest-site selection and the influence of habitat choice on nest survival, however, are unknown for Red-breasted Mergansers breeding on barrier islands. Likewise, habitat selection by merganser broods originating from barrier islands is poorly understood, although Titman (1999) speculated that broods use tidal lagoon habitats near nest sites, and forage in shallow waters with submergent vegetation accommodating small fish.

Adult and subadult (second-year) male Red-breasted Mergansers undergo a molt migration from at least some breeding sites in the Canadian Maritime Provinces (R. D. Titman, unpubl. data), but where specific birds travel for the wing molt is not understood, and until recently, it was unknown whether male mergansers undergo the period of flightlessness in the Gulf of St. Lawrence. Summer sea duck surveys conducted by the Canadian Wildlife Service in the upper Gulf of St. Lawrence in 2003 and 2004 confirmed large concentrations

(100-1000 birds flock^{-1}) of flightless male Red-breasted Mergansers in several coastal bays of Anticosti Island, Québec (Buidin et al. 2009, J.-P. L. Savard, unpubl. data). The precise molting schedule of flightless male Red-breasted Mergansers, however, is unknown, and this precludes the examination of habitat use during wing molt because the requirements of flightless Anatinae may vary from those of pre- and postflightless individuals (Adams et al. 2000). Thus, the duration and chronology of wing molt must be delineated before habitat use can be quantified.

TARGET POPULATIONS

BREEDING

From 2002 to 2006, I studied nest-site- and brood habitat selection by a population of Red-breasted Mergansers that breed colonially on coastal barrier islands at Kouchibouguac National Park, New Brunswick (Tern Islands; 46°46' N, 64°52' W; Fig. 2). Tern Islands is a 2.8-ha complex of three nearshore islands (<1 km from continent) at the mouth of Kouchibouguacis River, and in Saint-Louis Lagoon. The islands consist of sand stabilized primarily by marram grass (*Ammophila breviligulata*) and sea lyme grass (*Leymus mollis*). I chose the site because it represents one of the few areas in the Gulf of St. Lawrence where Red-breasted Merganser nesting has been confirmed (Erskine 1992). From 1992 to 2001, between 25 and 98 merganser nesting attempts were observed annually on Tern Islands (Bouchard 2001). Red-breasted Mergansers nest on the islands in association with a large colony of Common Terns (*Sterna hirundo*; 3500-7300 nests year^{-1}; 1981-2004; É. Tremblay, pers. comm.). Potential egg and duckling predators at the study area include Herring (*Larus argentatus*) and Great Black-backed (*L. marinus*) gulls, American Crow (*Corvus brachyrhynchos*), Common Raven (*C. corax*), Northern Harrier (*Circus cyaneus*), and red fox (*Vulpes vulpes*; Young and Titman 1986, Janishevski 2000). Topography of Tern Islands is low-lying (<2 m above sea level), so tern and merganser nests are at risk of flooding during spring storm surges (Hanson et al. 2006).

MOLTING

In 2005 and 2006, I examined molt chronology and habitat use by flocks of subadult and adult male Red-breasted Mergansers undergoing wing molt in eight coastal bays along the western shorelines of Anticosti Island (Fig. 2): Anse aux Fraises (49°49' N, 64°28' W), Baie Ste-Claire (49°54' N, 64°30' W), Chute à Boulay (49°55' N, 64°26' W), Baie du Grand Makasti (49°56' N, 64°16' W), Baie McDonald (49°45' N, 63°03' W), Baie Caplan (49°44' N, 63°00' W), Anse Gibbons (49°22' N, 63°29' W), and Rivière Ste-Marie (49°40' N, 63°56' W). I chose these bays because their use by flightless male Red-breasted Mergansers was confirmed in both 2003 and 2004 (J.-P. L. Savard, unpubl. data). Female Red-breasted Mergansers, however, do not concentrate at these sites during the male wing molt period. The coasts of Anticosti Island support concentrations (>100 birds flock^{-1}) of molting male Common Eiders (*Somateria mollissima*), and Black (*Melanitta nigra*), Surf (*M. perspicillata*), and White-winged (*M. fusca*) scoters (Buidin et al. 2009). Bald Eagles (*Haliaeetus leucocephalus*) are potential predators on flightless sea ducks at Anticosti Island (Guillemette and Guillemette 1983).

OBJECTIVES AND HYPOTHESES

My overall aim was to determine patterns of habitat use among 1) nesting, 2) brood-rearing, and 3) molting male Red-breasted Mergansers in the Gulf of St. Lawrence. I questioned whether these birds demonstrate habitat selection. To accomplish this, I considered objectives and hypotheses specific to each of the three stages:

Nest-site selection (Chapter 2). My main objectives were: 1) to determine use of nesting cover types (macrohabitat) relative to availability on Tern Islands, 2) to compare microhabitat between a) nests and random sites and b) successful and unsuccessful nests, and 3) to investigate the influence of habitat, intraspecific nest parasitism, and temporal trends (nest age, initiation date) on nest survival. I predicted that Red-breasted Mergansers would select macro- and microhabitat features that reduce nest detection and accessibility by predators, parasitic females, and other conspecifics. Specifically, I hypothesized that concealment and vegetation density at nest sites would be greater than that at random locations.

Brood habitat selection (Chapter 3). Following egg hatching and nest exodus by merganser broods from Tern Islands, I examined patterns of habitat use by broods throughout the rearing period. My main objectives were: 1) to measure distances traveled by radio-marked broods from Tern Islands to initial brood-rearing habitat (primary movements) and to subsequent rearing locations (secondary movements), 2) to examine patterns of habitat use relative to availability at two spatial scales: a) home range (second order) and b) sites within the home range (third order), and 3) to examine brood-age related changes in daily movements and habitat use. I predicted that broods would select specific habitat types among those available within the study site and in their home ranges. I suspected that selected habitats would consist of high densities of food resources (e.g., small fish), relatively low duckling predation pressure, and safe loafing sites for broods.

Molt chronology (Chapter 4). During the brood-rearing period, male Red-breasted Mergansers undergo wing molt at sites away from Kouchibouguac National Park. Prior to examining habitat use by flightless male mergansers at Anticosti Island, I delineated the duration and chronology of wing molt at this site.

Habitat use by flightless males (Chapter 5). I used a combination of microhabitat measurements, time-activity budgets, and diet information to help understand patterns of habitat use by flocks of flightless male Red-breasted Mergansers at Anticosti Island. My main objectives were: 1) to measure microhabitat at sites used by flocks of males, 2) to compare microhabitat between foraging and nonforaging flock locations, 3) to examine the effects of tide, weather, diurnal period, and period of the flightless season on foraging intensity, and 4) to examine prey items from esophagi of collected males. I predicted that foraging flocks would use shallow, nearshore sites with abundant food, whereas nonforaging flocks (e.g., loafing, undergoing comfort movements) would frequent offshore areas with little exposure to avian predators.

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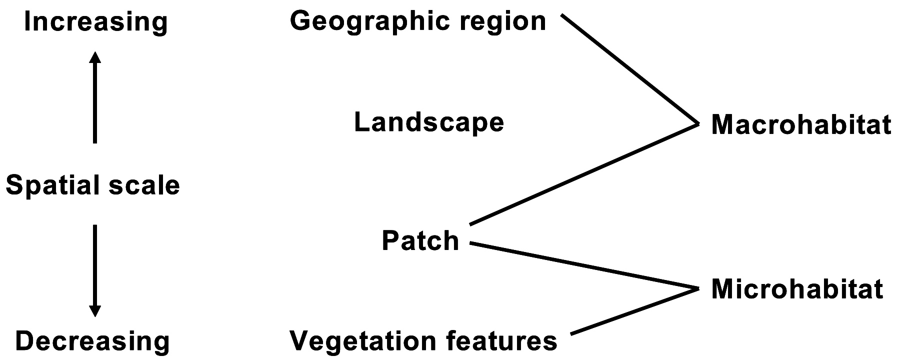

FIGURE 1. Spatial scales for the study of avian habitat use. Modified from Block and Brennan (1993).

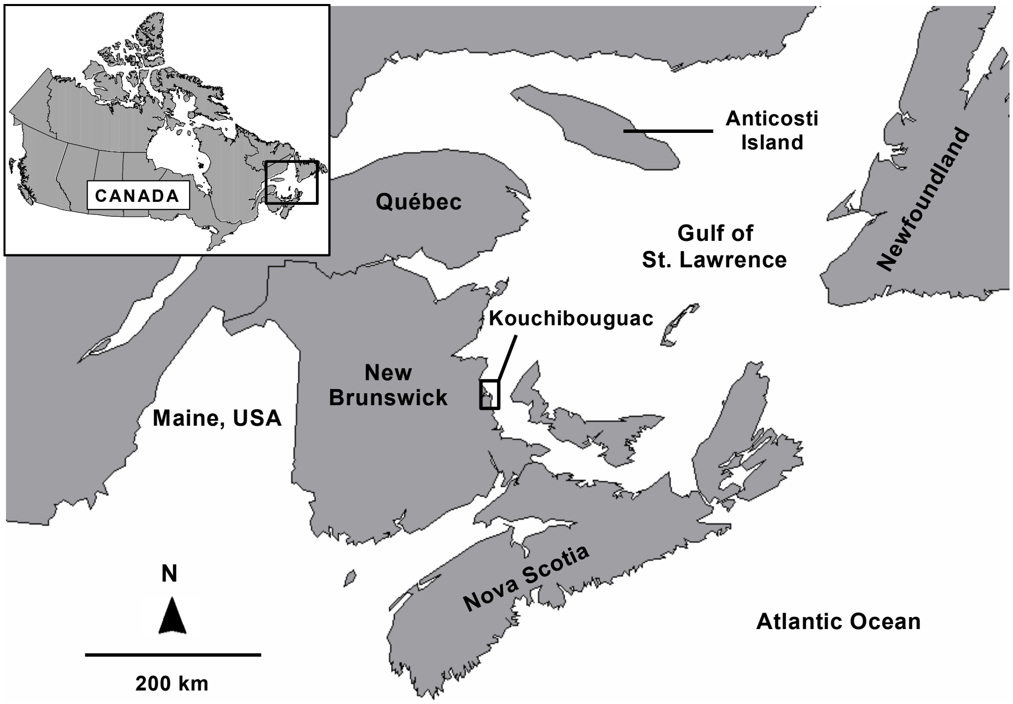

FIGURE 2. Red-breasted Merganser (*Mergus serrator*) study sites at Kouchibouguac National Park, New Brunswick (breeding), and Anticosti Island, Québec (molting). The Gulf of St. Lawrence is highlighted in the inset figure.

CONNECTING STATEMENT 1

This is the first of two chapters that examine habitat selection by breeding Red-breasted Mergansers at Kouchibouguac National Park, New Brunswick. I use macro- and microhabitat information to identify factors that potentially influence nest-site use among Red-breasted Mergansers that breed colonially with Common Terns on Tern Islands. Using a habitat use-versus-nonuse approach, I test the prediction that Red-breasted Mergansers select habitat features that reduce nest detection and accessibility by predators and conspecifics. I also attempt to identify factors affecting nest survival.

CHAPTER 2

NEST-SITE SELECTION AND NEST SUCCESS OF RED-BREASTED MERGANSERS IN A COMMON TERN COLONY IN EASTERN NEW BRUNSWICK

Abstract. Nest-site selection and nest success for Red-breasted Mergansers (*Mergus serrator*) breeding on a barrier island complex (Tern Islands) with >10,000 Common Terns (*Sterna hirundo*) in eastern New Brunswick, Canada, were studied in 2005 and 2006. Concealment was the most important feature for nest placement as 153 of 156 nests were in dense stands of marram grass (*Ammophila breviligulata*), and overhead concealment, vegetation density, and vegetation height were all greater at nests than at random locations. Apparent success for all nests was 57% and was similar between years. Few nests were depredated (*n* = 3), but abandonment was responsible for 95% of nest losses and was most common early in the season. Nest success was <45% for nests initiated before 25 May but >75% for nests initiated after 10 June. Nest abandonment was influenced by intraspecific nest parasitism and investigator activity. Red-breasted Mergansers selected nest sites adaptively on Tern Islands because 1) nests were more concealed than random sites, 2) avian predation at nests in the Common Tern colony was lower than that at nests on nearby islands without terns, 3) nests were not exposed to mammalian predators, and 4) nest success and nest densities were high.

INTRODUCTION

Nest success is influenced by nest-site choices (Johnson et al. 1992, Clark and Shutler 1999). Concealment and greater distance from edge reduce nest detection and accessibility by avian and terrestrial egg predators (Martin 1993, Larivière 2003), parasitic females (Giroux 1981a), and conspecifics (Lokemoen et al. 1984). Poorly elevated nests near water are at risk of flooding (Walker et al. 2005, Hanson et al. 2006). Nest success on islands far from shore (>1 km) is often higher than on the mainland and on islands near shore with mammalian predators (Giroux 1981b, Duebbert et al. 1983). Nests are also protected when associated with larids that mob avian predators, although some gulls (*Larus* spp.) prey upon waterfowl eggs and terns (*Sterna* spp.) may mob nesting females (Dwernychuk and Boag 1972, Young and Titman 1986, Kellett and Alisauskas 1997). Nest abandonment at sites frequently visited by humans may be higher than at undisturbed sites (Newton and Campbell 1975).

Population declines are known for at least 10 of the 15 nearctic sea ducks (Mergini; Sea Duck Joint Venture Management Board 2008), and lower nest success is contributing to at least some declines (e.g., Ely et al. 1994, Traylor et 2004). Most merganser (*Mergus* spp.) populations appear to be stable, but lack of differentiation among species during suveys prohibits reliable range-wide evaluations (Sea Duck Joint Venture 2007). Nesting ecology of the Red-breasted Merganser (*Mergus serrator*) remains one of the least understood among nearctic waterfowl, partly because of the species' remote breeding range and its low importance as a game bird (Titman 1999). Attention needs to be given to nest-site selection and factors influencing nest success, particularly for coastal breeding populations (Sea Duck Joint Venture Management Board 2008). Breeding sites have been described in general fashion at several palearctic freshwater (Russia: Dement'ev and Gladkov 1967, Iceland: Bengtson 1970, Á. Einarsson, pers. comm.) and coastal (Finland: Bergman 1939, Hildén 1964) locations where nests occur on islands occasionally with larids, and are concealed either under shrubs and boulders or in grasses and crevices.

In eastern New Brunswick, Canada, Red-breasted Mergansers breed on barrier islands with larids (Erskine 1992), including Tern Islands at Kouchibouguac National Park (Young and Titman 1988). Our objectives were: 1) to determine the type(s) of preferred nesting cover (macrohabitat) for Red-breasted Mergansers on Tern Islands, 2) to compare microhabitat between: a) nests and random sites, b) successful and unsuccessful nests, and c) parasitized and normal nests, 3) to estimate nest initiation dates and clutch sizes, and 4) to investigate the influence of habitat, intraspecific nest parasitism, temporal trends (nest age, initiation date), and investigator activity on nest survival. We predicted that Red-breasted Mergansers would select macro- and microhabitat features that reduce nest detection and accessibility by predators, parasitic females, and other conspecifics.

METHODS

STUDY SITE

We studied the nesting ecology of Red-breasted Mergansers from late May to early August in 2005 and 2006. Tern Islands is a 2.8-ha complex of three barrier islands in Saint-Louis Lagoon (46°46' N, 64°52' W; Fig. 1). Topography is low-lying (<2 m above sea level; Hanson et al. 2006) and sand is stabilized primarily by marram grass (*Ammophila breviligulata*), sea lyme grass (*Leymus mollis*), common yarrow (*Achillea millefolium*), and pigweed (*Chenopodium album*). Red-breasted Merganser nests were associated with nests of Common Terns (*Sterna hirundo*), which numbered 5045 and 6734 (1800-2500 nests ha^{-1}) in 2005 and 2006, respectively (É. Tremblay, pers. comm.). One or two gull nests were on Tern Islands each year. Avian egg predator species included Herring (*Larus argentatus*) and Great Black-backed (*L. marinus*) gulls, American Crow (*Corvus brachyrhynchos*), Common Raven (*C. corax*), and Northern Harrier (*Circus cyaneus*). Mammalian predators were absent from Tern Islands.

DATA COLLECTION

We found Red-breasted Merganser nests by systematically walking Tern Islands between 07:00 and 17:00 AST once a week from late May to early July. Most, if not all nests (bowl with ≥1 egg) were found. We marked each nest with an unpainted lathe placed 1 m north of the bowl and recorded nest coordinates with a global positioning system (GPS model eTrex, Garmin Ltd., Olathe, KS). We estimated nest initiation dates by backdating, assuming one egg was laid every 1.5 days, and determined stage of embryonic development by floating 2-3 incubated eggs, assuming a 30-day incubation period (Westerskov 1950, Titman 1999). We revisited nests every 5-15 days but made more frequent visits near hatching dates. The fate of a nest was considered 1) successful, if at least one egg hatched, 2) abandoned, if eggs were not added, an incubated clutch was cold, or if embryonic development was unchanged through two subsequent visits, or 3) depredated, if all eggs were removed or egg fragments remained (Young and Titman 1986). We classified a nest as parasitized if it had ≥13 Red-breasted Merganser eggs (dump nest; Janishevski 2000). Normal nests had <13 eggs.

Macrohabitat selection. We classified each nest into one of four macrohabitat types: 1) marram grass, 2) sea lyme grass, 3) common yarrow, and 4) miscellaneous. Miscellaneous was primarily pigweed but included sparse (<10 stems in 1 m^2) tumble mustard (*Sisymbrium altissimum*), evening primrose (*Oenothera* spp.), seaside goldenrod (*Solidago sempervirens*), common sow-thistle (*Sonchus oleraceus*), Norway cinquefoil (*Potentilla norvegica*), common yarrow, and marram grass. We delineated macrohabitats on Tern Islands by recording coordinates of stand perimeters with a GPS. We then calculated the total area (ha) of each macrohabitat with ArcView GIS 3.1 (Environmental Systems Research Institute Inc., Redland, CA).

Microhabitat selection. Seven nest-site features were examined. We measured maximum live and dead vegetation height (±1 cm) and vegetation density (number of stems) within a 40 cm^2 quadrat centered on the nest (Traylor et al. 2004). A black disc with five 6.5 cm^2 white squares was inserted into the nest bowl and overhead concealment was estimated as the average percentage of each square that was hidden by vegetation from 1 m above (Clark and Shutler 1999). We measured distance to water (±1 cm), where the edge was indicated by accumulation of dead eel grass (*Zostera marina*). We calculated nearby nest density as the number of active Red-breasted Merganser nests within a 5-m radius. Elevation (±1 cm above sea level) was obtained from light detection and ranging (LiDAR) data (Hanson et al. 2006). We calculated nearby nest density at the end of the nesting season, but all other microhabitat features were measured once nest fate was determined. Following measurements at a nest site, microhabitat at a single random site was examined. The direction and distance from the nest to a random site were obtained with a random function in a spreadsheet; random numbers were assigned to the eight cardinal directions and a random number between 1 and 68 designated distance (m). We chose ≤68 m because it was the greatest distance between a nest and water (R. D. Titman, unpubl. data 2002-2004). S. R. Craik (SRC) measured microhabitat from 3 June to 2 July and R. D. Titman (RDT) from 17 July to 2 August.

STATISTICAL ANALYSES

Nest-site selection. We compared proportional use and availability of the four macrohabitats with a Chi-square goodness-of-fit test (White and Garrott 1990). If nonrandom selection occurred, Bonferroni confidence intervals determined preference(s) (Byers and Steinhorst 1984).

Microhabitat variables were assessed for normality with Shapiro-Wilks tests. We arcsine square-root transformed overhead concealment, square-root transformed distance to water, and log transformed elevation and nearby nest density. Several variables were still not normally distributed following transformation, but these departures did not substantially violate assumptions for parametric tests because with the exception of nearby nest density, Shapiro-Wilks statistics were ≥0.98 (nearby nest density = 0.75; Clark and Shutler 1999). There was no improvement in normality after transformation of live and dead vegetation height, so analyses proceeded with untransformed data (Shapiro-Wilks test statistics ≥0.96).

We tested microhabitat variables for multicollinearity with principal component analysis (PCA). The data were orthogonal because the first component explained less variation (33%) than could occur by chance (37%; Frontier 1976). Discriminant function analyses (DFA) identified microhabitat features that best discriminated nests and random sites, successful and unsuccessful nests, and incubated dump and normal nests (Hair et al. 1995). To control for season effects, we saved residuals from linear regressions with microhabitat features as dependent variables and Julian date as the independent variable. We calculated standard normal deviates of residuals to combine data from both years and to control for year effects. We used group-specific covariance matrices to improve classification probabilities, which were set proportional to group sample sizes (Hair et al. 1995). Discriminant loadings of ≥|35| were important (Hair et al. 1995), and probability values for discriminations were calculated with chance-corrections (Titus et al. 1984). After controlling for season effects, vegetation heights obtained by RDT were generally greater than those obtained by SRC because RDT measured the tallest blade from its point of emergence to the tip, whereas SRC considered height of the tallest blade left to hang naturally. We therefore analyzed RDT and SRC datasets separately, but considered only dump/normal nest data from RDT because SRC measured few incubated dump nests ($n = 7$).

Nest success. We calculated apparent nest success as the number of successful nests divided by the total number of nests. Apparent nest success is a reliable estimator when most nests are found (Johnson and Shaffer 1990).

Hatching success for each successful nest was the number of hatched eggs divided by the total number of eggs. We examined factors that may influence daily survival rate (DSR) of nests with program MARK (White and Burnham 1999). We excluded 21 nests (*n* = 10 in 2005, *n* = 11 in 2006) that were found abandoned or were abandoned between the first and second visits because they were missing encounter histories. We also excluded three nests with unknown fates. Dates of nest initiation were standardized ($\bar{x}$ = 0, SD = 1) to avoid convergence problems, and the logit-link function forced estimates of DSR to the interval (0, 1).

We used an information-theoretic approach, based on Akaike's Information Criterion (AIC_c), to select among competing nest survival models (Akaike 1973, Burnham and Anderson 1998). We developed nine candidate models with a three-step process (Traylor et al. 2004). First, we compared six simple models with temporal trends: 1) constant DSR across the nesting season (26 May-12 August; {S.}), 2) constant DSR across the nesting season in each year (year effects; $\{S_{year}\}$), and 3) linear and quadratic trends of date of nest initiation $\{S_{init}\}$, $\{S_{init+init2}\}$ and nest age $\{S_{age}\}$, $\{S_{age+age2}\}$ across the nesting season (Dinsmore et al. 2002). Second, we considered additive and interactive effects of dump nesting to the most parsimonious model after the first step $\{S_{init+dump}\}$, $\{S_{init+dump+init*dump}\}$. Finally, we added effects of investigator activity to the most parsimonious model after the second step $\{S_{init+investigator}\}$. Dummy variables coded for whether a nest was visited on each day of the nesting season (0 = not visited, 1 = visited; Rotella et al. 2004). We considered a nest as 'visited' on each day that we landed on the nest's island, regardless of whether the nest was actually visited because attending female Red-breasted Mergansers often react to alarm calls of Common Terns by flushing before nests are visited (Young and Titman 1986). Human presence was limited to our visits because Parks Canada prohibits public access to Tern Islands. Habitat was not included in model selection analyses because microhabitat at successful nests was similar to that at unsuccessful nests (see Results), and investigator-biased height data (SRC/RDT) would have generated unrealistic models.

We summed weights (w_i) of models with a particular parameter to assess its importance to DSR (Σw_i; Burnham and Anderson 1998). Also, we model-averaged $\hat{\beta}$ of each parameter and generated unconditional standard errors and 95% confidence intervals to accommodate model uncertainty ($\bar{\hat{\beta}}$; Burnham and Anderson 1998). We concluded lack of fit of parameters ($\hat{\beta}$ or $\bar{\hat{\beta}}$) when their 95% confidence intervals included zero. Intercept and slope estimates from the most parsimonious model on the logit scale were back-transformed to estimates of DSR on the probability scale to predict effects of important factors (Walker et al. 2005). We obtained transformed estimates using:

$$\mathrm{DSR} = 1 + \exp[-(\hat{\beta}_0 + \hat{\beta}_1 X_1 + \hat{\beta}_2 X_2, \ldots + \hat{\beta}_n X_n)]^{-1}$$

where $\hat{\beta}_i$ are the estimated regression coefficients and X_i are parameter values. We scaled parameter values to 10% increments and estimated confidence intervals with the Delta method (Seber 1982). We used DSR^{45} to estimate nest success for each 10% increment, based on an average normal clutch of 10 eggs and an incubation period of 30 days (Johnson 1979, Titman 1999). We performed analyses with SPSS 11.5 (SPSS Inc., Chicago, IL), SAS 9.1 (SAS Institute Inc., Cary, NC), and program MARK 5.1 (White and Burnham 1999). We set significance levels at $P < 0.05$ and present values as means ± 95% confidence intervals (CI).

RESULTS

GENERAL NESTING ECOLOGY

We found 73 nests in 2005 and 83 nests in 2006 (Table 1). Nest densities in each year were similar (27-29 nests ha^{-1}). Over 35% of incubated nests in each year had ≥13 eggs (Table 1). Nest initiation date averaged 4 June (95% CI: 3-6 June, range 16 May-27 June, $n = 134$) with little difference between years ($F_{1,132} = 0.6$, $P = 0.46$). The peak nest initiation period in each year was similar; 65% of nests were initiated between 24 May and 8 June (Fig. 2). Initiation dates of incubated normal nests ($\bar{x}$ = 8 June, 95% CI: 6-10 June, $n = 63$) were later than those of incubated dump nests ($\bar{x}$ = 2 June, 95% CI: 30 May-5 June, $n = 43$; $F_{1,104} = 16.6$, $P < 0.001$). Initiation dates of successful nests ($\bar{x}$ = 6 June, 95% CI: 4-8 June, $n = 87$) were later than those of unsuccessful nests ($\bar{x}$ = 31 May, 95% CI: 29 May-2 June, $n = 44$; $F_{1,129} = 13.9$, $P < 0.001$). Mean hatch date was 22 July (95% CI: 20-23 July, range 6 July-12 August, $n = 87$) with little difference between years ($F_{1,85} = 0.1$, $P = 0.73$; Table 1). Clutch size of dump nests averaged 15.2 (95% CI: 14.6-15.7, median = 15, $n = 43$) and for normal nests averaged 9.7 (95% CI: 9.2-10.2, median = 10, $n = 63$). Clutch size declined by 0.18 (95% CI: -0.25--0.12) for each day that nest initiation was delayed ($F_{1,103} = 33.8$, $r^2 = 0.25$, $P < 0.001$).

NEST-SITE SELECTION

Marram grass and miscellaneous vegetation were the most common macrohabitats on Tern Islands (Table 2). Red-breasted Mergansers preferred to nest in marram grass (n = 153 nests), avoided sea lyme grass (n = 3 nests), and did not use common yarrow and miscellaneous vegetation ($\chi^2_3 = 60.8$, $P < 0.001$; Table 2).

Nest sites were more concealed than random locations (SRC: Wilks' λ = 0.4, $\chi^2_7 = 113.0$, $P < 0.001$; RDT: Wilks' λ = 0.4, $\chi^2_7 = 161.9$, $P < 0.001$). Overhead concealment at nests was >2× greater than at random sites (Table 3). Vegetation density and height at nests were greater than at random locations, indicating that females preferred sites with lateral concealment (Table 3). Microhabitat at successful nests was similar to that at unsuccessful nests (abandoned and depredated) (SRC: Wilks' λ = 0.9, $\chi^2_7 = 3.7$, $P = 0.81$; RDT: Wilks' λ = 0.9, $\chi^2_7 = 8.1$, $P = 0.33$; Table 3). Microhabitat at incubated dump nests was similar to that at incubated normal nests (Wilks' λ = 0.9, $\chi^2_7 = 2.7$, P = 0.92), although nearby nest densities for dump nests were generally greater than those for normal nests (Table 3).

NEST SUCCESS

Apparent success for all nests was 57% (87/153), and nest success in each year was similar (Table 4). Abandonment was responsible for 95% (63/66) of nest losses, and only three nests were depredated. Nest success of incubated dump nests (72%; 31/43) was lower than that of incubated normal nests (89%; 56/63), and >40% of nests lost during the laying stage had ≥13 eggs (9/25 in 2005 and 11/25 in 2006). Success of early dump nests (initiated <1 June; 45%, 14/31) was lower than that of later dump nests (≥1 June; 62%, 16/26). A total of 613 ducklings hatched from 1788 eggs (2.9 ducklings nest^{-1}) and 143 eggs (8%) were lost; many of these eggs were likely removed by breeding females. Hatching success for successful nests was 74% (95% CI: 70-79%, *n* = 78; Table 4). Nest losses during laying (*n* = 50) were more common than during early (<15 days, *n* = 8) and late incubation (≥15 days, *n* = 8).

Daily nest survival increased linearly with later dates of nest initiation ($\bar{\hat{\beta}}_{\text{init}} = 0.58$, 95% CI: 0.20-0.97, $\Sigma w_i = 0.97$; Table 5). Nest success was <45% for nests initiated before 25 May but >75% for nests initiated after 10 June (Fig. 3). Nest survival was unaffected by dump nesting (unincubated and incubated dump nests; $\bar{\hat{\beta}}_{\text{dump}} = 0.30$, 95% CI: -0.37-0.96, $\Sigma w_i = 0.29$), and investigator activity had little impact on DSR ($\hat{\beta}_{\text{investigator}} = 0.23$, 95% CI: -3.19-3.66, $\Sigma w_i = 0.21$; Table 5). Models with dump nesting and investigator activity received some support, but these parameters did not improve the fit of the most parsimonious model ($\{S_{\text{init}}\}$; Table 5).

DISCUSSION

NEST-SITE SELECTION

Few Red-breasted Merganser nests were depredated because mammalian egg predators were absent from Tern Islands and avian egg predators encountered high nest concealment and aggressive Common Terns. Females selected sites in stands of marram grass with new growth and residual stems that formed a dome of vegetation over the nest requiring access by grass tunnels. Overhead and lateral concealment reduced detection and accessibility of nest sites by local avian predators (Clark and Nudds 1991, Young and Titman 1986), and would hinder search efficiency of terrestrial predators (e.g., red fox *Vulpes vulpes*) if and when they occurred on Tern Islands (Martin 1993, Janishevski 2000). In contrast, sea lyme grass and pigweed provided little cover and were along island peripheries at risk of flooding during high tide. Common yarrow offered little overhead concealment until after the nest initiation period.

Common Terns protected Red-breasted Merganser nests because they defended their own nests. Terns mob avian predators in great numbers, driving them away from Tern Islands (Young and Titman 1986). As a result, avian predation is lower at Red-breasted Merganser nests in the Common Tern colony on Tern Islands than at nests on nearby Kouchibouguac barrier islands without terns (Young and Titman 1986; R. D. Titman, unpubl. data). Also, Common Tern eggs may act as a buffer for Red-breasted Merganser eggs because exposed tern eggs may be favored over concealed merganser eggs when a predator's search time is limited by mobbing (Titman 1999). Nevertheless, some Red-breasted Merganser nests in each year were initiated before Common Terns nested, when avian predator access to Tern Islands is likely easy. Therefore, concealment is particularly important to survival of Red-breasted Merganser nests early in the season.

NEST ABANDONMENT

We recorded some of the highest rates of nest abandonment among nearctic ground-nesting waterfowl as >40% of Red-breasted Merganser nests in each year were deserted (Titman and Lowther 1975, Duebbert et al. 1983). The cause of abandonment was unknown for most nests, but 1) frequent intraspecific nest parasitism, 2) female harassment, and 3) investigator disturbance influenced some desertion (Young and Titman 1986). Abandonment was common when many conspecific eggs were added to an unincubated clutch over a short period (≥2 eggs day^{-1}; Andersson and Eriksson 1982) and among early initiated nests with large clutch sizes (>16 eggs; Eadie 1989). Some parasitized nests with <13 eggs were also abandoned on Tern Islands (Young and Titman 1988). In Iceland, parasitized Red-breasted Merganser nests are abandoned twice as often as normal nests (Bengtson 1972). Abandonment may be an adaptive host response when frequent parasitism is detected early during nesting and sufficient time is available to renest (Sayler 1992). The number of renests on Tern Islands was unknown. Quantifying merganser nest losses due to dump nesting, however, is not possible because many eggs may have been added to a clutch after the nest was abandoned or a host may have deserted a parasitized nest for another reason (Sayler 1992). Furthermore, the negative effects of nest parasitism may be exaggerated when parasitized nests are distinguished by large clutch size alone because parasitized Red-breasted Merganser nests with smaller clutches (<13 eggs) are often successful (Young and Titman 1988).

Nest densities and abandonment on Tern Islands are higher than on nearby islands without terns (Young and Titman 1986, R. D. Titman, unpubl. data). Female waterfowl interfere with each other and are harassed by drakes in dense breeding situations where intraspecific aggression may lead to above-average nest abandonment (>15% of nests; Newton and Campbell 1975, Titman and Lowther

1975, Duebbert et al. 1983). Restricted movements in grass tunnels and other well-defined pathways on Tern Islands may yield conflicts among breeding Red-breasted Mergansers (Young and Titman 1986). Female Red-breasted Mergansers were also harassed by mobbing Common Terns and reacted by taking refuge in vegetation or by leaving the islands. Young and Titman (1986) suggested that mobbing attacks may be responsible for some merganser nest abandonment, but this has yet to be confirmed. Concealment around nest sites, however, helps screen females from conspecifics and provides shelter from aggressive terns (Lokemoen et al. 1984).

We influenced some nest abandonment because at least four females deserted their nests after being captured in a nest trap. Also, morning nest visits early in the season likely disturbed some laying females, which are more likely to abandon their nests than those incubating (Livezey 1980, Gloutney et al. 1993). The frequency of nest abandonment on Tern Islands is reduced when nest searching is delayed until incubation (Bouchard 2001), but the extent of this reduction is still unclear. Common Terns are particularly agitated during our visits, which may provoke them to mob female Red-breasted Mergansers (Young and Titman 1986). Despite this, results suggest that DSR of merganser nests was unaffected by our visits to Tern Islands. Studies that consider whether females are flushed from their nests during investigator visits (e.g., Rotella et al. 2004, Donehower 2006) provide more direct evidence for human disturbance than our method, which only considered whether we landed on a nest's island.

CONCLUSIONS

We provide evidence for adaptive nest-site selection by a ground-nesting sea duck because 1) Red-breasted Merganser nests were more concealed than random sites, 2) avian predation at nests in the Common Tern colony was lower than that at nests on nearby islands without terns, 3) nests were on islands without mammalian predators, and 4) apparent nest success was high (Young and Titman 1986, Clark and Shutler 1999). Persistence of adaptive nest-site placement on Tern Islands was also associated with high nest densities, which are promoted by natal and breeding philopatry (Clark and Shutler 1999, see Appendix I). In contrast, recent declines for several breeding populations of nearctic sea ducks are linked to increased nest depredation (Ely et al. 1994, Traylor et al. 2004), and there are concerns that changing predator regimes are lowering nest success and nest densities at many breeding sites (Quakenbush et al. 2004, Sea Duck Joint Venture Management Board 2008).

More attention is needed to unravel the cause-and-effect relationships for abandoned Red-breasted Merganser nests on Tern Islands. Accordingly, reducing investigator disturbance will assist in an effort to better understand the natural factors that influence nest success for Red-breasted Mergansers breeding on barrier islands with large numbers of Common Terns.

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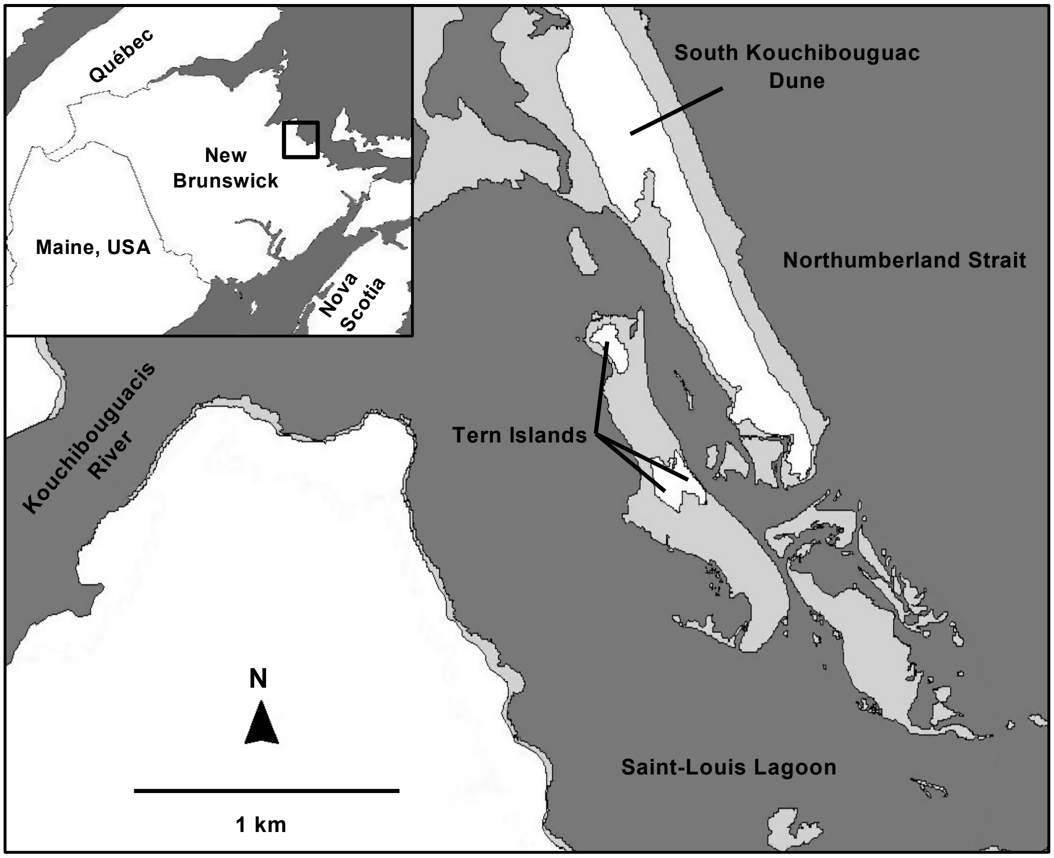

FIGURE 1. Study site on Tern Islands, Kouchibouguac National Park, New Brunswick, 2005 and 2006. Shaded areas are intertidal regions.

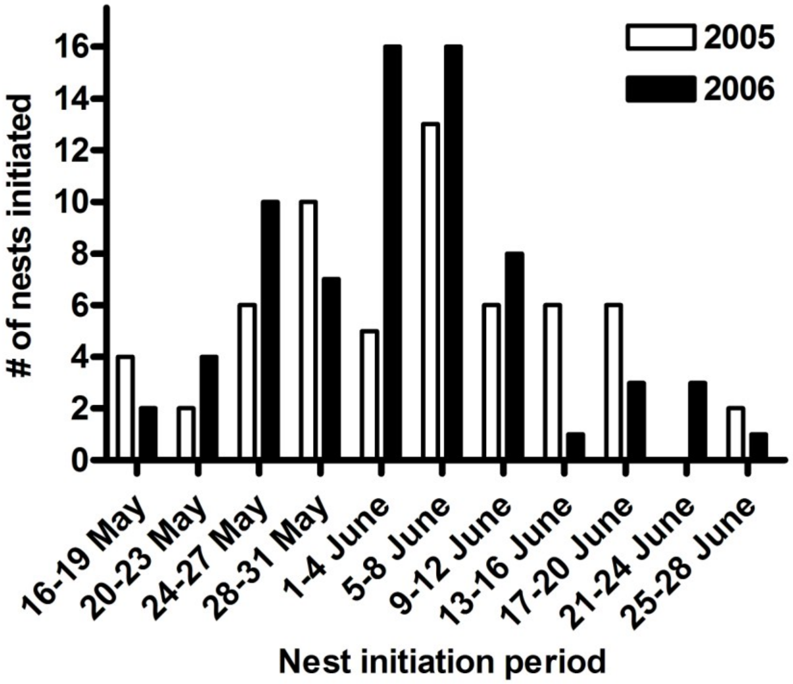

FIGURE 2. Number of Red-breasted Merganser (*Mergus serrator*) nests initiated during eleven periods through the nesting season on Tern Islands, Kouchibouguac National Park, New Brunswick, 2005 and 2006.

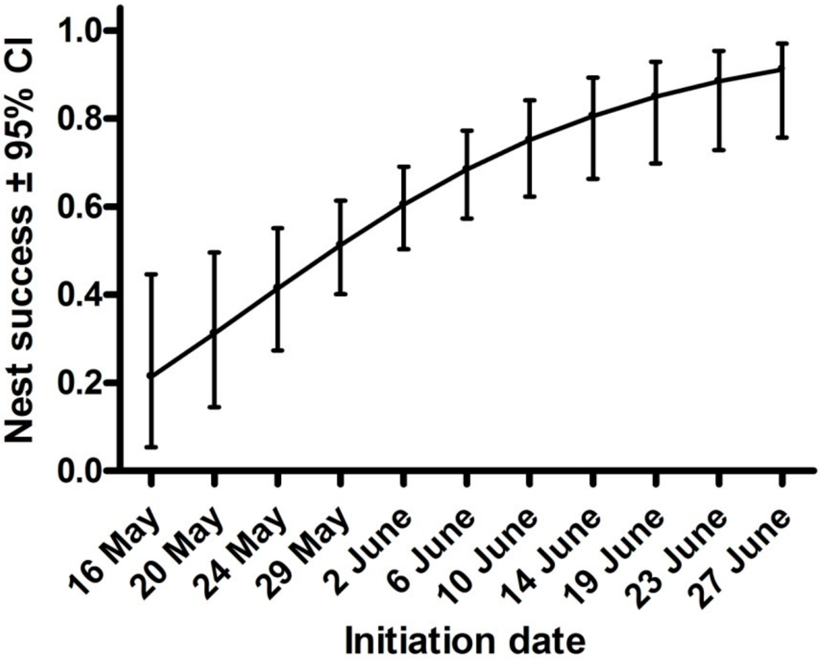

FIGURE 3. Influence of date of nest initiation on success of Red-breasted Merganser (*Mergus serrator*) nests on Tern Islands, Kouchibouguac National Park, New Brunswick, 2005 and 2006. Nest success estimates (± 95% CI) were obtained from the most parsimonious model {S_{init}} on the logit scale.

TABLE 1. Number of nests, mean nest initiation and hatch dates, and mean clutch size for Red-breasted Mergansers (*Mergus serrator*) on Tern Islands, Kouchibouguac National Park, New Brunswick, 2005 and 2006.

Parameter	2005	2006
Number of nests	73	83
Number of dump nests[a]	19/49 (39%)	24/57 (42%)
Mean nest initiation date	5 June	4 June
95% CI	2-7 June	1-6 June
range	16 May-27 June	17 May-27 June
n	62	72
Mean hatch date	21 July	22 July
95% CI	19-24 July	20-24 July
range	6 July-7 August	7 July-12 August
n	42	45
Mean clutch size[b]	11.9	11.8
95% CI	10.8-12.8	11.0-12.6
range	3-20	5-18
n	49	56

[a] ≥13 eggs; for incubated nests.

[b] For incubated nests.

TABLE 2. Macrohabitat types and availabilities, expected use, number of nests in each macrohabitat, observed use, and Bonferroni confidence intervals for Red-breasted Mergansers (*Mergus serrator*) on Tern Islands, Kouchibouguac National Park, New Brunswick, 2005 and 2006.

Macrohabitat[a]	Availability (ha)	Expected use (%)	Nests (*n*)	Observed use (%)	Bonferroni confidence intervals
Marram	1.94	70	153	98	$0.95 \leq P \leq 1.00$[b]
Sea lyme	0.18	6	3	2	$0.00 \leq P \leq 0.05$[c]
Common yarrow	0.03	1	0	0	-[d]
Miscellaneous	0.64	23	0	0	-[d]
Total	2.79	100	156	100	

[a] Marram (*Ammophila breviligulata*); sea lyme (*Leymus mollis*); common yarrow (*Achillea millefolium*); miscellaneous (see Methods for description).

[b] Preferred ($P < 0.05$).

[c] Avoided ($P < 0.05$).

[d] Not calculated given no use of macrohabitat.

TABLE 3. Microhabitat ($\bar{x}$ ± 95% CI) at nests and random sites, successful and unsuccessful (abandoned and depredated) nests, and incubated dump (≥13 eggs) and normal nests for Red-breasted Mergansers (*Mergus serrator*) on Tern Islands, Kouchibouguac National Park, New Brunswick, 2005 and 2006. Discriminant function loadings are listed for analyses of nest and random sites. Significant loadings of ≥|35| are underlined.

Site type	Elevation (m)	Overhead concealment (%)	Vegetation density (stems in 40 cm^2)	Maximum live height (cm)	Maximum dead height (cm)	Distance to water (m)	Number of nests within a 5 m radius
Nest (*n* = 69)[a]	2.25 ± 0.12	78 ± 4	81.48 ± 6.33	75.39 ± 2.83	58.32 ± 4.13	13.13 ± 1.81	0.86 ± 0.23
Random (*n* = 69)[a]	2.07 ± 0.10	27 ± 7	49.00 ± 6.48	61.29 ± 5.01	33.13 ± 4.66	12.75 ± 2.06	0.36 ± 0.16
Nest (*n* = 87)[b]	2.21 ± 0.08	55 ± 4	97.16 ± 6.62	117.16 ± 2.44	83.14 ± 2.62	13.93 ± 1.77	0.75 ± 0.20
Random (*n* = 87)[b]	2.09 ± 0.09	23 ± 4	57.63 ± 4.90	92.41 ± 3.65	60.89 ± 4.93	12.93 ± 1.65	0.55 ± 0.15
DFA loadings[c,d]	0.17, 0.14	0.90, 0.71	0.53, 0.59	0.41, 0.69	0.62, 0.48	0.05, 0.06	0.28, 0.09
Successful nest (*n* = 17)[a]	2.09 ± 0.23	73 ± 11	84.29 ± 17.96	83.41 ± 5.33	59.94 ± 6.81	9.74 ± 3.58	0.71 ± 0.40
Unsuccessful nest (*n* = 50)[a]	2.30 ± 0.14	80 ± 4	80.94 ± 6.70	72.60 ± 3.18	58.24 ± 5.27	14.47 ± 2.13	0.92 ± 0.28
Successful nest (*n* = 70)[b]	2.22 ± 0.10	56 ± 5	95.09 ± 7.84	116.49 ± 2.87	83.31 ± 3.05	14.03 ± 1.98	0.81 ± 0.23
Unsuccessful nest (*n* = 16)[b]	2.14 ± 0.23	57 ± 9	107.13 ± 11.05	121.06 ± 3.93	83.13 ± 5.37	13.27 ± 4.68	0.38 ± 0.27
Dump nest (*n* = 36)[b]	2.21 ± 0.12	55 ± 6	96.50 ± 10.51	117.39 ± 3.86	83.50 ± 4.48	14.53 ± 2.76	0.92 ± 0.36
Normal nest (*n* = 48)[b]	2.20 ± 0.12	56 ± 6	96.65 ± 9.24	116.23 ± 3.35	82.90 ± 3.42	13.72 ± 2.49	0.63 ± 0.25

[a] Data collected from 3 June to 2 July.

[b] Data collected from 17 July to 2 August.

[c] First loading from data collected between 3 June and 2 July and second loading from data collected between 17 July and 2 August.

[d] 3 June-2 July data: 87% of cases classified correctly ($\kappa = 0.74$, 95% CI: 0.68-0.80, $z = 8.7$, $P < 0.001$); 17 July-2 August data: 91% of cases classified correctly ($\kappa = 0.82$, 95% CI: 0.78-0.86, $z = 10.8$, $P < 0.001$).

TABLE 4. Apparent nest success for all nests and incubated dump (≥13 eggs) and normal nests, hatching success (± 95% CI), and rates of abandonment and depredation for Red-breasted Merganser (*Mergus serrator*) nests on Tern Islands, Kouchibouguac National Park, New Brunswick, 2005 and 2006.

Parameter	2005	2006
Nest success (%)		
all nests	59 (42/71)	55 (45/82)
dump nests	63 (15/24)	84 (16/19)
normal nests	91 (30/33)	87 (26/30)
Hatching success (%)[a]		
successful nests	80 ± 8 (36)	70 ± 6 (42)
dump nests	85 ± 10 (15)	64 ± 9 (15)
normal nests	76 ± 10 (21)	73 ± 8 (27)
Nest losses (% of nests)		
abandoned	41 (29/71)	42 (34/82)
depredated	0 (0/71)	4 (3/82)

[a] # of hatched eggs/eggs laid for successful nests.

TABLE 5. Summary of model selection results for daily survival of Red-breasted Merganser (*Mergus serrator*) nests on Tern Islands, Kouchibouguac National Park, New Brunswick, 2005 and 2006. Symbols "+" and "*" indicate additive and interactive relationships, respectively.

Model[a]	Deviance[b]	*K*[c]	ΔAIC_c[d]	w_i[e]
$\{S_{init}\}$	278.26	2	0.00	0.38
$\{S_{init+dump}\}$	277.42	3	1.17	0.21
$\{S_{init+init^2}\}$	277.95	3	1.70	0.16
$\{S_{init+investigator}\}$	278.23	3	1.98	0.14
$\{S_{init+dump+init*dump}\}$	277.41	4	3.16	0.08
$\{S_{age+age^2}\}$	282.85	3	6.59	0.01
$\{S_.\}$	289.92	1	9.67	0.00
$\{S_{year}\}$	289.74	2	11.48	0.00
$\{S_{age}\}$	289.92	2	11.66	0.00

[a] Model factors were constant daily survival (.), year effects (year), linear nest initiation date trend (init), quadratic nest initiation date trend ($init^2$), linear age trend (age), quadratic age trend (age^2), dump nesting (dump), investigator activity (investigator).

[b] Computed as difference in -2log-likelihood values between the model in question and the saturated model.

[c] Number of parameters in model.

[d] Difference in Akaike's Information Criterion (corrected for small sample

sizes) values between the model in question and the most parsimonious model. AIC$_c$ value for model {S$_{init}$} was 282.26.

[e] Measure of relative support for the model in question.

CONNECTING STATEMENT 2

In the previous chapter, I used a multi-scale approach to study nest-site selection by Red-breasted Mergansers on Tern Islands at Kouchibouguac National Park. In this chapter, I examine movements and habitat use by Red-breasted Merganser broods originating from nests on Tern Islands. I use a habitat use-versus-availability approach to test the hypothesis that broods select among coastal habitat types available within the study area (second-order selection) and in their home ranges (third-order selection). I examine patterns of brood habitat use at population and individual (e.g., radio-marked brood) levels.

CHAPTER 3

MOVEMENTS AND HABITAT USE BY RED-BREASTED MERGANSER BROODS IN EASTERN NEW BRUNSWICK

Abstract. Little is known of the brood-rearing activities of the Red-breasted Merganser (*Mergus serrator*) throughout much of its range, and particularly in coastal environments. We measured daily movements and habitat use of radio-marked female Red-breasted Mergansers with broods ($n = 17$) originating from coastal barrier islands at Kouchibouguac National Park, New Brunswick, Canada, from 2002 to 2004. Primary brood movements from nest sites to initial rearing areas were often extensive, averaging 3.5 km ($n = 15$), since many broods crossed Saint-Louis Lagoon to continental rearing sites. Broods remained mobile throughout the rearing period as there was little difference in daily movements between age class I (days 1-10 post-nest exodus), class II (days 11-20), and class III (>20 days) broods. Broods frequented shallow ($\bar{x} = 51$ cm), nearshore ($\bar{x} = 47$ m) waters that often supported submergent eel grass (*Zostera marina*). Broods selected estuarine intertidal regions in Saint-Louis and Kouchibouguac lagoons, as well as wetlands at the mouths of tidal streams. Few broods were found in tidal river and marine habitats. Continental estuarine intertidal, tidal stream, and saltmarsh habitats were selected by age class I broods, whereas estuarine intertidal and subtidal habitats were selected by age classes II and III. This study highlights the importance of estuarine habitats in lagoons and

at the mouths of streams for brood-rearing Red-breasted Mergansers in eastern New Brunswick.

INTRODUCTION

Adult female ducks (Anatinae) enhance juvenile recruitment by assisting young in locating suitable habitats throughout the brood-rearing period (Afton and Paulus 1992). Parents select wetlands where food quality and abundance are greatest to meet the energetic and nutritional requirements of developing young (Minot 1980, Talent et al. 1982), and use areas that provide safe loafing sites for resting broods (Bengtson 1971b). Movements and habitat selection by brood-rearing females have been well documented for a variety of dabbling (Anatini) and diving (Aythyini) duck species, including Mallard (*Anas platyrhynchos*; Krapu et al. 2006), Wood Duck (*Aix sponsa*; Granfors and Flake 1999), Redhead (*Aythya americana*; Yerkes 2000a, Yerkes 2000b), and Canvasback (*Aythya valisineria*; Austin and Serie 1991). Few studies, however, have investigated brood habitat selection by sea ducks (Mergini) breeding at inland and, in particular, at coastal sites, despite this tribe representing over 40% of duck species breeding in North America (Palmer 1976, Pöysä and Virtanen 1994). The brood-rearing activities of most sea duck populations are poorly known because they generally breed at low densities across remote areas where studies are logistically difficult (Décarie et al. 1995). Characterization of important breeding sites is needed given increased concern about population declines among most species of sea ducks (Sea Duck Joint Venture Management Board 2008).

The Red-breasted Merganser (*Mergus serrator*) is a piscivorous sea duck with a holarctic breeding distribution in which it is associated with brackish and salt waters and large freshwater wetlands (Titman 1999). The breeding population of Red-breasted Mergansers in the Gulf of St. Lawrence region of the Canadian Maritime Provinces exceeds 5000 birds (Titman 1999), many of which nest colonially on barrier islands in estuaries throughout eastern New Brunswick (Erskine 1992, Chapter 2). Little is known of the activities of merganser broods at these sites, which include a variety of riverine, estuarine, and marine wetlands. Information on movements and habitat use by Red-breasted Merganser broods is limited primarily to Iceland where Bengtson (1971b) studied movements of newly hatched young and documented the general distribution of broods around Lake M'yvatn.

Brood movements from nest sites to initial rearing habitats (primary movements) and subsequent movements to alternate areas (secondary movements) generally indicate that Anatinae actively select habitats throughout the rearing period (Mauser et al. 1994, Granfors and Flake 1999). Movements and habitat use may vary with brood age and result from varying physiological, nutritional, and behavioral requirements of Anatinae from hatching to fledging (Berg 1956, Beard 1964, Rotella and Ratti 1992).

We investigated movements and habitat selection by Red-breasted Merganser broods originating from a nesting colony at Kouchibouguac National Park, New Brunswick (Chapter 2). Specific objectives were: 1) to measure distances traveled to initial brood-rearing locations and to subsequent rearing sites, 2) to examine patterns of habitat use relative to availability at two spatial scales: a) home range (second-order selection) and b) sites within the home range (third order), and 3) to examine brood-age related changes in daily movements and habitat use. We hypothesized that broods would select specific habitat types among those available within the study site and in their home ranges. We suspected that important habitats would consist of high densities of small fish, safe loafing sites for broods, and relatively low duckling predation pressure.

METHODS

STUDY SITE

We conducted work from late May to mid-September 2002 to 2004. Kouchibouguac National Park (46°46' N, 64°52' W; Fig. 1) occupies an area of 239 km^2 on the coast of the Magdalene Shallows Natural Marine Region; the marine waters of Northumberland Strait are separated from an estuary by a 26-km crescent of barrier islands. The estuary consists of Saint-Louis and Kouchibouguac lagoons and the tidal regions of several rivers and streams, including the Kouchibouguacis and Kouchibouguac rivers and Major Kollock Creek (Fig. 1). Submergent eelgrass (*Zostera marina*) occurred over shallows of much of the area (salinity >7%), but widgeon grass (*Ruppia maritima*) dominated brackish waters (Beach 1988). Average water depths in the estuary were shallow (<1 m) except for several channels (2-6 m) and over unvegetated intertidal flats (0.3 m; Beach 1988). Substrates were primarily organic matter or sand (1-2 mm particle size; Hanson and Calkins 1996). Saltmarsh, consisting of two zones, fringed much of the continental side of the lagoons. The low marsh was flooded daily by tides (<0.7 m tidal amplitude) and was dominated by saltwater cordgrass

(*Spartina alterniflora*), whereas the upper marsh was only infrequently flooded by the highest tides and saltmeadow cordgrass (*S. patens*), saltmarsh sedge (*Carex paleacea*), and prairie cordgrass (*Spartina pectinata*) were most common (Beach 1988).

Red-breasted Mergansers nested colonially on Tern Islands, a 2.8-ha island complex consisting of three barrier islands in Saint-Louis Lagoon (Fig. 1). The islands are composed of sand and stabilized primarily by marram grass (*Ammophila breviligulata*; Chapter 2). Potential duckling predators at the site included Herring (*Larus argentatus*) and Great Black-backed (*L. marinus*) gulls, American Crows (*Corvus brachyrhynchos*), Common Ravens (*C. corax*), Northern Harriers (*Circus cyaneus*), and red fox (*Vulpes vulpes*).

DATA COLLECTION

We found Red-breasted Merganser nests in each year by systematically searching Tern Islands on foot between 07:00 and 11:00 AST once a week from late May to early July (Chapter 2). Nest coordinates were obtained using a global positioning system (GPS model eTrex, Garmin Ltd., Olathe, KS). We estimated hatching date for each incubated nest by floating 2-3 eggs in water and assuming an incubation period of 30 days (Westerskov 1950, Titman 1999). We captured females on their nest during the last week of incubation using a dip net or automatic trap (Weller 1957), and equipped hens with radio transmitters implanted immediately posterior to the nape (model PD-2, Holohil Systems Ltd., Carp, ON; Korschgen et al. 1996). Transmitters weighed between 3.1 and 3.8 g, which represented <1% of the body mass of the lightest marked female (680 g).

We captured and radio-marked females throughout the hatching season (early July-early August).

We attempted to locate marked broods (hen and ≥1 duckling) once daily post-nest exodus (White and Garrott 1990). Locations were obtained from a sea kayak or small motorboat (3 m) throughout the diurnal period (06:00-21:00). We tried to monitor broods up to 45 days post-nest exodus, after which brood-hen bonds generally deteriorated. We assumed total brood mortality or abandonment when a marked hen was observed post-nest exodus either alone or with other female Red-breasted Mergansers. We excluded travel locations between rearing sites ($n = 2$) and locations that may have been influenced by our activity ($n = 8$). We assumed that investigator disturbance occurred when broods were initially observed swimming directly away from the boat. We observed broods with binoculars from as great a distance as possible (>500 m). This was feasible given the open environment and often linear shorelines of the estuarine and marine habitats at Kouchibouguac National Park. We approached brood locations only when broods had moved >200 m to further reduce the possibility of investigator influence on brood movements.

We obtained coordinates (e.g., where brood was observed initially) of each location with a GPS, and broods were assigned to an age class: (I) days 1-10 post-nest exodus, (II) days 11-20, and (III) >20 days (Austin and Serie 1991). We measured water depth (±1 cm) and distance to shore (±1 cm) at each location, and estimated the proportion of cover in 5% increments for each of three submergent vegetation types (eelgrass, widgeon grass, macro algae) within a 10-m diameter area centered on the location.

HABITAT MAP

We delineated coastal habitat types in the study area according to the Wetlands of the Maritime Provinces classification system (Hanson and Calkins 1996). Habitats were classified as 1) tidal river, 2) tidal stream (1st-3rd order), 3) saltmarsh, 4) estuarine intertidal flat in the lagoons, 5) estuarine subtidal flat in the lagoons, 6) marine intertidal flat, or 7) marine subtidal flat. We divided estuarine intertidal flat into continental estuarine intertidal and barrier island estuarine intertidal to reflect variation in landscape and physiognomic features between estuarine intertidal habitats. Estuarine intertidal habitats were distinguished from estuarine subtidal by the absence of extensive eelgrass meadows at intertidal areas (Hanson and Calkins 1996). Marine intertidal habitat included nearshore, foreshore, and backshore regions (Godfrey 1976). We excluded barrier island and nearby upland habitats (e.g., forests, freshwater wetlands) from analyses given their avoidance by merganser broods. Candidate habitats (*n* = 8) were identified on a mosaic of digital geo-referenced orthophotographs provided by Parks Canada. Habitats were digitized from the mosaic using Cartalinx 1.04 (Clark Laboratories, Worcester, MA).

STATISTICAL ANALYSES

We measured primary and secondary movements for each brood as straight-line distances (±0.1 km) with ArcView GIS 3.1 (Environmental Systems Research Institute Inc., Redland, CA). A secondary movement was calculated only when a brood was located on consecutive days. We summarized movement data by pooling locations among broods so that daily movements were compared between the three brood age classes. Data were square-root transformed to improve normality (Shapiro-Wilks statistic = 0.95) prior to a one-way analysis of variance (ANOVA). We defined a home range as the area where broods restricted their activities during observation (Mauser et al. 1994). We calculated home range size (±1 ha) for broods that were assumed to have fledged at least one duckling (e.g., survived to at least 30 days post-nest exodus) using the minimum convex polygon method with the Animal Movement Program 2.0 (Hooge and Eichenlaub 2000) in ArcView. Before estimating home ranges, we removed 5% of outlying locations for each brood using the harmonic mean method (Dixon and Chapman 1980). We also measured the total distance moved (± 1 km) throughout the observation period for each of these broods.

We compared habitat use to availability at two spatial scales (Johnson 1980). First, proportions of each habitat within brood home ranges were compared to those available in the study area (second-order selection). Second, we compared proportions of telemetry locations that occurred in each habitat type to proportions of each habitat within home ranges (third-order selection; Johnson 1980). We calculated habitat availability for each brood by creating a thematic map in ArcView that contained used habitats surrounding the brood's nest and within a radius equivalent to the distance between the nest and the brood's farthest location from the nest (Granfors and Flake 1999, Chouinard and Arnold 2007). Thematic maps were clipped in the habitat map to estimate the proportion of each habitat type available in the study area. Thematic maps containing brood home ranges were also clipped in the habitat map to estimate the proportion of each habitat type within individual home ranges. We overlaid telemetry locations onto the habitat map to estimate the proportion of locations that occurred within each habitat for each brood.

We used the Friedman ranking procedure (Friedman 1937) to examine individual variation in availability and use of each habitat type, which resulted in habitats being ranked at the second and third orders of selection. We used compositional analysis (CA) to test for habitat selection at the two spatial scales (Aebischer et al. 1993, Smith 2003). We replaced habitat proportions consisting of zero values with 0.00001 to calculate log-ratios (Aebischer et al. 1993). We used randomization procedures to avoid inflated type I error rates produced by CA (Bingham and Brennan 2004, Thomas and Taylor 2006). We generated 2500 data sets of the same size (number of broods) and number of locations as the original data but under the hypothesis of random habitat use (Pendleton et al. 1998, Granfors and Flake 1999). If habitat use was nonrandom ($P < 0.05$), we constructed a matrix of t-tests using differences of log-ratios so that we could rank habitat preferences and examine where ranks differed (Aebischer et al. 1993). Broods tracked for fewer days provided less information, thus, observations were weighted by the square-root of the number of days a brood was under observation (Granfors 1996). We considered broods that were assumed to have fledged young ($n = 6$) or were observed on at least eight occasions ($n = 2$) prior to total brood mortality or abandonment for analyses of habitat selection.

We evaluated the effects of brood age on habitat use using a Chi-square goodness-of-fit test for each of the three brood age classes (White and Garrott 1990). Few broods ($n = 6$) provided information about each age class and many broods had few locations (<6) within a given age class, so locations were pooled among broods (Alldredge and Ratti 1986, Gammonley 1990). We estimated available habitat by creating a thematic map in ArcView that contained used habitats surrounding the nest of the brood with the largest radius between the broods's nest and its farthest location from the nest. The thematic map was clipped in the habitat map to calculate the proportion of each habitat type available in the study area. We overlaid all brood locations onto the habitat map to calculate the proportion of locations in each habitat for each brood age class. We used an exact test to compare use of habitats within each age class because of many small expected frequencies (<5) in the Chi-square table (Sokal and Rohlf 1981). If nonrandom habitat use occurred, we calculated Bonferroni confidence intervals to identify preferred habitat(s) (Byers and Steinhorst 1984). Data analyses were conducted using SPSS 11.5 (SPSS Inc., Chicago, IL) and SAS 9.1 (SAS Institute Inc., Cary, NC). We set all significance levels at $P < 0.05$ and present values as means ± 95% confidence intervals (CI).

RESULTS

MARKING AND TRACKING

Twenty-seven female Red-breasted Mergansers were fitted with transmitters. Nests of three marked females were unsuccessful, three females were observed without a brood post-nest exodus, and four females were not found following nest exodus. We obtained 233 locations ($\bar{x} = 13.7$ locations brood^{-1}, range 1 to 45) from 17 broods. The mean brood age at last observation was 16.2 days post-nest exodus and ranged from 0 to 51 days (day 0 = day of nest exodus). Ninety (38%)

locations were recorded for age class I broods, 49 (21%) for class II broods, and 95 (41%) for class III broods.

MOVEMENTS

Primary movements averaged 3.5 km (95% CI: 2.8-4.2 km, $n = 15$) and ranged from 0.6 to 5.9 km. Most broods crossed Saint-Louis Lagoon from Tern Islands to reach estuarine bays and mouths of tidal streams along the continent. One hen in 2003 led her brood <1 km from her nest to initial rearing habitat along the shorelines of Tern Islands. One female, radio-marked in both 2003 and 2004, led her broods to Anse à Simon Michel, a shallow bay in Saint-Louis Lagoon (Fig. 1).

Secondary movements averaged 1.0 km day^{-1} (95% CI: 0.8-1.2 km, $n =$ 157 locations) and ranged from localized movements (<0.1 km) to 7.9 km. Secondary movements were typically not directional (e.g., consistently moving away from Tern Islands) as broods often returned to previous rearing sites. Overall, brood movements were greatest immediately post-nest exodus (Table 1), but there were no differences in daily movements between age class I, class II, and class III broods ($F_{2,202} = 0.5$, $P = 0.62$). Mean home range size for those broods that were assumed to have fledged young ($n = 6$) was 806 ha (95% CI: 40-1572 ha) and ranged from 196 to 2199 ha. Total straight-line distance traveled by these broods averaged 44.0 km (95% CI: 20.2-67.7 km) and ranged from 17.4 to 81.2 km.

HABITAT USE AND SELECTION

Microhabitat at brood locations varied between habitat types (Table 2). Overall, broods frequented shallow waters ($\bar{x}$ = 51 cm, 95% CI: 44-58 cm, *n* = 191 locations) near shore ($\bar{x}$ = 47 m, 95% CI: 33-60 m, *n* = 157 locations). The proportion of submergent vegetation at locations averaged 38% (95% CI: 34-43%, *n* = 212 locations). Eelgrass occurred at 85% of 216 brood locations whereas macro algae and widgeon grass each occurred at <20% of locations. Eelgrass cover at brood locations was considerably higher ($\bar{x}$ = 35%, 95% CI: 31-39%) than that of macro algae ($\bar{x}$ = 3%, 95% CI: 2-5%) or widgeon grass ($\bar{x}$ = 1%, 95% CI: 0-1%; $\chi^2_2 = 299.5$, $P < 0.001$).

Broods loafed on shore typically <1 m from water. Broods on the continental side of lagoons rested on sandy intertidal areas surrounded by saltwater cordgrass and on peat deposits with cordgrass. Broods resting on the barrier islands loafed on intertidal beaches that lacked vegetative concealment.

We observed little variability in ranks of habitats across broods (Table 3). Estuarine subtidal was ranked first (most used) for all eight broods at the second order of selection, and continental estuarine intertidal was ranked at least third for all broods at the third order of selection (Table 3). Use of habitats was proportional to availability at the second order of selection (Wilk's $\lambda = 0.002$, $\chi^2_7 = 50.8$, randomized $P = 0.26$). However, marine (*n* = 5 locations) and tidal river (*n* = 4 locations) habitats were not important in brood home ranges (Table 4). River locations were within 2.8 km of a lagoon.

Marine and tidal river habitats were excluded from analysis of third-order selection as at least six non-missing log-ratio differences, necessary for randomization to show a difference from zero at $P < 0.05$ (df ≥ 5 for *t*-tests), were unavailable. Removal of these habitats, however, did not affect ranking among remaining habitats. Habitat use was nonrandom (weighted mean Wilk's $\lambda = 0.1$, $\chi^2_4 = 16.5$, randomized $P = 0.03$) at the third order of selection (Table 4). Continental estuarine intertidal was ranked first but was not used more than tidal stream ($P = 0.52$). Broods used shallow intertidal areas in continental bays, including Grande Anse and Anse à Simon Michel, and at the mouths of streams (<675 m from a lagoon), particularly Duck Brook and Major Kollock Creek (Fig. 1). Estuarine subtidal was ranked last and was used less than continental estuarine intertidal ($P = 0.008$) and barrier island estuarine intertidal ($P = 0.02$). The relatively little use of estuarine subtidal habitat reflected large areas of relatively deep (>75 cm), offshore (>100 m) waters that were not important in brood home ranges. However, most broods regularly used shallow, nearshore estuarine subtidal habitats (Table 4).

Use of habitats was nonrandom for brood age class I ($\chi^2_7 = 1318.0$, $P < 0.001$). Continental estuarine intertidal, tidal stream, and saltmarsh habitats were selected (Table 5). Habitat use was also nonrandom for brood age classes II ($\chi^2_7 = 452.2$, $P < 0.001$) and III ($\chi^2_7 = 1723.0$, $P < 0.001$) as continental estuarine intertidal, barrier island estuarine intertidal, and estuarine subtidal habitats were selected (Table 5).

DISCUSSION

MOVEMENTS

Distances traveled by Red-breasted Merganser broods from nests on Tern Islands to rearing areas were variable but often exceeded 3 km. Extensive travels are common for broods moving from nesting islands to continental wetlands (Munro and Bédard 1977, Sayler and Willms 1997). In Lake Michigan, Braun et al. 1980 reported travel by a Red-breasted Merganser brood of nearly 1 km from its nesting island to rearing habitat along the continent. Primary movements by Common Eider (*Somateria mollissima*) broods may exceed 10 km toward continental rearing areas (Munro and Bédard 1977).

Movements to the continent by newly hatched Red-breasted Merganser broods may have been necessary if suitable brood-rearing conditions near the nesting islands were not available. Predation pressure on broods was relatively high along the barrier islands since predatory gulls are more common around Tern Islands than along the continent. Great Black-backed Gulls harassed Red-breasted Merganser broods as they left Tern Islands, and on two occasions, we observed a gull preying on a newly hatched merganser duckling. In their study, Young and Titman (1986) suggested that Red-breasted Merganser duckling survival at Kouchibouguac National Park was reduced by the numerous gulls along the barrier islands, and that broods moved quickly from island nests to continental shorelines, possibly to avoid predation. Predation pressure by gulls was likely higher during Young and Titman's (1986) study in 1984 than in 2002-2004, when <5 nests and small numbers of gulls were observed on Tern Islands.

Nevertheless, as many as 500 gull nests occurred annually on Tern Islands during the late 1990s (R. Ouellette, pers. comm.).

Daily movements by Red-breasted Merganser broods were most extensive within 10 days post-nest exodus (age class I), which at least partially reflected the extensive primary movements. Movements of the youngest age class in our study were greater than those reported at Lake M'yvatn, Iceland, where daily travel by newly hatched Red-breasted Merganser broods averaged 265 m (Bengtson 1971b). Bengtson (1971b) was not able to follow broods throughout the entire rearing period, but Red-breasted Merganser broods at Kouchibouguac National Park remained highly mobile in age classes II and III, often traveling >1 km day^{-1}. This mobility may be linked to foraging since mergansers (*Mergus* spp.) use extensive paths along shorelines in search of fish (Wood and Hand 1985), particularly when previous sites are unprofitable (Wood 1985).

Multiple Red-breasted Merganser broods often occupied nearby loafing and foraging sites, suggesting that encounters between broods were common. We are uncertain whether brood movements were triggered by agonistic behavior between broods, but on 22 August 2004, an amalgamated brood of 23 young was aggressively displaced from the mouth of Major Kollock Creek by the hen of an older brood of 7 ducklings. Aggression between brood-rearing female Red-breasted Mergansers was reported in Denmark, but this behavior did not lead to extensive brood movements (Kahlert 1993).

We eliminated the brood locations that were apparently influenced by investigator activity (e.g., boat tracking). However, our activities may have resulted in undetected brood displacement on a small number of occasions, such as during motorboat departures from brood locations following habitat measurements. Fast-moving motorboats in Denmark were twice as likely to disturb Red-breasted Merganser broods than smaller boats, but broods quickly resumed their activities once the disturbance had passed (Kahlert 1993). It is unlikely that our tracking efforts played a major role on merganser brood movements, given that disturbed broods did not move large distances (<200 m) and that some broods made extensive secondary movements (>2 km) regardless of whether they were followed by kayak or motorboat.

HABITAT USE AND SELECTION

Red-breasted Merganser broods used predominantly shallow, nearshore intertidal and subtidal habitats throughout Saint-Louis and Kouchibouguac lagoons and at the mouths of tidal streams that emptied into the lagoons. These habitats provide an abundance of small fish throughout the brood-rearing period. Threespine (*Gasterosteus aculeatus*), blackspotted (*G. wheatlandi*), fourspine (*Apeltes quadracus*), and ninespine (*Pungitius pungitius*) sticklebacks, mummichog (*Fundulus heteroclitus*), Atlantic silverside (*Menidia menidia*), and cunner (*Tautogolabrus adspersus*) are common in the lagoons throughout summer and represent much of the total fish biomass present within the park's estuarine system (Klassen 2001, Joseph et al. 2006). Broods were observed foraging (*n* = 36 locations) over stands of submergent eelgrass in shallow (<1 m) subtidal areas. Eelgrass meadows provide sticklebacks and other small fish with nursery habitat that generally produces more adult recruits than other juvenile fish habitats (Beck et al. 2001, Joseph et al. 2006).

Habitat selection by mergansers is affected by the availability and abundance of fish (Kaminski and Weller 1992). Abundance of Common Merganser (*Mergus merganser*) broods in British Columbia is linked to abundance of juvenile Pacific salmon (*Oncorhyncus* spp.; Wood 1986) and the distribution of Red-breasted Merganser broods has been related to the distribution and abundance of small fish (<15 cm), particularly sticklebacks (White 1957, Bengtson 1971a, Råd 1980). Sjöberg (1989) suggested that the breeding period for the Red-breasted Merganser in Sweden is synchronized with movements of threespine sticklebacks; broods forage on juvenile sticklebacks that move downstream to coastal regions. Sticklebacks are the most abundant fish in the lagoons at Kouchibouguac National Park throughout the Red-breasted Merganser brood-rearing period (Klassen 2001).

Continental estuarine intertidal, tidal stream, and saltmarsh habitats were selected by age class I broods. These habitats provided newly hatched ducklings with shallow waters that are sheltered from wind and larger waves, which likely improved brood foraging given the limited diving abilities of young mergansers (Beard 1964). These areas also provided young broods with loafing sites in saltwater cordgrass. Vegetative concealment likely reduced predator detection of age class I broods, a period when mortality of young Anatinae is usually highest (Flint and Grand 1997, Guyn and Clark 1999). We observed little use of stream and saltmarsh habitats by brood age classes II and III, and these broods often used more open estuarine subtidal and barrier island intertidal areas. Bengtson (1971b) observed young Red-breasted Merganser broods in restricted areas near continental and island shorelines of Lake M’yvatn, whereas older broods occurred in more open areas. Older merganser broods (>2 weeks) likely use deeper, more open habitats since shallow waters and concealment are of less importance than for younger broods. Age-related shifts in habitat use may be influenced by changes in duckling food requirements (Bengtson 1971a, Gammonley 1990, Afton and Paulus 1992); the diet of Red-breasted Merganser ducklings at Kouchibouguac National Park warrants investigation.

CONCLUSIONS

Red-breasted Merganser broods at Kouchibouguac National Park used shallow, nearshore estuarine habitats with an abundance of economically unimportant fish, including sticklebacks and mummichogs (Klassen 2001). Commercially- and recreationally important fish (e.g., Atlantic salmon *Salmo salar* parr), however, are uncommon in the park's lagoons in summer (Klassen 2001), and few of these fish move downstream during the late summer merganser brood-rearing period (Delaney et al. 1993). It is therefore unlikely that Red-breasted Merganser broods at Kouchibouguac National Park affected populations of economically important fish species.

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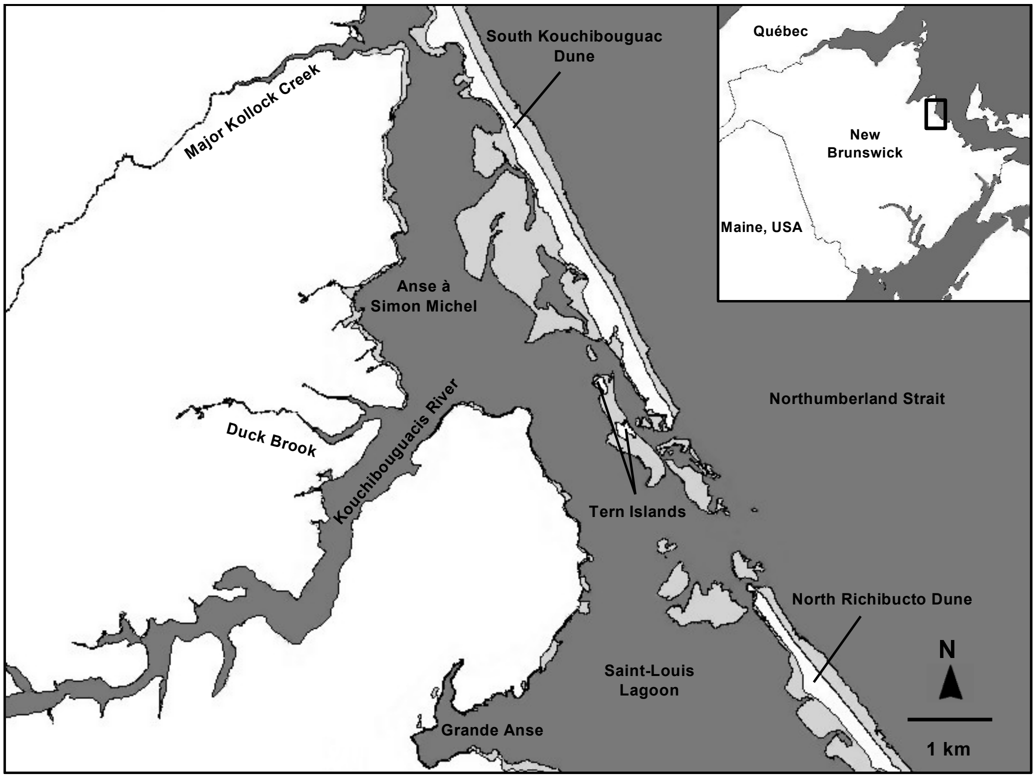

FIGURE 1. Study site at Kouchibouguac National Park, New Brunswick, 2002-2004. Red-breasted Merganser (*Mergus serrator*) brood-rearing sites included Grande Anse, Duck Brook, Anse à Simon Michel, and Major Kollock Creek. Shaded areas are intertidal regions.

TABLE 1. Distances moved by Red-breasted Merganser (*Mergus serrator*) broods for three age classes at Kouchibouguac National Park, New Brunswick, 2002-2004.

Age class[a]	Mean distance moved day^{-1} (km)	95% CI (km)	Range (km)	Broods[b]	Observations
I	1.3	1.0-1.7	0.0-5.9	15	76
II	1.1	0.7-1.4	0.1-7.9	5	52
III	1.1	0.9-1.3	0.0-3.5	6	77

[a] I = days 1-10 post-nest exodus, II = days 11-20, III = >20 days.

[b] Number of broods that provided movement data within each brood age class

TABLE 2. Microhabitat characteristics at Red-breasted Merganser (*Mergus serrator*) brood locations within four habitat types at Kouchibouguac National Park, New Brunswick, 2002-2004. From 17 broods.

	Habitat type[a]			
	STR	ES	IFB	IFC
Mean water depth (cm)	30.3	65.3	38.2	33.3
95% CI	20.4-40.2	52.7-77.8	24.9-51.3	27.2-39.5
range	4.9-64.1	2.7-475.0	2.2-122.6	2.0-91.8
n	20	86	20	46
Mean distance to shore (m)	22.0	77.5	13.3	16.0
95% CI	6.3-37.7	53.5-101.3	7.6-18.9	12.4-19.7
range	2.1-45.3	0.9-771.0	0.3-39.2	0.1-45.1
n	7	80	22	41
Mean vegetative cover (%)[b]	34	44	20	37
95% CI	21-47	38-51	7-33	28-45
range	5-95	0-100	0-100	0-100
n	20	94	24	55
Percent occurrence (%)[b]				
eelgrass	100 (20/20)	89 (84/94)	65 (15/23)	85 (45/53)
macro algae[c]	30 (6/20)	7 (7/94)	13 (3/23)	9 (5/53)
widgeon grass	15 (3/20)	2 (2/94)	0 (0/23)	4 (2/53)

TABLE 2 (continued). Habitat characteristics at Red-breasted Merganser (*Mergus serrator*) brood locations within four habitat types at Kouchibouguac National Park, New Brunswick, 2002-2004. From 17 broods.

	Habitat type[a]			
	STR	ES	IFB	IFC
Cover (%)[b]				
eelgrass				
mean	26	43	18	33
95% CI	17-36	36-50	6-30	26-41
range	5-70	0-100	0-100	0-100
n	20	94	24	55
macro algae[c]				
mean	6	1	2	3
95% CI	0-13	0-2	0-6	1-6
range	0-50	0-40	0-40	0-50
n	20	94	24	55
widgeon grass				
mean	2	0	0	0
95% CI	0-4	0.0-1	-	-
range	0-15	0-20	-	-
n	20	94	24	55

[a] STR = tidal stream, ES = estuarine subtidal, IFB = barrier island estuarine intertidal, and IFC = continental estuarine intertidal. Other habitats excluded since few locations (≤6) were available.

[b] Obtained from within a 10-m diameter area centered on each location. Includes live and dead vegetation.

[c] Families Phaeophyta, Rhodophyta, Cyanophyta, and Chlorophyta.

TABLE 3. Habitat ranks for eight Red-breasted Merganser (*Mergus serrator*) broods at Kouchibouguac National Park, New Brunswick, 2002-2004. Ranks calculated at the second and third orders of habitat selection. Number of telemetry locations are in parentheses.

	Habitat type[a]							
Brood ID	STR	ES	IFB	IFC	MI	MS	RIV	SM
150 (*n* = 39)	5 / 2[b]	1 / 6	2 / 5	4 / 1	6 / n	8 / n	7 / 3	3 / 4
131 (*n* = 13)	6 / 2	1 / 7	3 / 1	5 / 3	2 / 4	8 / 6	7 / n	4 / 5
711 (*n* = 8)	4 / 2	1 / 5	7 / 4	2 / 1	5 / n	8 / n	6 / n	3 / 3
638 (*n* = 29)	4 / n	1 / 6	2 / 1	5 / 3	3 / 2	8 / 4	6 / n	7 / 5
500 (*n* = 38)	5 / 3	1 / 6	2 / 4	4 / 1	7 / n	8 / n	6 / 2	3 / 5
209 (*n* = 22)	5 / 3	1 / 7	2 / 6	3 / 1	6 / 5	8 / n	7 / 4	4 / 2
529 (*n* = 31)	5 / 2	1 / 8	2 / 6	4 / 1	7 / 4	8 / 3	6 / 5	3 / 7
120 (*n* = 8)	4 / 2	1 / 3	7 / n	3 / 1	5 / n	8 / n	6 / n	2 / 4

[a] STR = tidal stream, ES = estuarine subtidal, IFB = barrier island estuarine intertidal, IFC = continental estuarine intertidal, MI = marine intertidal, MS = marine subtidal, RIV = tidal river, and SM = saltmarsh.

[b] 5 / 2, where 5 is habitat rank (derived from observed – expected frequencies) at second order of selection, and 2 is rank at third order of selection. Rank of 1 = most used. (n) denotes no rank since habitat was not available.

TABLE 4. Mean percentage (± 95% CI) of each habitat type available, within home ranges, and at telemetry locations among eight Red-breasted Merganser (*Mergus serrator*) broods at Kouchibouguac National Park, New Brunswick, 2002-2004 (n = 188 locations).

	Habitat type[a]							
	STR	ES	IFB	IFC	MI	MS	RIV	SM
Available	0.4 ± 0.1	24.0 ± 6.2	4.2 ± 2.1	1.0 ± 0.1	1.4 ± 0.3	62.8 ± 8.1	2.5 ± 0.6	3.8 ± 0.8
Home range	0.6 ± 0.5	65.9 ± 13.7	10.7 ± 6.2	6.0 ± 5.9	3.0 ± 2.5	4.5 ± 10.7	0.9 ± 1.1	9.9 ± 6.5
Locations	11.0 ± 11.0	26.1 ± 17.8	17.7 ± 15.9	29.4 ± 11.8	0.9 ± 2.0	2.9 ± 6.8	2.1 ± 2.9	9.9 ± 8.1
Rank: 2nd order[b]	N/A							
Rank: 3rd order[c]	IFC > STR > IFB > SM > ES[d]							

[a] STR = tidal stream, ES = estuarine subtidal, IFB = barrier island estuarine intertidal, IFC = continental estuarine intertidal, MI = marine intertidal, MS = marine subtidal, RIV = tidal river, and SM = saltmarsh.

[b] Home ranges vs. available habitat. Randomized $P = 0.26$, so habitats were not ranked.

[c] Telemetry locations vs. home ranges. Habitats are presented in rank order where they are separated with > symbols, those to the left being of higher rank. Habitats that share an underline were used equally ($P < 0.05$).

[d] Randomization indicated greater use of IFB in comparison to ES ($P = 0.02$).

Table 5. Characteristics of available habitats for three age classes of Red-breasted Merganser (*Mergus serrator*) broods at Kouchibouguac National Park, New Brunswick, 2002-2004. From 17 broods.

	Habitat type[a]							
	STR	ES	IFB	IFC	MI	MS	RIV	SM
Class I[b]								
# of locations	18	19	8	18	0	0	4	16
% of locations	22	23	10	22	0	0	5	19
Bonferroni CI	0.09-0.34	0.10-0.36	0.01-0.19	0.09-0.34	0-0.001	0-0.001	0-0.02	0.07-0.31
selected/avoided[c]	selected	-	-	selected	-	avoided	-	selected
Class II[b]								
# of locations	2	16	16	22	0	0	2	3
% of locations	5	36	23	25	0	0	5	7
Bonferroni CI	0-0.13	0.17-0.56	0.05-0.40	0.07-0.43	0-0.001	0-0.001	0-0.13	0-0.17
selected/avoided	-	selected	selected	selected	-	avoided	-	-
Class III[b]								
# of locations	1	26	19	33	2	3	1	2
% of locations	49	30	22	38	2	3	1	2
Bonferroni CI	0-0.11	0.17-0.43	0.10-0.34	0.24-0.52	0-0.07	0-0.09	0-0.11	0-0.07
selected/avoided	-	selected	selected	selected	-	avoided	-	-
% available	<1	15	2	1	1	75	4	2

[a] STR = tidal stream, ES = estuarine subtidal, IFB = barrier island estuarine intertidal, IFC = continental estuarine intertidal, MI = marine intertidal, MS = marine subtidal, RIV = tidal river, and SM = saltmarsh.

[b] Class I = days 1-10 post-nest exodus, Class II = days 11-20, Class III = >20 days.

[c] (-) denotes no preference or avoidance for habitat type.

CONNECTING STATEMENT 3

By the early brood-rearing period, most male Red-breasted Mergansers have departed Kouchibouguac National Park for molting sites. The following two chapters focus on molting male Red-breasted Mergansers at Anticosti Island, Québec, the only important molting site known for this species in the Gulf of St. Lawrence. My main objective was to examine patterns of habitat use during male wing molt, and the first step to accomplish this was to delineate the flightless period. In this chapter, I determine the duration and chronology of wing molt among male Red-breasted Mergansers using the western shorelines of Anticosti Island. I also characterize body molt in relation to growth of new remiges because variation in molt intensities may reflect physiological pressures encountered during the period of flightlessness.

CHAPTER 4

WING AND BODY MOLTS OF MALE RED-BREASTED MERGANSERS IN THE GULF OF ST. LAWRENCE

Abstract. Little is known of the chronology of wing molt and the intensity of body molt among flightless Red-breasted Mergansers (*Mergus serrator*) in North America. We examined molt of 39 postbreeding male mergansers collected at Anticosti Island, Québec, Canada, from July to September 2005 and 2006. We estimated that birds were flightless for 30-33 days. Nearly 75% of males initiated the flightless period between 20 July and 3 August and >90% were flightless from 8 to 25 August. Subadult males became flightless slightly earlier ($\bar{x}$ = 28 July, n = 7) than adult males ($\bar{x}$ = 1 August, n = 28). Most of the head and neck attained the cryptic alternate plumage before remiges were lost, which was consistent with observations at a nearby breeding site in eastern New Brunswick, where >75% of adult males were undergoing prealternate molt on the head region by late June. Molt intensities declined on the side, collar, and back and increased on the belly and tail throughout the period of flightlessness. Greater coverts generally molted in synchrony with new flight feathers and most median and lesser coverts initiated replacement within 10 days of loss of remiges. This study provides evidence that the prealternate molt functions effectively to replace bright upperpart feathers with cryptic plumage prior to the flightless period. We suggest that the staggered pattern of molt among feather regions minimizes energetic and nutrient demands

associated with feather replacement and changes in plumage insulation among flightless male Red-breasted Mergansers in the upper Gulf of St. Lawrence.

INTRODUCTION

Male ducks (Anatinae) generally leave their mates following the onset of incubation and gather to undertake a molt of remiges that renders birds flightless for several weeks (Hohman et al. 1992). While flightless, males complete the prealternate body molt (Pyle 2005), which includes a replacement of bright contour plumage with cryptic feathers that may begin prior to movements to molting sites (Wishart 1985, Howell et al. 2003). The flightless period may also include initial stages of the prebasic body molt (Young and Boag 1981, Wishart 1985), although this feather transition typically continues well after flight is regained (Hohman et al. 1992, Pyle 2005). Molting is a major metabolic event as feather production is associated with increased protein and amino acid synthesis, enlarged blood volume, alteration of water balance, and increased thermostatic costs and nutrient demands for feather and nonfeather components (King 1980, Murphy and King 1992). Given the relatively high intensities of feather replacement during the wing molt period (Thompson and Drobney 1995), energetic and nutrient demands associated with molt may be higher during the period of flightlessness than during other periods of the annual cycle (Hohman and Crawford 1995).

Adult male and subadult (second-year) sea ducks (Mergini) often move considerable distances (>500 km; Salomonsen 1968, Phillips et al. 2006) to gather in large concentrations at marine sites during the flightless period (>10 000 birds;

Frimer 1994, Petersen et al. 1999). These habitats provide food resources to help meet costs of wing feather replacement, but they may also be important during the pre- and postflightless stages, including throughout winter for some populations of sea ducks (Petersen 1981, Robertson et al. 1997, Fox et al. 2008). Food availability, ice formation, and other habitat and climatic factors, as well as behavioral requirements may influence the seasonal distribution of coastal waterfowl (van Eerden 1984, Guillemette and Himmelman 1996, Bourget et al. 2007), so patterns of habitat use at a site may vary during different stages of the postbreeding period. Thus, duration and chronology of the wing molt should be understood prior to examining habitat use, nutrient acquisition, and other aspects of the ecology of flightless Anatinae. Also, characterization of body molt in relation to growth of new remiges provides information on the chronology and intensity of molt in different feather regions, and may reflect varying physiological pressures encountered throughout the flightless period (Heitmeyer 1987, Lovvorn and Barzen 1988).

In contrast to some tribes of nearctic waterfowl, little is known about the flightless period of male sea ducks, which often occur in remote areas (Hohman et al. 1992). Thousands of postbreeding male Red-breasted Mergansers (*Mergus serrator*) replace their remiges at Anticosti Island, Québec, Canada, one of the few major molting sites known for this holarctic sea duck in eastern North America. The precise molting schedule of nearctic male Red-breasted Mergansers is not known, however, and the timing of wing molt has been described only generally in Denmark (Joensen 1973). The objectives of our study were: 1) to determine the duration and chronology of the flightless period for male

Red-breasted Mergansers at Anticosti Island and 2) to describe the chronology and intensity of body molt in relation to the length of growing remiges. We also observed adult male Red-breasted Mergansers at a breeding site 300 km from Anticosti Island to gather evidence of prealternate body molt prior to migration to molting sites. Molt and plumage nomenclature follow Pyle's (2005) modification of the Humphrey-Parkes system (Humphrey and Parkes 1959).

METHODS

STUDY SITES

Breeding. We investigated the molt status of adult male Red-breasted Mergansers at Kouchibouguac National Park, New Brunswick, Canada, from 2004 to 2006 (Fig. 1). Red-breasted Mergansers nested colonially on Tern Islands (≥46 nests year^{-1}; 46°46' N, 64°52' W), a 2.8-ha complex of barrier islands in Saint-Louis Lagoon (Chapter 2). A few mergansers (≤4 nests year^{-1}) also nested on Kelly's Island (2.0 ha; 46°47' N, 65°52' W), 6.1 km north of Tern Islands. We studied feather molt from before laying through the early incubation period, 2-29 June 2004, 20 May-17 June 2005, and 11 May-23 June 2006 (Chapter 2, R. D. Titman, unpubl. data). We regularly observed at least 35-40 adult males on the islands and in nearby intertidal and subtidal waters. We occasionally observed groups of <15 subadult males during this period.

Molting. Anticosti Island is in the upper Gulf of St. Lawrence and approximately 300 km northeast of Kouchibouguac National Park (Fig. 1). Several bays along the western shores of the 7943-km^2 island support >2500 flightless male Red-breasted Mergansers during summer (Buidin et al. 2009).

We collected males from July to September 2005 and 2006 by shooting from blinds or from a boat near shore (<150 m) at eight sites within 120 km of each other (Fig. 1): Anse aux Fraises (49°49' N, 64°28' W), Baie Ste-Claire (49°54' N, 64°30' W), Chute à Boulay (49°55' N, 64°26' W), Baie du Grand Makasti (49°56' N, 64°16' W), Baie McDonald (49°45' N, 63°03' W), Baie Caplan (49°44' N, 63°00' W), Anse Gibbons (49°22' N, 63°29' W), and Rivière Ste-Marie (49°40' N, 63°56' W). It is unknown whether males that occur at Kouchibouguac National Park during the breeding season undergo wing molt at Anticosti Island.

DATA COLLECTION

Breeding site. We observed adult male Red-breasted Mergansers with a 60× spotting scope by day at four sites. Two observation sites were on the south tip of South Kouchibouguac Dune and within 150-200 m of the eastern shores of Tern Islands; the others were either on the north tip of South Kouchibouguac Dune or on the nearby mainland and within 500 m of Kelly's Island. We attempted to use the sites equally and made observations every 1-7 days. We distinguished adult males from subadult males by plumage characteristics (Titman 1999), although we did not consider the molt status of subadults. It was difficult to determine whether adult males were paired because they often loafed in small groups (<10 birds) with females and other adult males, but this difficulty led to little chance that we mistakenly studied a male on more than one occasion during an observation session. We observed each adult male within sufficient viewing distance (50-200 m) until all aspects of plumage were visible on the head region

(Cooke et al. 1997), which included the crown, cheek, throat, and upper and lower ventral and dorsal sides of the neck. Among male Anatinae, these areas are generally the first to begin the prealternate molt (Weller 1957, Young and Boag 1981, Howell et al. 2003). We did not quantify molt status in other feather regions because relatively subtle differences between alternate and basic plumages made accurate assessment difficult. When an assessment of molt status on the head was made with confidence, we categorized this feather region as 1) in old basic plumage when the head, upper neck, and central dorsal neck were black or purple, the crown was green, and the lower neck was white, or 2) undergoing the prealternate molt when any amount of brown plumage on the head and neck and some white feathering on the throat and center of ventral neck were visible (Titman 1999). We could distinguish the much drabber alternate plumage from old basic plumage. Only S. R. Craik made observations. The designation of basic plumage did not imply that prealternate molt was not occurring at other feather regions of the body. Observation sessions ended when we assessed the molt status of all adult males within sufficient viewing distance. We compared the percentages of adult males in basic plumage and undergoing prealternate molt for five 10-day periods. Our data likely represent the minimum proportions of birds undergoing feather replacement in the head region because we were unable to identify the earliest stages of molt (first blood quills). We combined observations from the three years because annual chronology of molt in each year was similar.

Molting site. We randomly collected males from flocks while birds were in various stages of the flightless period (except preshedding), from just following loss of old remiges through feather growth and reattainment of flight. We used characteristics of wing plumage (before loss of old lesser coverts) and/or depth of the bursa of Fabricius to age birds (Titman 1999). We classified males with a bursal depth of ≥9.5 mm as subadults and those with depths of <9.5 mm as adults (Mather and Esler 1999). Males were in active wing molt when the ninth primary had a vascularized calamus (Morton et al. 1969). We determined the stage of wing molt for each bird by measuring the length (±1 mm) of a growing ninth primary from its point of emergence to the tip of the rachis (van de Wetering and Cooke 2000). Also, occasional observations of males at close distance (<100 m) at our study sites provided evidence of newly shed remiges during wing flapping (Frimer 1994, Chapter 5) and by the absence of long black primaries overlying a variably gray back (Titman 1999).

We delineated 11 feather regions on each bird: head, side, collar, back, belly, leg, tail, scapular/humeral, and greater, median, and lesser coverts (Billard and Humphrey 1972). We divided the head into seven subregions, sides into three, collar into four, belly into five, and back into five because molt within a region was often heterogeneous (Titman et al. 1990). Except for the tail and wing coverts, we plucked 1-2 cm^2 of contour feathers from the skin of each region or subregion to determine numbers of growing and old feathers (Miller 1986, Titman et al. 1990). We examined the calamus of smaller feathers under a dissecting microscope to help identify the later stages of feather development. For all feathers, we noted new growth when vascularization was present or old feathers when the calamus was clear and dry. We calculated the percentage of growing feathers for each region by dividing the sum of growing feathers from all subregions by the sum of feathers plucked from those subregions. We determined the percentage of growing feathers in the tail and coverts by examining all (tail, greater and median coverts) or most (lesser coverts) feathers in each tract (Bailey 1981).

STATISTICAL ANALYSES

We estimated the length of the flightless period as: length of a full-grown ninth primary (mm) × estimated percent regrowth needed to regain flight/feather growth rate (mm day^{-1}). Approximately 2-4 days elapse between shedding of old remiges and emergence of new feathers (Balát 1970, Bowman 1987), so we extended our estimate of the flightless period to accommodate this interval. We determined the mean length of a full-grown ninth primary from five preflightless adult males that we collected in July and August 2006 at Anticosti Island and from skins of 18 adult males at the Canadian Museum of Nature in Gatineau, Québec. These birds were collected from March to early July in Nova Scotia (n = 2), New Brunswick (n = 4), Québec (n = 4), Ontario (n = 3), Manitoba (n = 3), and Saskatchewan (n = 2). We used a growth rate of 4.04 ± SE 0.05 mm day^{-1} estimated from the ninth primary of adult male Barrow's Goldeneyes (*Bucephala islandica*; van de Wetering and Cooke 2000), and assumed that feather growth remained constant and was representative of primary feather growth (Hay 1974, Boyd and Maltby 1980). We assumed that most males could fly when the ninth primary reached 75% of its final length (Sjöberg 1988, Hohman et al. 1992).

We estimated the date of initiation of the flightless period for each bird as: date of collection – [length of ninth primary (mm)/feather growth rate (mm day^{-1})]. We extended this estimate by three days to account for the period between loss of remiges and emergence of new feathers (Bowman 1987). Also, we estimated the date that each bird would have regained flight as: date of collection + [(length of a full-grown ninth primary (mm) × estimated percent regrowth needed to regain flight) – length of ninth primary (mm)/feather growth rate (mm day^{-1})]. We used general linear models to compare dates of initiation of the flightless period and reattainment of flight between subadult and adult birds since data were normally distributed (Shapiro-Wilks statistics = 0.98). We used weighted average percentiles to determine dates of initiation of the flightless period and reattainment of flight at the 5th, 10th, 25th, 50th, 75th, 90th, and 95th percentiles and to estimate the period when most birds (>90%) were flightless.

Inspection of data suggested that relationships between body molt intensity and ninth primary length were not always linear. We used forward-selection polynomial regression to examine these relationships (Zar 1996). We fit data with linear and quadratic models and determined whether the addition of a quadratic function improved model fit by obtaining the *F*-statistic from the following equation:

$$F = \frac{\text{regression SS for linear model} - \text{regression SS for quadratic model}}{\text{residual MS for quadratic model}}$$

We did not consider higher-degree models to avoid overfitting the data. We assessed normality of residuals from the best model for each feather region with Shapiro-Wilks tests. We arcsine square-root transformed the percentages of growing feathers in the head and greater coverts. Transformation of residuals for median and lesser coverts did not improve normality, but departures from normality when untransformed data were used did not substantially violate assumptions for parametric regressions since Shapiro-Wilks test statistics were ≥0.91 (Clark and Shutler 1999). We performed statistical analyses with SPSS 11.5 (SPSS Inc., Chicago, IL). We set significance levels at $P < 0.05$, and unless otherwise stated, we present values as means ± 95% confidence intervals (CI).

RESULTS

FLIGHTLESS PERIOD

We collected six flightless male Red-breasted Mergansers from 3 August to 7 September 2005 and 33 flightless males from 10 August to 12 September 2006. Twenty-eight (72%) were adults, 7 (18%) were subadults, and 4 (10%) were of unknown age since measurements of bursal depth were not reliable. The mean length of a full-grown ninth primary from five males that we collected at Anticosti Island ($\bar{x}$ =154.3 mm, 95% CI: 151.5-157.1 mm) was similar to that of the 18 museum specimens ($\bar{x}$ =154.5 mm, 95% CI: 153.0-156.1 mm; $F_{1,21} = 0.1$, $P = 0.90$). We estimated the flightless period to be 30-33 days (2-4 days of no visible regrowth + 28.7 ± SE 0.4 days of regrowth), assuming a constant growth rate of the ninth primary of 4.04 ± SE 0.5 mm day^{-1} and that males regained flight when the ninth primary reached 75% of its final length ($\bar{x}$ = 154.5 mm, n = 23 birds). Thus, we estimated that primaries completed development in about 40-43 days.

The flightless period was synchronous. We estimated that the mean initiation date of wing molt was 1 August (95% CI: 30 July-2 August, n = 39 birds) and ranged from 20 July to 10 August, but nearly 75% of males lost old remiges by 3 August (Table 1). Anecdotal field observations also indicated a synchronous wing molt as we first noted newly shed remiges during the last 1-1.5 weeks of July (after 21 July) in both years, but over 90% of 440 males that we observed between 8 and 14 August were growing new primaries. Peak flightlessness (>90% of collected birds) was from 8 to 25 August (Table 1). Subadult males became flightless slightly earlier ($\bar{x}$ = 28 July, 95% CI: 23 July-1 August, *n* = 7) than adult males ($\bar{x}$ = 1 August, 95% CI: 31 July-3 August, *n* = 28; $F_{1,33} = 5.3$, $P = 0.03$). The estimated mean date that birds would have regained flight was 1 September (95% CI: 31 August-3 September, *n* = 39 birds) and ranged from 21 August to 11 September. Over 70% of males would have regained flight by 5 September (Table 1), a date consistent with observations that most males could fly by 10 September. Dates of initiation of the flightless period and reattainment of flight in both years were similar ($F_{1,37} = 1.5$, $P = 0.23$), but we collected few birds in 2005. Female Red-breasted Mergansers did not concentrate at our study sites from late June to mid-September.

BODY MOLT

At Kouchibouguac National Park, at least 50% of adult males were undergoing prealternate molt on the head region by late May 2004-2006, prior to incubation of nests on Tern Islands and Kelly’s Island (Table 2). Over 75% of males were wearing some alternate plumage in this region before the first nests hatched in early July (Table 2). Observations of molt of males collected at Anticosti Island indicated that much of the head and neck underwent prealternate molt before old remiges were lost (Fig. 2). The slight feather replacement in this region during the flightless period typically occurred through the upper and lower neck, and particularly once ninth primary length exceeded 40 mm. Molt intensities on the side, collar, and back were greatest (>50% of feathers) during initial stages of wing molt and generally declined throughout the flightless period (Fig. 2, Table 3). Some feathers in these regions were replaced before loss of old remiges; at least some adult males at the Kouchibouguac breeding site were replacing cinnamon breast feathers by late June (S. R. Craik, pers. obs.). Molt intensities on the belly increased linearly during the flightless period, and feather replacement likely continued following the development of remiges (Fig. 2, Table 3). Varying percentages of leg feathers molted during the flightless period (Fig. 2).

Ninth primary length explained >70% of the variation in molt intensity on the tail (Table 3). Molt on the tail was generally greatest once the ninth primary exceeded 50% of its final length, but some rectrices molted during earlier stages of wing molt (Fig. 2). Tail feathers generally molted in waves (often alternately); in most cases, nearly half of the rectrices initiated molt just prior to or immediately following loss of remiges, and the remainder began molting during later stages of the flightless period.

Greater coverts were shed in synchrony with flight feathers, but most new greater coverts completed development before the ninth primary reached its final length (Fig. 2). Most median and lesser coverts molted within 10 days of loss of remiges, and >50% were molting through much of the remainder of the flightless period (Fig. 2). Wing coverts either completed growth or were near full length before birds regained flight. Molt intensities in the scapular/humeral region were variable throughout the flightless period (Fig. 2).

DISCUSSION

FLIGHTLESS PERIOD

We estimated that the flightless period for male Red-breasted Mergansers at Anticosti Island was 30-33 days, but this estimate excludes the preshedding interval when old flight feathers are too loose to withstand flight. Little is known about the duration of the preshedding period for most nearctic Anatinae [see Shewell (1959) for some African waterfowl], but Bowman (1987) estimated 2-3 days for the American Black Duck (*Anas rubripes*). Thus, we may have slightly underestimated the flightless period for some male Red-breasted Mergansers. Palmer (1976), however, suggested that male Red-breasted Mergansers are likely flightless for about four weeks, a period similar to that of adult male Common Mergansers (*Mergus merganser*) in eastern Canada (~1 month; Erskine 1971) and other medium to large male Anatinae that molt in temperate regions (Owen and King 1979, Hohman et al. 1992).

We based our estimate of the length of the flightless period on three assumptions: 1) that the daily growth rate of the ninth primary was similar to that of adult male Barrow's Goldeneyes, 2) that daily growth rate was constant, and 3) that birds regained flight when the ninth primary reached 75% of its final length. Mean daily growth rate of the ninth primary of adult male Red-breasted Mergansers and Barrow's Goldeneyes is likely similar since daily percent change in the length of wing feathers varies little among waterfowl (2-3%; Hohman et al.

1992) and the length of a full-grown ninth primary in the two species is similar ($\bar{x}$ = 154.5-155.0 mm; 2.6% change day^{-1}; van de Wetering and Cooke 2000, this study). Even the most extreme remigial growth rates for medium to large sea ducks and diving ducks [Aythyini: 4.70 mm day^{-1} for captive Redheads (*Aythya americana*; Bailey 1981)] yields estimates of the flightless period within 2-3 days of our estimate. However, there is conflicting evidence for constancy in the daily growth rate of remiges (Bailey 1981, Sjöberg 1988). Growth may be faster during early stages of flight-feather development, possibly owing to greater body weight early on (Owen and King 1979, but see Taylor 1995), and growth rates of subadults and adults and of individuals with varying body conditions may vary, or they may vary according to nutrient availability (Swaddle and Witter 1997, van de Wetering and Cooke 2000). Van de Wetering and Cooke's (2000) estimate of 4.04 ± SE 0.05 mm day^{-1} was from Barrow's Goldeneyes that they captured throughout the flightless period, yet they did not find an association between growth rate and stage of wing molt. An estimate of 75% wing regrowth for flight is slightly higher than that for some other Anatinae, particularly dabbling ducks (Anatini: 70%; Young and Boag 1981, Hohman et al. 1992). Given their relatively heavy wing loading and shorter remiges, sea ducks and diving ducks appear to require a more developed wing to regain flight than do some dabblers (Robertson et al. 1997). The use of >75% regrowth likely overestimates the duration of the flightless period for male Red-breasted Mergansers at Anticosti Island. Three males were observed flying with remiges <80% of their full length prior to collection, and we suspect that many males were capable of flight once their primaries reached at least 75% of their final length. Before regaining flight, however, heavier birds probably require a more developed wing than do lighter individuals (Taylor 1995, Guillemette et al. 2007).

The flightless period was relatively synchronous as we estimated that >75% of 39 males lost their remiges between 20 July and 5 August. Large numbers (<800) of preflightless subadult and adult male Red-breasted Mergansers occur in scattered groups at some Anticosti Island molting sites from at least late June (Buidin et al. 2008, J.-P. L. Savard, unpubl. data), indicating that some male Red-breasted Mergansers likely complete the molt migration at least 2-3 weeks before the flightless period. In Denmark, most adult male Red-breasted Mergansers are flightless between late July and mid-August, despite large concentrations at molting sites by late June (Joensen 1973). This further suggests that wing molt is highly synchronous among Red-breasted Mergansers that gather well in advance of the flightless period. Synchronous wing molt occurs among other male Anatinae that gather before the flightless period (Bailey 1981, Robertson et al. 1997), but proximal factors, including physiological condition and geographic differences in breeding chronology, habitat conditions, and postbreeding movements may produce variation in the chronology of molt between individuals (Petersen 1981). Although predation on sea ducks molting in coastal areas may be extremely low (e.g., Iverson and Esler 2007), a synchronous wing molt within large flocks may increase individual survival through greater vigilance and predator dilution over that in smaller groups or solitary birds that are flightless (Pulliam 1973, Cooke et al. 1997). These strategies may be of particular importance because flightless Red-breasted Mergansers do not seek cover (Chapter 5), and given their limited mobility, they may be more likely to be affected by disturbance and predation pressure than during other periods of the annual cycle (Hohman et al. 1992). Flightless male Red-breasted Mergansers were generally in groups of >5-10 birds whereas preflightless males were often alone, in small groups (<5 birds), or loosely associated with flightless flocks. For mergansers (*Mergus* spp.), a synchronous molt may also be important for food acquisition during the flightless period. Groups of flightless Red-breasted Mergansers often fed by cooperatively herding fish into shallow waters (S. R. Craik, pers. obs.), and this foraging method may be efficient for exploiting local food resources since birds searching for areas where fish concentrate are less mobile when flightless than when they can fly (Emlen and Ambrose 1970, Wood 1985).

Subadult males began the remigial molt nearly five days before adult males, but we identified only seven subadults from those collected. Field observations also indicated that many early flightless males were in their second year (S. R. Craik, unpubl. data). Subadult males losing remiges earlier than adult males has been documented in other sea ducks, including Steller's Eider (*Polysticta stelleri*; Petersen 1981) in Alaska, King Eider (*Somateria spectabilis*; Frimer 1994) in Greenland, and Common Goldeneye (*Bucephala clangula*) and Common or Black Scoter (*Melanitta nigra*) in Denmark (Jepsen 1973, Joensen 1973). The timing of wing molt is under hormonal control (Payne 1972), but breeding chronology and length of molt migration may create variation in timing of the flightless period between subadults and adults (Salomonsen 1968, Petersen 1981). Petersen (1980) suggested that a separation of the molt of subadult and adult male Steller's Eiders by nearly four weeks may have evolved to reduce competition for food resources at molting habitats, but this does not appear to be the case in our study given the extensive overlap of the flightless period among male Red-breasted Mergansers. Little is known of the chronology of arrival of subadult and adult male Red-breasted Mergansers at Anticosti Island, but most males leave breeding sites at Kouchibouguac National Park by mid-July (R. D. Titman, unpubl. data).

BODY MOLT

All regions of the body molted during the flightless period, but the timing and extent of molt varied between regions. During prealternate molt, most bright feathers on the head and many on the side, collar, and back were replaced with cryptic plumage prior to loss of remiges, a pattern similar to that reported for male Red-breasted Mergansers in the Palearctic (Dement'ev and Gladkov 1967). This plumage transition likely functions to reduce detection of flightless birds when they may be more vulnerable to predators (Heitmeyer 1987, Hohman et al. 1992). We found molt intensities to increase on the belly after birds became flightless, providing further evidence that the prealternate molt is incomplete (e.g., only involves bright upperparts) and that feathering on the belly may be replaced only once during the annual cycle of Anatinae (Erskine 1971, Pyle 2005). Molting on the belly, and perhaps some on the leg, scapular/humeral tract, side, and back of flightless male Red-breasted Mergansers likely represented the earliest stages of the complete prebasic body molt (P. Pyle, pers. comm.), indicating that the prealternate and prebasic body molts may overlap by a small amount. This prebasic plumage likely has little effect on the conspicuousness of flightless birds since it is limited to underparts and regions where alternate and basic plumages are relatively similar in appearance (Titman 1999).

Male Red-breasted Mergansers reduced overlap of body feather-replacement with wing molt by initiating the prealternate molt in advance of the flightless period (e.g., on breeding grounds) and by limiting the extent of prebasic body molt while flightless, as demonstrated by increases in intensities of feather replacement on only the belly and tail. This strategy can allow birds to begin wing molt shortly after arrival at molting sites (Petersen 1980, Frimer 1994) and may help to minimize costs associated with feather synthesis and other metabolic processes during the flightless stage, a period demanding of energy and nutrients (Heitmeyer 1987, Lovvorn and Barzen 1988, Hohman and Crawford 1995). Likewise, staggered feather replacement spreads costs associated with molt among feather regions of the body. We observed little overlap in molt between the head and belly, and these are two of the largest areas of feathering on Anatinae (Heitmeyer 1987).

A staggered pattern of body molt may lessen thermoregulatory costs associated with changes in plumage insulation for flightless ducks in cold marine waters, such as the upper Gulf of St. Lawrence (Schieltz and Murphy 1997, Howell et al. 2003). Water-surface temperatures at molting sites at Anticosti Island were generally <10 °C by mid-to late August and often dropped to 5-6 °C (Chapter 5). Jenssen et al. (1989) demonstrated that thermal conductance is highest for wintering Common Eiders (*Somateria mollissima*) exposed to water temperatures <10 °C and that heat production increases significantly when water temperatures are <15 °C. Decreased plumage insulation as a result of feather replacement, however, may result in elevated lower critical temperatures and increased energy expenditure associated with thermoregulation (Schietlz and Murphy 1997). Flightless male Red-breasted Mergansers at Anticosti Island spend relatively little time on shore (Chapter 5), suggesting that while they are in the water their plumage may provide insulation and waterproofing sufficient to minimize thermal conductance.

CONCLUSIONS

We provide the first estimate of the chronology of the flightless period for male Red-breasted Mergansers in eastern North America. However, this estimate needs to be verified since it is based on several assumptions derived from data obtained from other Anatinae. The recapture of flightless and postflightless males can provide information on remigial growth rates and stage of primary feather development necessary to restore flight (e.g., Bowman 1987, van de Wetering and Cook 2000). Regrettably, our efforts to capture flightless Red-breasted Mergansers at Anticosti Island were unsuccessful. Nevertheless, estimates of the flightless period for collected males and our field observations agree that most males became flightless between late July and early August and that many birds were flying by the first week of September. With the wing molt delineated, we now can examine aspects of the ecology of flightless male Red-breasted Mergansers at Anticosti Island, including habitat use (see Chapter 5).

Our study provides evidence that the prealternate molt of male Anatinae is incomplete, although it functions effectively to replace bright upperpart feathers with cryptic plumage prior to the flightless period (Pyle 2005). The patterns of prealternate and prebasic molts exhibited by flightless male Red-breasted Mergansers may minimize energetic and nutritional demands associated with feather replacement and changes in plumage insulation in the cold waters of the upper Gulf of St. Lawrence.

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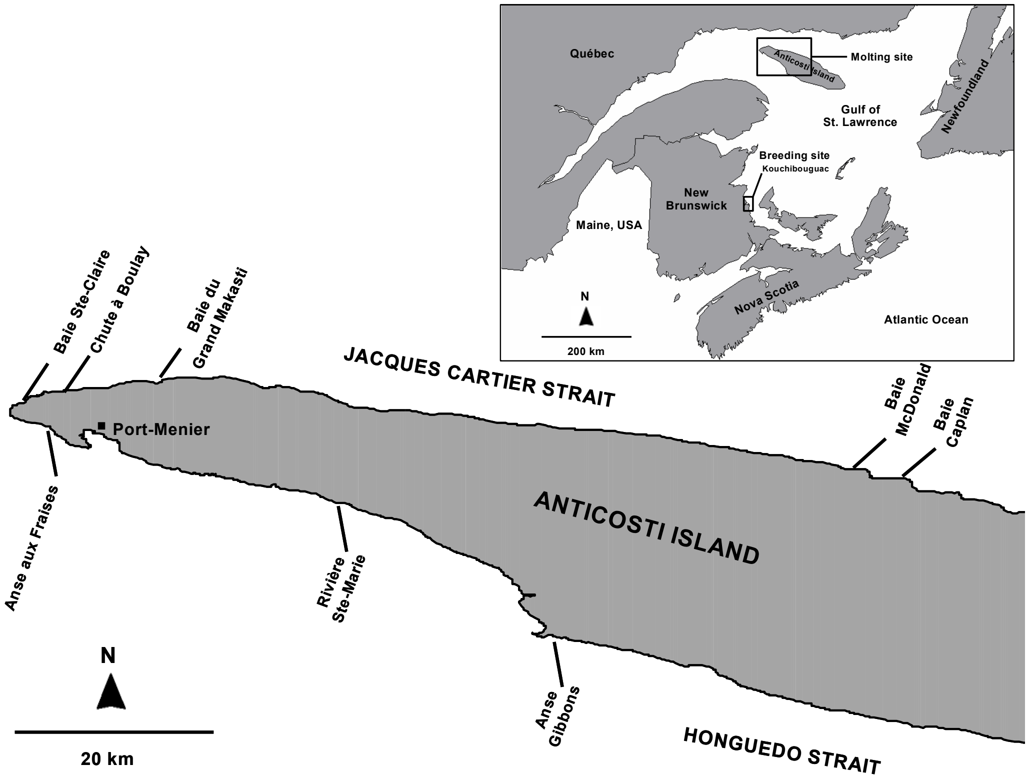
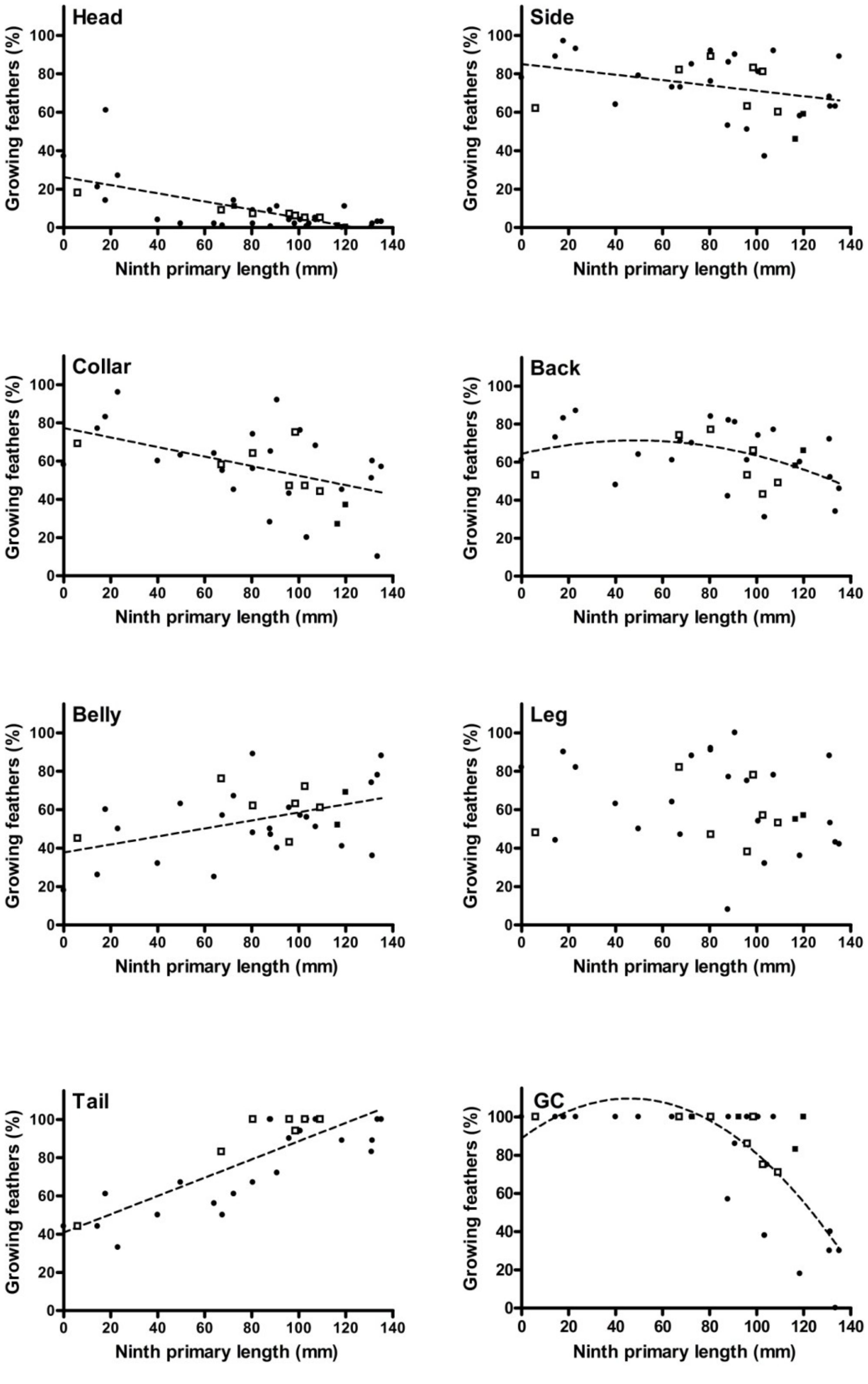


FIGURE 1. Sites of Red-breasted Merganser (*Mergus serrator*) breeding at Kouchibouguac National Park, New Brunswick, and molting at Anticosti Island, Québec, 2004-2006 (inset). Collection sites are highlighted on map of Anticosti Island.


Head
Side
Collar
Back
Belly
Leg
Tail
GC
Growing feathers (%)
0
20
40
60
80
100
Ninth primary length (mm)
0
20
40
60
80
100
120
140

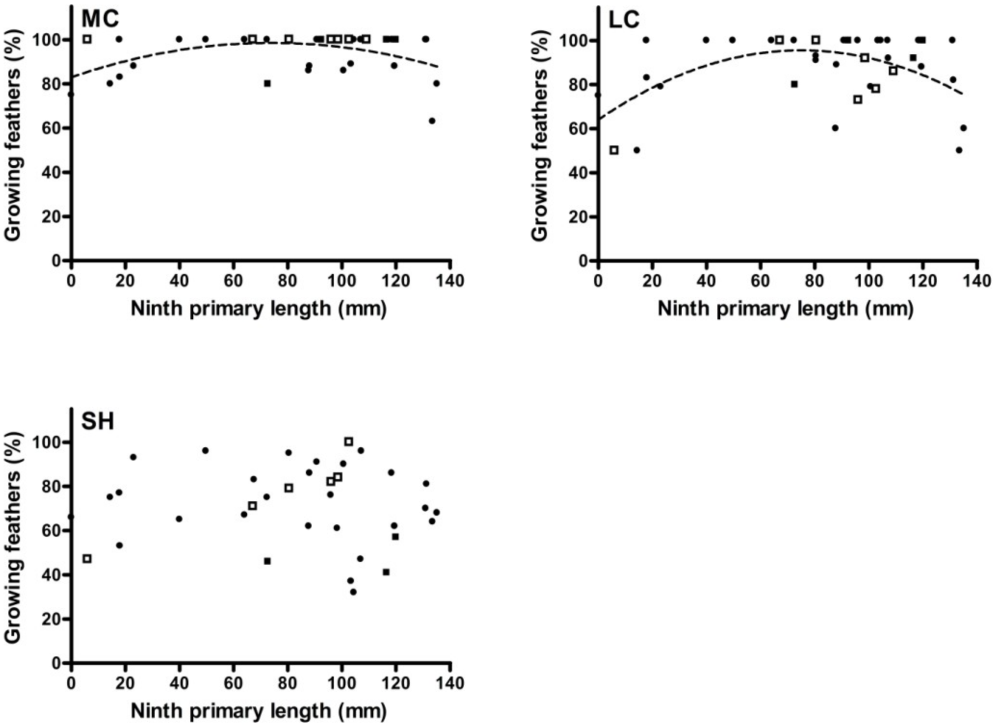


FIGURE 2. Relationships between percentage of growing feathers in 11 feather regions and length of ninth primary (mm) for male Red-breasted Mergansers (*Mergus serrator*): head, side, collar, back, belly, leg, tail, greater coverts (GC), median coverts (MC), lesser coverts (LC), and scapular/humeral (SH). Birds were collected at Anticosti Island, Québec, 2005 and 2006. Adult males (*n* = 28) are represented by black circles, subadult males (*n* = 7) by white squares, and males of unknown age (*n* = 4) by black squares. Lines of fit are provided for the best significant polynomial functions (linear or quadratic). Significant functions were not observed for the leg and scapular/humeral regions.

TABLE 1. Weighted average percentiles for dates of initiation of the flightless period and reattainment of flight for male Red-breasted Mergansers (*Mergus serrator*) collected at Anticosti Island, Québec, 2005 and 2006. From 28 adults, 7 subadults, and 4 of unknown age.

	Percentile of birds (*n* = 39)						
	5	10	25	50	75	90	95
Flightless	21 July	25 July	29 July	1 Aug.	4 Aug.	7 Aug.	9 Aug.
Flight regained	22 Aug.	26 Aug.	30 Aug.	1 Sep.	5 Sep.	8 Sep.	10 Sep.

TABLE 2. Proportions of adult male Red-breasted Mergansers (*Mergus serrator*) undergoing prealternate molt on the head region during five periods through laying and incubation on Tern Islands and Kelly's Island, Kouchibouguac National Park, New Brunswick, 2004-2006.

Period	Observations[a]	Birds molting (%)
11-20 May	108	34
21-30 May	159	49
31 May-9 June	125	79
10-19 June	129	78
20-29 June	33	88

[a] Number of birds observed. Some males were likely observed on >1 occasion during an observation period.

TABLE 3. Relationships between percentage of growing feathers (Y) in 11 feather regions and length of ninth primary (*i*) for male Red-breasted Mergansers (*Mergus serrator*) collected at Anticosti Island, Québec, 2005 and 2006. From 28 adults, 7 subadults, and 4 of unknown age.

Feather region	Regression equation	β_{SE}	β^2_{SE}	r^2	F	P
Head	$Y = 50.43 - 0.31 (i)$	0.05	-	0.51	37.9	<0.001
Side	$Y = 85.05 - 0.14 (i)$	0.07	-	0.12	4.1	0.05
Collar	$Y = 78.17 - 0.26 (i)$	0.08	-	0.26	10.8	0.003
Back	$Y = 64.35 + 0.29 (i) - 0.01 (i^2)$	0.24	0.01	0.19	3.4	0.04
Belly	$Y = 37.70 + 0.21 (i)$	0.07	-	0.22	8.3	0.007
Leg	$Y = 72.19 - 0.12 (i)$	0.10	-	0.05	1.4	0.24
Tail	$Y = 40.87 + 0.48 (i)$	0.06	-	0.68	58.2	<0.001
Greater coverts	$Y = 113.86 + 0.95 (i) - 0.01 (i^2)$	0.32	0.01	0.61	27.0	<0.001
Median coverts	$Y = 82.97 + 0.42 (i) - 0.01 (i^2)$	0.14	0.01	0.21	4.6	0.02
Lesser coverts	$Y = 64.00 + 0.84 (i) - 0.01 (i^2)$	0.22	0.01	0.29	7.0	0.003
Scapular/humeral	$Y = 72.37 - 0.01 (i)$	0.08	-	0.00	0.1	0.88

CONNECTING STATEMENT 4

In the last chapter, I delineated the chronology of wing molt for male Red-breasted Mergansers using several bays along the western shorelines of Anticosti Island, Québec, in 2006. In this chapter, I determine patterns of habitat use by flocks of males in wing molt at these sites in 2006 by examining three sources of data: 1) microhabitat, 2) time-activity budgets, and 3) stomach contents. I use a foraging habitat-versus-nonforaging habitat approach to test the prediction that foraging flocks use shallow, nearshore sites, whereas nonforaging flocks frequent offshore areas.

CHAPTER 5

HABITAT USE BY MALE RED-BREASTED MERGANSERS MOLTING IN THE GULF OF ST. LAWRENCE

Abstract. We examined habitat use by flocks of male Red-breasted Mergansers (*Mergus serrator*) undergoing wing molt in three coastal bays at Anticosti Island, Québec, Canada, by obtaining information on microhabitat features, prey items, and diurnal behavior. Males used clear, shallow waters (≤12 m) near shore (<850 m), and often over a sand-rock substrate with submergent algae. Foraging flocks were generally restricted to intertidal and shallow subtidal areas (<4 m depth), whereas nonforaging flocks often used deeper subtidal sites. Intertidal bedrock reefs adjacent to the bays were rarely used by foraging birds. Male Red-breasted Mergansers fed primarily on small, inshore fish, particularly grubby (*Myoxocephalus aenaeus*) and sandlance (*Ammodytes* spp.), but also obtained clam worms (Nereidae) and rock crabs (*Cancer irroratus*), indicating that they fed opportunistically on inshore benthivores. Males spent <25% of the diurnal period foraging and likely did not feed at night. The proportion of time spent feeding in the morning and evening was 3× greater than at mid-day, when flocks often loafed offshore. Feeding intensity in the first half of the flightless season (18%) was lower than that in the second half (30%). Feeding intensity was highest (>60%) when the tide was low in the morning and evening during the second half of the season. We suggest that flightless male Red-breasted Mergansers spent little time feeding because they devoted >50% of the diurnal period to energy inexpensive activities (e.g., resting) and used habitats with an

abundance of prey, allowing birds to meet the energetic and nutrient demands of wing and body molts.

INTRODUCTION

Male ducks (Anatinae) generally leave their mates prior to brood-rearing and gather for the wing molt, which renders birds flightless for 3-5 weeks (Salomonsen 1968, Hohman et al. 1992). While flightless, males replace most feathers of the wing, complete the prealternate body molt, and may initiate the prebasic body molt (Howell et al. 2003, Pyle 2005, Chapter 4). Feather replacement is a major metabolic event (Walsberg 1983) that involves increased protein synthesis and associated metabolic processes (King 1980, Murphy and King 1992). Thus, molt intensity and energetic and nutrient demands associated with feather replacement are likely highest during wing molt (Austin and Fredrickson 1987, Thompson and Drobney 1995). Flightless birds, however, are constrained to a local food supply and are unable to escape from predators by flight. Selection should therefore favor individuals that resume flight as quickly as possible, achieved by using undisturbed areas where food sources help meet costs of feather replacement (Bailey 1985, Thompson and Drobney 1996, Fox et al. 2008).

Flightless sea ducks (Mergini) often forage in shallow waters (Joensen 1973, Frimer 1995), which minimizes the energetic demands of diving (Wilson et al. 1992, Lovvorn 1994) or allows birds to obtain food without diving (Petersen 1980, Sjöberg 1988). These nearshore sites, however, may be at risk to avian predation (Fox and Mitchell 1997), so birds benefit by gathering into offshore rafts between feeding periods (Fox et al. 1994). Accordingly, differences in patterns of habitat use between foraging and nonforaging flocks may reflect strategies to maximize the efficiency of energy and nutrient intake and to minimize exposure to predation (Reed and Flint 2007).

In contrast to some tribes of Anatinae, patterns of habitat use among populations of flightless male sea ducks are relatively unknown (Hohman et al. 1992). The distribution of flightless Red-breasted Mergansers (*Mergus serrator*) has only been described in general terms at several palearctic sites (Dement'ev and Gladkov 1967, Joensen 1973, Kumari 1979). However, habitat requirements for molting Red-breasted Mergansers have not been identified (Salter et al. 1980, Sea Duck Joint Venture Management Board 2008), including in eastern Canada where >2500 subadult (second-year) and adult male Red-breasted Mergansers undergo wing molt and associated body molts at Anticosti Island, Québec (Chapter 4).

We used a combination of microhabitat measurements, time-activity budgets, and diet analyses to help understand patterns of habitat use by flightless male Red-breasted Mergansers at Anticosti Island. The objectives of our study were: 1) to measure microhabitat at sites used by flocks of males, 2) to compare microhabitat between foraging and nonforaging flock locations, 3) to examine the effects of tide, weather, time of day, and period of the flightless season on the proportion of time that males spent feeding, and 4) to examine prey items from esophagi of collected males. We predicted that foraging flocks would use shallow, nearshore sites, whereas nonforaging flocks (e.g., loafing, undergoing comfort movements) would use offshore areas with little exposure to avian predators.

METHODS

STUDY SITE

Anticosti Island is in the upper Gulf of St. Lawrence (Fig. 1). We studied flightless male Red-breasted Mergansers in three coastal bays at the western tip of the island (Fig. 1): Anse aux Fraises (49°49' N, 64°28' W), Baie Ste-Claire (49°54' N, 64°30' W), and Chute à Boulay (49°55' N, 64°26' W). The bays are bordered by intertidal bedrock reefs that are mostly unvegetated, although rockweeds (*Fucus* spp.) occur in poorly elevated areas (Guillemette and Guillemette 1983). The nearshore (<1 km) bottom of each bay slopes gently, substrate varies from sand to bedrock, and marine algae include rockweeds in the intertidal zone and kelps (*Laminaria* spp.) in the lower intertidal and subtidal areas. Tidal amplitude averaged 1.7 m (semi-diurnal; Canadian Tide and Current Tables 2006), and water-surface salinities were 27-29 psu (Fisheries and Oceans Atlantic Zone Monitoring Programme 2006). Adjacent shorelines accommodated spruce forests (*Picea* spp.) or meadows. Human activity at each site was generally limited to our research. Female Red-breasted Mergansers did not concentrate at our sites during male wing molt.

DATA COLLECTION

Microhabitat. We measured microhabitat at sites used by flocks of male Red-breasted Mergansers from 15 July to 10 September 2006, which coincided with the wing molt period in that year (Chapter 4). At each site, we randomly selected flocks throughout the diurnal period (06:00-21:00 EST) from a blind by directing a spotting scope into the bay and choosing the flock of Red-breasted Mergansers closest to the center of view (Bergan et al. 1989). Selected 'flocks' occasionally included lone males (<10% of observations). Selected flocks (hereafter including observations of lone males) were classified immediately as either 1) foraging, when at least the majority of birds swam with head submerged, dove, or consumed prey (Sjöberg 1988) or 2) nonforaging, when birds primarily rested (loafing, sleeping) or performed comfort movements (stretching, cleaning, preening, bathing; McKinney 1965). We censored flocks of swimming birds because they may have been moving between foraging and nonforaging sites, or were disturbed by our presence.

We recorded the position of selected flocks from shore with laser range-finding binoculars (Leica Vector 1000, Leica Geosystems AG, Heerbrugg, Switzerland), which calculated distance and azimuth between the observation site and selected flock (Guillemette and Larsen 2002). We recorded a position near the center of each flock and often obtained a second position to verify accuracy of the first. For the largest flocks (>100 birds), we recorded 2-3 positions throughout the flock. We reached the determined position(s) in a 2-m boat within 30 min of recording the position(s), and subsequently measured eight microhabitat features. We recorded water depth (±0.1 m) and water-surface temperature (±0.1 °C) with a portable depth-finder. Water depth was corrected by considering the time from when the position was recorded to when the measurement was obtained (≤0.4 m difference; Canadian Tide and Current Tables 2006). Tidal regime was classified as either intertidal/upper subtidal (0.0-3.0 m depth at low tide) or subtidal (>3.0 m; Canadian Tide and Current Tables 2006). We estimated light penetration as the largest proportion of water depth in which a submerged Secchi disk was visible from the boat. Distance to shore was the shortest distance (±0.1 m) to the high-tide line and was obtained with a global positioning system (GPS model eTrex, Garmin Ltd., Olathe, KS). We classified substrate type and estimated cover of submergent marine algae (5% increments taxon^{-1}) by SCUBA diving over a 20-m diameter area centered on the location. Substrate classes were 1) sand (1-2 mm particle size), 2) sand-rock (1->300 mm), 3) rock (>300 mm), 4) bedrock, and 5) sand-rock-bedrock (Hanson and Calkins 1996). To minimize disturbance to ducks, we tried to use the study sites equally, restricted measurement sessions to ≤3 days week^{-1}, and generally separated sessions at a site by ≥3 hr.

Time-activity budgets. We studied behavior of male Red-breasted Mergansers from 19 July to 5 September 2006 at the three sites, as well as at nearby Baie du Grand Makasti (49°56' N, 64°16' W) and Anse Gibbons (49°22' N, 63°29' W; Fig. 1). Flocks were selected randomly (see method above) and observed with a 60× spotting scope from blinds. We recorded activity from instantaneous scan samples during 10-min observation sessions distributed throughout the diurnal and crepuscular periods (Altmann 1974). During each session, we recorded activity of each individual in small flocks (≤5 birds) every 30 sec, but increased the interval between consecutive scans to >1 min for larger flocks. Adult males were not distinguished from subadult males because of subtle differences in plumage characteristics during wing molt (Titman 1999, Chapter

4). We studied a flock until it was out of viewing distance or for up to 3 hr (≤18 sessions). If a flock split into groups, we continued by randomly selecting a group. We assigned activity to one of seven categories: 1) foraging, 2) locomotion (primarily swimming), 3) resting, 4) comfort movement, 5) display (Salute-Curtsy, Head-Shake), 6) aggression (Crouch, Sprint), and 7) alert (McKinney 1965, Titman 1999). For foraging flocks, the number of submerged birds was the difference between total flock size (obtained before the scan) and the number of birds counted at the surface.

We divided the flightless season into early (19 July-12 August) and late periods (13 August-5 September; Chapter 4), and divided the diurnal period into morning (morning twilight-11:00), mid-day (11:01-16:00), and evening (16:01-evening twilight). We did not quantify activity at night. Prior to each 10-min session, we recorded wind velocity (km hr^{-1}), cloud cover as 0-50% or >51%, and precipitation as none, light, moderate, or heavy. We delineated tidal stage as rising, high, falling, or low (Canadian Tide and Current Tables 2006).

Diet and body mass. We collected subadult and adult male Red-breasted Mergansers in various stages of wing molt from 10 August to 12 September 2005 and 2006 by shooting from blinds or from a boat at the five sites, as well as at Baie McDonald (49°45' N, 63°03' W), Baie Caplan (49°44' N, 63°00' W), and Rivière Ste-Marie (49°40' N, 63°56' W; Fig. 1) to minimize disturbance to ducks at sites where habitat and behavioral data were collected. We flooded the upper digestive tract with a 95% ethyl alcohol solution to minimize postmortem digestion and autolysis (Swanson and Bartonek 1970), and weighed carcasses (±5 g). Within 10 hr of collection, contents of the esophagus (including proventriculus) were removed and preserved in 70-80% ethyl alcohol. We measured tarsal length (±0.1 mm) and recorded stage of wing molt by measuring the length (±0.1 mm) of a ninth primary from its point of emergence to the tip of the rachis (van de Wetering and Cooke 2000). We identified whole specimens and partially digested items from the esophagus. Examination of saccular otoliths with a dissecting microscope assisted with identification of partially digested fish (Campana 2004). Fish identification was occasionally confirmed by comparing morphological features with those of specimens at the Canadian Museum of Nature in Gatineau, Québec.

STATISTICAL ANALYSES

Microhabitat. For each flock with ≥2 positions, we calculated an average for each continuous microhabitat variable and if necessary, assigned a substrate class that reflected variability among the positions. We combined data from the three sites because sample sizes were low ($\bar{x} = 28$ flock locations site^{-1}). We tested for multicollinearity among continuous and binary microhabitat variables by examining tolerance statistics from a multiple linear regression model (Menard 2002). We collapsed each continuous microhabitat variable into a four-level categorical variable derived from quartiles of the data and used Kendall's τ-b to examine their level of correlation with substrate type. Water depth and tidal regime were correlated (Kendall's τ-b = 0.83, $P < 0.001$), so we excluded tidal regime from analysis because water depth was used to classify tidal regime. We retained all other variables (tolerances ≥0.65).

We used binary logistic regression to identify microhabitat features that best discriminated foraging and nonforaging flock locations (Hosmer and Lemeshow 2000). To control for season effects, we saved residuals from linear regressions with microhabitat as dependent variables and Julian date as the independent variable. We considered a three-step approach to select variables for the final logistic regression model (Hosmer and Lemeshow 2000). First, we fit univariate logistic regression models to examine the level of association between each microhabitat variable and flock type (foraging or nonforaging). We determined the significance of each estimated coefficient ($\hat{\beta}$) with likelihood ratio tests; variables with *P*-values of ≥0.25 were unimportant (Hosmer and Lemeshow 2000). Second, we fit an additive multivariate logistic regression model to the microhabitat variables remaining after step one (water depth, light penetration, water-surface temperature, distance to shore). We assessed the importance of each variable in the model by examining significance of $\hat{\beta}$ with Wald statistics; variables with *P*-values of ≥0.10 were not considered in a revised model (Menard 2002). Finally, we compared the revised model (water depth) with 1) the original multivariate model, 2) all single and multiple variable combinations of the original multivariate model, and 3) an additive multivariate model with water depth and the variables eliminated during the first step (substrate class, % vegetative cover). These comparisons ensured that the final model (water depth) contained the important variables (Hosmer and Lemeshow 2000).

We tested for linearity in the logit of water depth by creating a four-level categorical variable derived from quartiles of the data (Hosmer and Lemeshow

2000). We fit the categorical variable to a univariate logistic regression model and linearity was confirmed by plotting $\hat{\beta}_{\text{depth}}$ with the midpoint of data for each category ($r^2 = 0.98$, $F_{1,2} = 122.3$, $P = 0.008$). We assessed goodness-of-fit of the final model with the Hosmer-Lemeshow decile of risks test (Hosmer and Lemeshow 2000). We inspected the Receiver Operating Characteristic (ROC) curve to derive an optimized cut-off (e.g., maximizing sensitivity and specificity) for classification of predicted probabilities. We examined whether the proportion of correctly classified cases exceeded chance alone by evaluating the significance of Cohen's Kappa (κ) statistic with a z-test (Titus et al. 1984).

For each marine algae taxon, we calculated frequency of occurrence as the proportion of flock locations associated with the taxon, and percent composition as the proportion of cover over all locations. We compared percent occurrence and composition of each taxon between foraging and nonforaging flock locations with z-tests for two proportions (Zar 1996).

Time-activity budgets. We used regression trees (CART Pro 6.0; Salford Systems, San Diego) to help identify factors contributing to variation in the proportion of time that male mergansers spent foraging during 10-min observation sessions (Breiman et al. 1984, Steinberg and Colla 1995). Independent variables were period of the flightless season, diurnal period, cloud cover, and tidal stage. Wind velocity and precipitation were excluded because few observations were recorded when winds were >20 km hr^{-1} or rain was moderate and heavy. We grew regression trees by iteratively splitting nodes to minimize within node sum of squares about group means (Breiman et al. 1984). To avoid spurious splits, node splitting stopped when a parent node had <55 cases and a child node had <10 cases (O'Connor 2008). For each tree size (defined by # of terminal nodes), we identified the most parsimonious tree by calculating an error-complexity measure (De'ath and Fabricius 2000). We chose an optimal tree from the sequence by performing 50 ten-fold cross-validations and selecting the most frequently occurring tree size within 1 SE of the tree with the minimum cross-validated error estimate (Breiman et al. 1984).

Diet and body mass. For each prey taxon, we calculated frequency of occurrence as the proportion of esophagi that contained the taxon, and average percent composition. We examined the relationship between corrected body mass (mass/tarsal length; van de Wetering and Cooke 2000) and length of the ninth primary using a linear regression model. We compared corrected body mass of males in wing molt with that of four preflightless adult males collected at Anticosti Island from 15 July to 19 August 2006. Analyses were performed with SPSS 11.5 (SPSS Inc., Chicago, IL). We set significance levels at $P < 0.05$, and unless otherwise stated, we present values as means ± 95% confidence intervals (CI).

RESULTS

MICROHABITAT

We measured microhabitat at 83 flock locations ($\bar{x} = 39$ birds flock^{-1}, 95% CI: 26-52, median = 14, range 1-322). Flocks used clear, shallow waters (≤12 m) near shore (<850 m), and often over a sand-rock substrate with stands of submergent algae (Table 1). Foraging flocks generally used intertidal and upper subtidal waters whereas nonforaging flocks often frequented subtidal areas (Table 1). Accordingly, sites of foraging flocks were generally half as deep (final logistic regression model: $\chi^2_1 = 13.2$, $P < 0.001$; Table 2) and closer to shore than sites used by nonforaging flocks (Table 1). Over 75% of foraging flocks were at sites where water depths were <4 m (Fig. 2). Males foraged along emerged shorelines and exposed rocks, but rarely fed over intertidal reefs adjacent to the bays. Thirty percent of nonforaging flocks were in shallow waters (<2.5 m; Fig. 2). These birds were often resting and preening around foraging sites or on nearby shores and exposed rocks for short periods (<0.5 hr) between feeding bouts.

Large kelps were at nearly 50% of all flock locations (Table 3). The proportion of foraging sites with rockweeds was greater than that for nonforaging locations (Table 3). The proportion of foraging sites with sea colander (*Agarum cribrosum*) and edible kelp (*Alaria* spp.) was smaller than that for nonforaging sites (Table 3). These differences reflected the distribution of each algae taxon.

TIME-ACTIVITY BUDGETS

We observed the diurnal behavior of male Red-breasted Mergansers for 54.2 hr (325 sessions). Flock size averaged 38 birds (95% CI: 26-50, median = 13, range 2-242). Males alternated between periods of loafing ($\bar{x} = 30\%$ of time, 95% CI: 26-33%), comfort movements ($\bar{x} = 20\%$, 95% CI: 18-23%), locomotion ($\bar{x} = 26\%$, 95% CI: 23-29%), and foraging ($\bar{x} = 23\%$, 95% CI: 20-27%). Little time (<1%) was spent displaying, alert, or exhibiting aggression toward other males.

Proportion of time spent foraging in the morning and evening was 2.5× and 4× greater, respectively, than at mid-day (Fig. 3), when flocks typically loafed and performed comfort movements offshore (Table 4). Feeding intensity in the first half of the flightless season was lower than that in the second half (Table 4). Feeding intensity was highest (>60%) when the tide was low in the morning and evening during the second half of the season (Fig. 3).

DIET AND BODY MASS

We collected 39 subadult and adult male Red-breasted Mergansers in wing molt, one flightless hatch-year male, and one flightless female. Subadult and adult males fed primarily on small, inshore fish (~80% of total prey items). Nearly 55% of 30 esophagi with prey contained grubby (*Myoxocephalus aenaeus*) and 40% had sandlance (*Ammodytes* spp.; Table 5). Clam worm (Nereidae) jaws were found in 40% of esophagi, but we likely underestimated the composition of Nereidae because we assumed each jaw should be paired with another in the esophagus (Table 5). Isopods (*Idotea baltica*) and amphipods (*Gammarus* spp.) were in at least nine esophagi, but their importance to merganser diet is questionable given that their remains were always associated with partially digested grubby, which preyed on the crustaceans (S. R. Craik, pers. obs.).

Body mass of 31 molting males averaged 1133 g (95% CI: 1101-1166, range 955-1335 g). Corrected body mass increased with greater ninth primary length ($r^2 = 0.20$, $F_{1,23} = 5.7$, $P = 0.03$), although our sample did not include birds with short primaries (0-40 mm; Fig. 4).

DISCUSSION

HABITAT USE

Habitat use by Red-breasted Mergansers is influenced by the availability of shallow wetlands with clear waters and abundant small fish (<15 cm; Bengtson 1971, Råd 1980, Chapter 3). At Anticosti Island, flocks of flightless male Red-breasted Mergansers used intertidal and shallow subtidal habitats (≤12 m) consisting of clear waters over a sand-rock substrate and stands of submergent algae. Little is known of the ichthyological communities in the shallow waters along Anticosti Island (G. Laprise, pers. comm.), but nearshore marine habitats are typically dominated by small fish in summer (Macdonald et al. 1984). We found that Red-breasted Mergansers foraged on inshore fish, particularly grubby and sandlance. Nearly 55% of esophagi contained the remains of small grubby (e.g., young-of-the-year; Roseman et al. 2005), which concentrate in shallow, coastal waters (Lazzari et al. 1989). Small sculpins appear to be an important prey item for coastal Red-breasted Mergansers (Munro and Clemens 1939), likely because they are often among the most common fish near shore (Macdonald et al. 1984, Roseman et al. 2005). Sandlance are abundant in summer along sand-rock shorelines (Robards et al. 1999), and burrowing densities in the Gulf of St. Lawrence may reach >250 individuals $(m^2)^{-1}$ (Saint-Pierre 1985).

Although fish were among the most common items captured by male Red-breasted Mergansers, we found evidence of grubby, clam worms, rock crabs (*Cancer irroratus*), or caridean shrimp (Hippolytidae) in >75% of esophagi, suggesting that mergansers feed opportunistically on small benthic animals. Accordingly, we observed males searching for prey while swimming with head submerged and randomly probing substrates while moving along shorelines (Munro and Clemens 1939, Sjöberg 1988). In the Gulf of St. Lawrence, the distribution of small, inshore, benthic fish, polychaetes, and crustaceans is associated with sand-rock substrate and marine algae (e.g., Scarratt and Lowe 1972, Miron and Desrosiers 1990), because rock crevices and vegetation serve as cover (Stott and Olson 1973) and sand provides burrowing habitat (Miron and Desrosiers 1990). Stott and Olson (1973) related the inshore distribution of wintering Red-breasted Mergansers in New England to the availability of irish moss (*Chondrus crispus*), which provides cover for fish and invertebrate prey at shallow depths (<10 m), but is nearly absent farther offshore. Likewise, Red-breasted Mergansers at Anticosti Island rarely foraged over the relatively featureless intertidal reefs as they likely support a lower abundance of fish and invertebrates than in adjacent bays with a sand-rock substrate (Guillemette and Guillemette 1983).

By foraging in shallow waters, Red-breasted Mergansers minimize the aerobic demands of diving (Lovvorn 1994) and heat loss from compression of air in feathers while underwater (Wilson et al. 1992). Reducing thermostatic costs of diving may be important for flightless Red-breasted Mergansers in the cold waters of the upper Gulf of St. Lawrence since plumage insulation is partially disrupted during wing and body molts (Schieltz and Murphy 1997, Chapter 4). Among Tufted Ducks (*Aythya fuligula*), diving costs in waters at <10°C are nearly twice as great as in waters of >20°C (de Leeuw 1996). Water-surface temperatures at Anticosti Island were <10°C by mid-August and often dropped to 5-6°C during the period of wing molt. Male Red-breasted Mergansers at Anticosti Island, however, may minimize plumage disruption during wing molt by staggering body feather replacement (Chapter 4). Furthermore, in the shallowest waters (<30 cm), Red-breasted Mergansers often obtain prey while at the surface, which requires less energy than diving (Sjöberg 1988).

Red-breasted Mergansers aggregated into rafts and remained offshore during periods of nonforaging (e.g., mid-day), when inter-bird distances were generally smaller than while foraging. Offshore resting bouts have been reported for flightless male Surf Scoters (*Melanitta perspicillata*; O'Connor 2008) and King (*Somateria spectabilis*; Frimer 1994) and Common (*S. mollissima*; Frimer 1995) eiders, as well as for wintering Steller's Eiders (*Polysticta stelleri*; Fox and Mitchell 1997) and Harlequin Ducks (*Histrionicus histrionicus*; Reed and Flint 2007), suggesting a common behavior that may serve to reduce predation pressure (Fox et al. 1994, Fox and Mitchell 1997). Bald Eagles (*Haliaeetus leucocephalus*) are common summer residents at Anticosti Island (Bird and Henderson 1996), where they are suspected of preying on sea ducks (Guillemette and Guillemette 1983). Eagle predation was not observed during our study, but their flights along shorelines induced flightless sea ducks to move farther offshore. By rafting offshore, flightless Red-breasted Mergansers thereby lower their risk of predation since Bald Eagles often hunt near shore (Buehler 2000). Resting birds may also prefer offshore sites because turbulence from wave action and tidal currents is often highest near shore (Guillemette and Himmelman 1996).

TIME-ACTIVITY BUDGETS

Male Red-breasted Mergansers foraged primarily in the morning and evening, particularly near sunrise and sunset. Mergansers (*Mergus* spp.) are capable of synchronizing feeding patterns with activity of their fish prey (Sjöberg 1989). In a Swedish river, Red-breasted Mergansers exhibit peaks in upstream flight activity near sunrise and sunset, which may be influenced by diurnal movements of three-spined stickleback (*Gasterosteus aculeatus*), an important prey item (Sjöberg 1985). Sandlance are vulnerable to predation around sunrise and sunset, when they move between offshore schooling sites and nighttime burrows near shore (Robards et al. 1999). Predatory fish attack partially buried sandlance during changeovers periods (Hobson 1986). Thus, intense foraging by Red-breasted Mergansers during periods of diminished daylight at Anticosti Island may be driven by the abundance of sandlance around burrowing sites. Grubby likely exhibit diurnal peaks in movements around sunrise and sunset (M. Lazzari, pers. comm.), although they only move short distances (Nickell and Sayer 1998), and are captured by flightless male Red-breasted Mergansers throughout the day (S. R. Craik, pers. obs). Wintering Red-breasted Mergansers in the Gulf of Mexico forage at similar intensities throughout the diurnal period, but they feed primarily on sedentary benthivores (e.g., gulf toadfish *Opsanus beta*; Bowles 1980).

Red-breasted Mergansers aggregated offshore within 30 min after sunset, and approached inshore feeding sites during morning twilight, suggesting males did not feed at night. Mergansers may therefore fast for up to 12 hr at Anticosti Island, and respond by feeding in the morning and evening to help meet energetic and nutrient demands of feather replacement and maintenance activities (K. Sjöberg, pers. comm.). Similar bimodal peaks in foraging activity occur among flightless male Surf Scoters and King Eiders that forage on sedentary benthivores in subtidal areas, and independent of tide level (Frimer 1994,. Male Red-breasted Mergansers foraged regardless of tidal stage, but their feeding intensity was greatest during a low tide in the evening. Greater investment in foraging at low water levels may reflect easier access to prey (Petersen 1980).

Foraging intensity in the second half of the flightless season was nearly twice as great as that in the first half, which was consistent with greater body mass among birds collected during the later stages of wing molt. Increased foraging during the later period of molt may be associated with hypertrophy of pectoral muscles (Bailey 1985) and accretion of lipids for thermoregulation (A. D. Fox, pers. comm.) and preparation for fall migration (Thompson and Drobney 1996). Most male Red-breasted Mergansers that undergo wing molt at Anticosti Island winter in other regions as only small numbers of mergansers are found along the island in winter (<200 birds; CWS-QC helicopter-survey data, M. Robert). Red-breasted Mergansers with long growing primaries were likely able to fly (>115 mm; Chapter 4), and our time-activity data may have included some birds that had regained flight (e.g., after 1 September). Nevertheless, body mass increased with stage of wing molt for males with ninth primary lengths of <110 mm. Also, the proportion of time spent foraging during the first portion of the second half of the flightless season (31%; 20-28 August) was similar to that during the second portion (28%; 29 August-5 September), suggesting weight gain and increased foraging intensity were associated with the later stages of flightlessness. Greater body mass may prolong the flightless period (Austin and Fredrickson 1987), but this may not have negative consequences for Red-breasted Mergansers molting in marine habitats where predation and other disturbances are likely low (Thompson and Drobney 1996).

Feeding intensity during wing molt was low in comparison to other nonbreeding periods for Red-breasted Merganser (winter: 34-80% of diurnal period; Titman 1999). Mobilization of lipid reserves, particularly during the early stages of wing molt, may allow some flightless Anatinae to reduce feeding (Hohman et al. 1992). We were unable to examine body mass during early wing molt. However, male Red-breasted Mergansers may have spent relatively little time feeding because they 1) devoted >50% of the diurnal period, and likely the entire night, to inexpensive activities (e.g., resting; Bailey 1985, Austin and Fredrickson 1987) and 2) used habitats with abundant food (Hohman et al. 1992, Fox et al. 2008). Males increased body mass when annual molt intensity is relatively high (Thompson and Drobney 1995, Chapter 4), suggesting these birds had little problem obtaining exogenous sources of energy and nutrients. Dietary protein, however, may be partially supplemented by catabolized pectoral muscle (Bailey 1985, Austin and Fredrickson 1987, but see Ankney 1979), and changes to digestive organs may increase alimentary efficiency and allow flightless waterfowl to reduce feeding activity (Thompson and Drobney 1996).

CONCLUSIONS

We provide the first information on patterns of habitat use among flightless male Red-breasted Mergansers. Patterns of use, however, may not reflect optimal choice(s) of habitat(s), and do not indicate whether habitat use is adaptive (Clark and Shutler 1999). Nevertheless, we advocate supplementing habitat measurement with time-activity budgets and diet analyses to interpret patterns of habitat use among nonbreeding Anatinae. Identifying factors affecting survival of flightless male Red-breasted Mergansers will provide a first step in understanding the processes that influence habitat use.

Male Red-breasted Mergansers relied on foods consumed while molting to help meet the energetic and nutrient demands of wing and body molts. However, it was unknown whether endogenous protein, lipids, and minerals were catabolized during the flightless period, and whether their mobilization influences feeding intensity and patterns of habitat use. Energetic and nutrient reserve dynamics among molting Red-breasted Mergansers warrant further attention.

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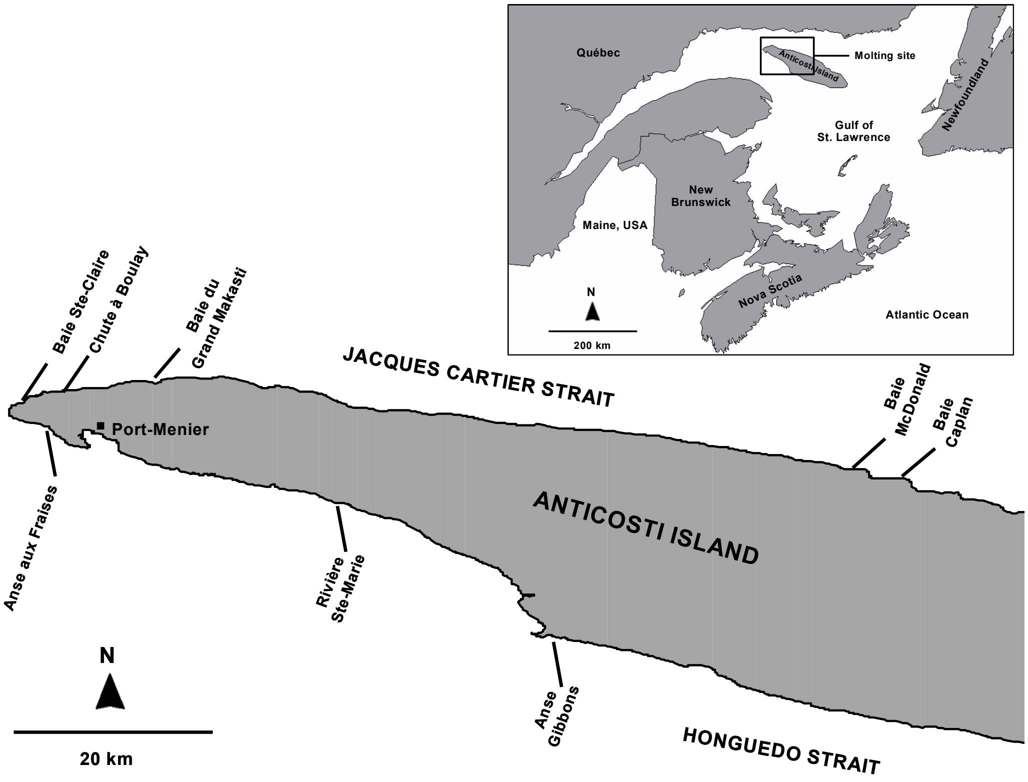

FIGURE 1. Study sites at Anticosti Island, Québec, 2005 and 2006.

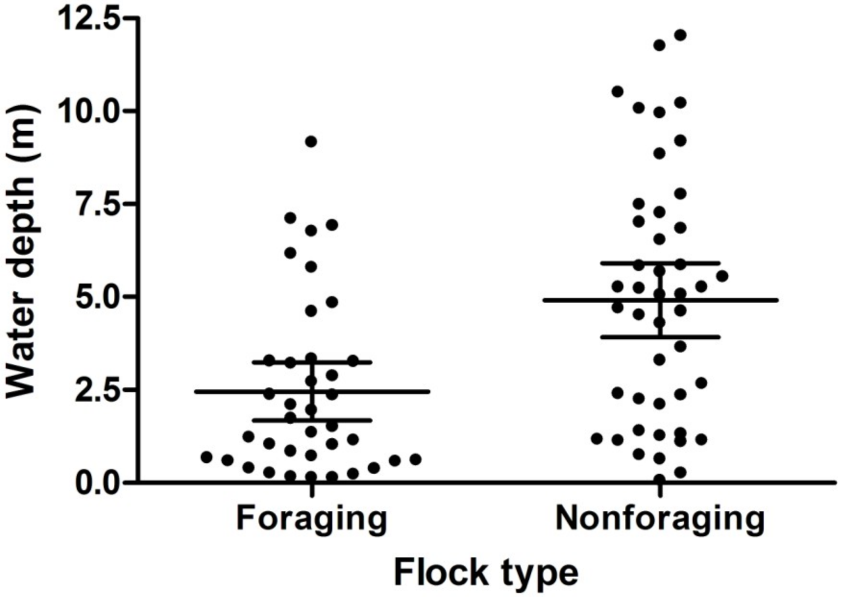

FIGURE 2. Water depths (m; x̄ ± 95% CI) at sites used by flocks of foraging and nonforaging male Red-breasted Mergansers (*Mergus serrator*) molting at Anse aux Fraises, Baie Ste-Claire, and Chute à Boulay, Anticosti Island, Québec, 2006.

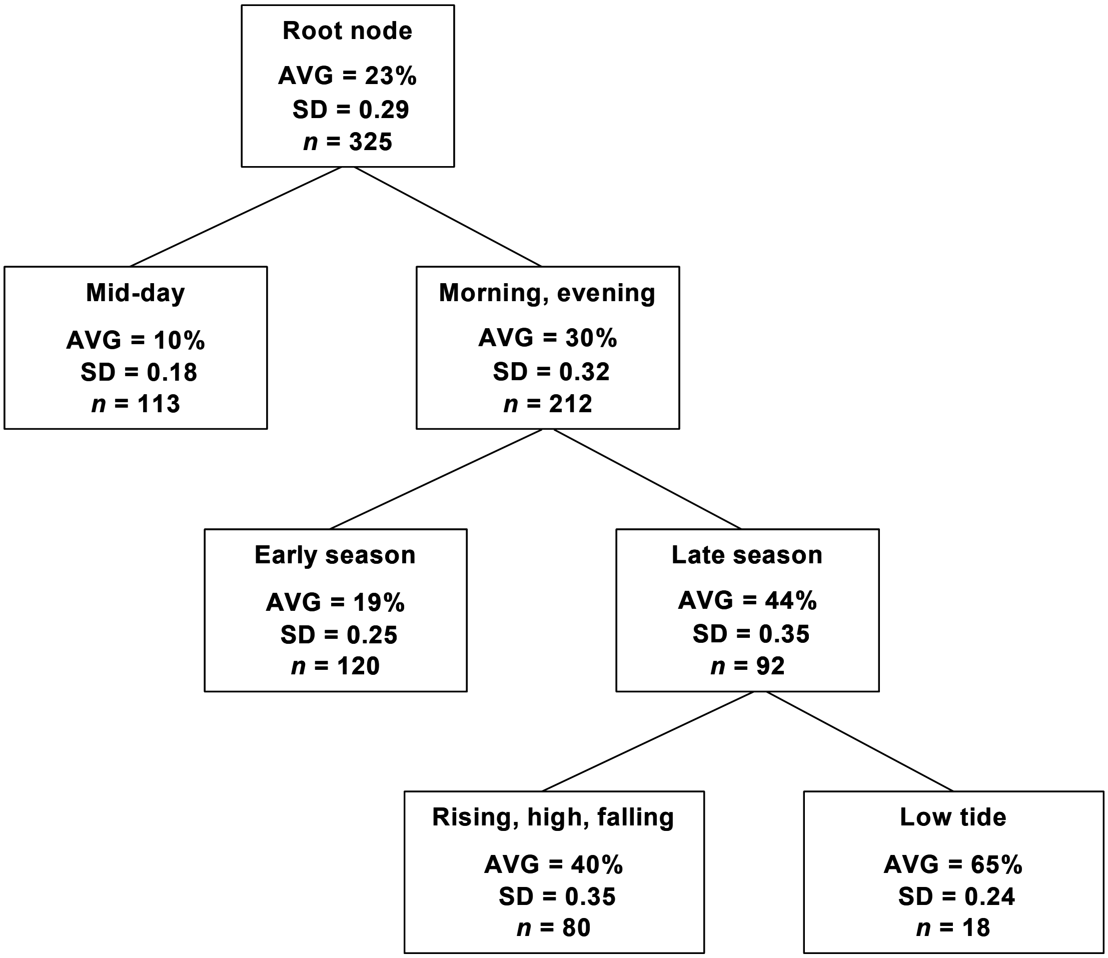

FIGURE 3. Regression tree explaining variation in the amount to time spent foraging during 10-min diurnal observation sessions for male Red-breasted Mergansers (*Mergus serrator*) molting at Anticosti Island, Québec, 2006. Each node contains the average proportion of time foraging (AVG) and standard deviation (SD) for observations (*n*) included in the node. Branching to the right indicates greater foraging intensities.

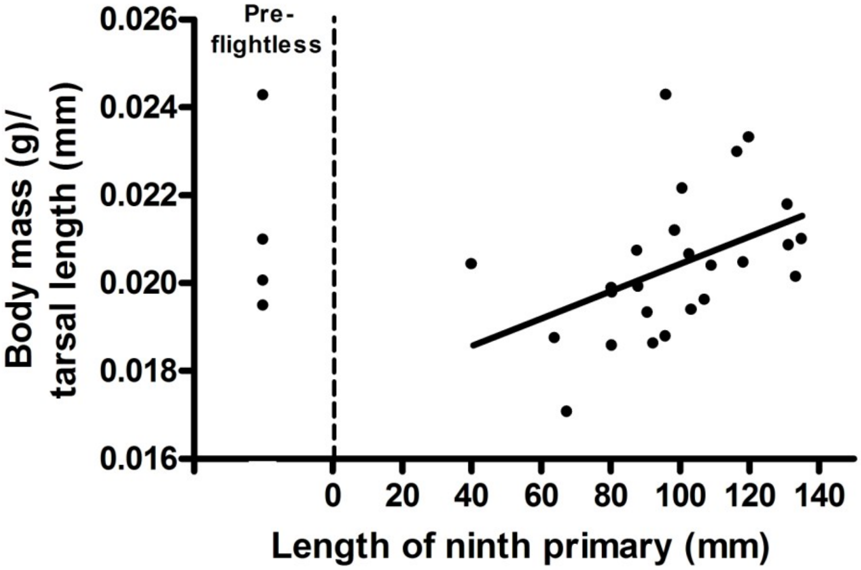

FIGURE 4. Relationship between corrected body mass and length of ninth primary (mm) for male Red-breasted Mergansers (*Mergus serrator*) molting at Anticosti Island, Québec, 2005 and 2006. Corrected body mass is shown for four preflightless adult male Red-breasted Mergansers.

TABLE 1. Microhabitat characteristics ($\bar{x}$ ± 95% CI) at sites used by flocks of male Red-breasted Mergansers (*Mergus serrator*) molting at Anse aux Fraises, Baie Ste-Claire, and Chute à Boulay, Anticosti Island, Québec, 2006. Sample sizes are in parentheses.

Habitat feature	All flocks (*n* = 83)	Foraging flocks (*n* = 38)	Nonforaging flocks (*n* = 45)
Water depth (m)	3.8 ± 0.7	2.5 ± 0.8	4.9 ± 1.0
Range	0.1-12.0	0.1-9.2	0.1-12.0
Proportion of sites by tidal regime			
intertidal/upper subtidal (≤3 m)[a]	0.57	0.76	0.40
subtidal (>3 m)[a]	0.43	0.24	0.60
Light penetration (% of depth)	98 ± 2	100 ± 0	97 ± 3
Range	50-100	100-100	50-100
Water-surface temperature (°C)	12.3 ± 0.8	12.6 ± 1.2	12.1 ± 1.2
Range	5.5-21.0	6.0-21.0	5.5-19.0
Distance to shore (m)	290.1 ± 39.2	244.9 ± 50.3	328.3 ± 57.8
Range	16.5-823.0	16.5-666.0	55.3-823.0
Proportion of sites by substrate class[b]			
Sand	0.00	0.00	0.00
sand-rock	0.62	0.71	0.54
Rock	0.05	0.03	0.07
Bedrock	0.15	0.13	0.16
sand-rock-bedrock	0.18	0.13	0.23

TABLE 1 (continued). Microhabitat characteristics ($\bar{x}$ ± 95% CI) at sites used by flocks of male Red-breasted Mergansers (*Mergus serrator*) molting at Anse aux Fraises, Baie Ste-Claire, and Chute à Boulay, Anticosti Island, Québec, 2006. Sample sizes are in parentheses.

Habitat feature	All flocks (*n* = 83)	Foraging flocks (*n* = 38)	Nonforaging flocks (*n* = 45)
Vegetative cover (%)[b]	53 ± 7	54 ± 11	51 ± 9
range	0-100	0-100	0-100

[a] Water depth at low tide.

[b] Obtained from within a 20-m diameter area centered on each location.

TABLE 2. Parameters of the final logistic regression model discriminating foraging and nonforaging flock locations of male Red-breasted Mergansers (*Mergus serrator*) molting at Anse aux Fraises, Baie Ste-Claire, and Chute à Boulay, Anticosti Island, Québec, 2006. From 38 foraging and 45 nonforaging flocks. The model fit the data well (Hosmer-Lemeshow test $\chi^2_8 = 5.2$, $P = 0.74$).

Variable	$\hat{\beta}$	95% CI ($\hat{\beta}$)	Wald χ^2_1	P	Odds ratio ($e^{\hat{\beta}}$)	95% CI ($e^{\hat{\beta}}$)
Intercept	0.21	-0.26-0.68	0.7	0.39	-	-
Water depth	1.03	0.43-1.63	11.2	0.001	2.80[a]	1.53-5.13

70% of cases classified correctly ($\kappa = 0.40$, 95% CI: 0.30-0.50, $z = 3.6$, $P < 0.001$; 60% cut-off).

[a] Odds of encountering a nonforaging flock for each unit of increase of water depth.

TABLE 3. Comparisons of frequency of occurrence and percent composition of marine algae between foraging and nonforaging flock locations of male Red-breasted Mergansers (*Mergus serrator*) molting at Anse aux Fraises, Baie Ste-Claire, and Chute à Boulay, Anticosti Island, Québec, 2006.

	Frequency of occurrence (%)			Percent composition		
Taxon	Foraging *n* = 37	Nonforaging *n* = 44	*P* (*z*-test)	Foraging *n* = 34	Nonforaging *n* = 43	*P* (*z*-test)
Brown algae						
Fucus spp.	41	18	0.06	15	16	0.90
Desmarestia viridis	8	14	0.39	5	3	0.50
Dictyosiphon foeniculaceus	22	11	0.18	7	3	0.41
Chordaria flagelliformis	19	14	0.55	7	7	1.00
Chorda filum	5	0	0.14	<1	0	0.77
Laminaria spp.	57	43	0.24	46	35	0.33
Agarum cribrosum	11	50	<0.001	13	27	0.13
Alaria spp.	0	23	0.002	0	4	0.23

TABLE 3 (continued). Comparisons of frequency of occurrence and percent composition of marine algae between foraging and nonforaging flock locations of male Red-breasted Mergansers (*Mergus serrator*) molting at Anse aux Fraises, Baie Ste-Claire, and Chute à Boulay, Anticosti Island, Québec, 2006.

	Frequency of occurrence (%)			Percent composition		
Taxon	Foraging *n* = 37	Nonforaging *n* = 44	*P* (*z*-test)	Foraging *n* = 34	Nonforaging *n* = 43	*P* (*z*-test)
Green algae						
Ulva lactuca	11	7	0.53	2	2	1.00
Total				95	97	

TABLE 4. Proportion of time (x̄ ± 95% CI) that male Red-breasted Mergansers (*Mergus serrator*) spent foraging, swimming, loafing, and in comfort movements throughout the flightless season and diurnal period at Anticosti Island, Québec, 2006. Other activities were not included given their low frequency of occurrence (<1% of diurnal period). Number of 10-min observation sessions are in parentheses.

	Activity			
Time period	Foraging	Locomotion	Loafing	Comfort
Early molt[a] (177)	0.18 ± 0.04	0.31 ± 0.05	0.28 ± 0.05	0.23 ± 0.04
Late molt[b] (148)	0.30 ± 0.06	0.21 ± 0.04	0.31 ± 0.06	0.18 ± 0.04
Mann-Whitney U test	$P = 0.005$	$P = 0.004$	$P = 0.43$	$P = 0.02$
Morning[c] (129)	0.25 ± 0.06	0.20 ± 0.04	0.33 ± 0.06	0.21 ± 0.04
Mid-day[d] (115)	0.10 ± 0.04	0.35 ± 0.06	0.34 ± 0.07	0.20 ± 0.04
Evening[e] (81)	0.39 ± 0.07	0.24 ± 0.05	0.19 ± 0.06	0.19 ± 0.05
Kruskall-Wallis H test	$P < 0.001$	$P = 0.002$	$P = 0.01$	$P = 0.51$

[a] 19 July-12 August.

[b] 13 August-5 September.

[c] Morning twilight-11:00 EST.

[d] 11:01-16:00.

[e] 16:01-evening twilight.

TABLE 5. Prey items recovered in the esophagi of male Red-breasted Mergansers (*Mergus serrator*) molting at Anticosti Island, Québec, 2005 and 2006. From 30 subadult and adult males.

				Fish length[b]/carapace width[c] (mm)		
Taxon	*n*	Frequency of occurrence (%)	Average % composition (± 95% CI)	Mean[d]	95% CI	Range
Fish						
Myoxocephalus aenaeus	113	53	29.1 ± 13.2	43.7 (19)	3.5	30.1-57.9
Ammodytes spp.	71	43	35.9 ± 16.8	-	-	-
Gasterosteus spp.	5	17	4.6 ± 4.6	59.9 (1)	-	-
Pleuronectes americanus	1	3	0.2 ± 0.4	94.6 (1)	-	-
Crustaceans						
Cancer irroratus	20	20	3.7 ± 4.5	28.3 (12)	4.9	16.7-40.1
caridean shrimp (Hippolytidae)	6	7	3.9 ± 6.9	-	-	-
Gammarus spp.	-[a]	-	-	-	-	-
Idotea baltica	-[a]	-	-	-	-	-
Polychaetes						
clam worm (Nereidae)	33	40	22.0 ± 13.8	-	-	-
Gastropods						
Littorina obtusata	1	3	0.2 ± 0.4	-	-	-
Bivalves						
Mytilus edulis	1	3	0.3 ± 0.7	-	-	-

[a] Frequency of occurrence and percent composition in merganser diet unknown because the species was preyed on by *Myoxocephalus aenaeus*.

[b] Distance from the most anterior part of the head to the tip of the longest caudal fin ray.

[c] For *Cancer irroratus.*

[d] Sample sizes in parentheses.

CONNECTING STATEMENT 5

In the previous chapters, I reviewed literature on habitat selection theory and habitat requirements of breeding and molting Anatinae, provided rationale for my study, outlined my objectives and hypotheses, and presented results from my research program. In this chapter, I summarize key findings, present final conclusions, identify priorities for future research, and describe the original aspects of my work.

CHAPTER 6

SUMMARY, CONCLUSIONS, AND STATEMENT OF ORIGINALITY

SUMMARY

I studied habitat use by Red-breasted Mergansers (*Mergus serrator*) breeding at Kouchibouguac National Park, New Brunswick, and molting at Anticosti Island, Québec, in 2002-2006. Nearly all Red-breasted Merganser nests on Tern Islands were in dense stands of marram grass (*Ammophila breviligulata*), whereas sparser vegetation types were avoided. This was consistent with observations that overhead concealment and vegetation density and height at nests were greater than that at random sites. These habitat features varied little between successful and unsuccessful nests because relatively unconcealed nests were not depredated more often than concealed nests. Marked broods originating from Tern Islands crossed Saint-Louis Lagoon toward continental estuarine intertidal and tidal stream rearing habitats. Broods also used shallow estuarine subtidal, barrier island intertidal, and saltmarsh wetlands, but avoided marine and river habitats.

I estimated that male Red-breasted Mergansers were flightless for 30-33 days at Anticosti Island, and that most males were in wing molt between late July and early September, indicating a synchronous molt. Males used clear coastal bays with a sand-rock substrate and submergent algae throughout wing molt, but were generally restricted to the shallowest nearshore areas while feeding (<4 m depth). Foraging was relatively intense early in the morning and in the evening, which may have been influenced by the crepuscular activity of merganser prey (e.g., sandlance *Ammodytes* spp.).

CONCLUSIONS AND PRIORITIES FOR FUTURE RESEARCH

During each stage of the annual cycle, ducks (Anatinae) make decisions regarding the use of habitats. I focused on examining patterns of habitat use by Red-breasted Mergansers throughout the interval of nesting to brood-rearing, which includes the male flightless period. I demonstrated that these birds exhibit habitat selection in the Gulf of St. Lawrence, and specifically, that barrier island-lagoon systems in eastern New Brunswick and coastal bays at Anticosti Island provide important merganser breeding and molting habitats, respectively. The following sections provide final conclusions and information needs specific to nesting, brood-rearing, and flightless Red-breasted Mergansers:

NESTING ECOLOGY

Nest success of Red-breasted Mergansers breeding on Tern Islands was higher than that reported for many other duck populations (Sargeant and Raveling 1992) because merganser nests were placed on islands without mammalian egg predators and with Common Terns (*Sterna hirundo*) that actively defend their nests from avian predators. Also, I suspect that at least some merganser nests were renests (see Bengtson 1972), so my estimates of nest success likely underestimated hen success (Johnson et al. 1992), although the extent of this discrepancy on Tern Islands remains unclear. Renesting propensity is an important determinant of the level of nest success necessary to sustain a breeding population (Klett et al. 1988). Thus, renesting potential among nearctic Red-breasted Mergansers warrants attention.

Nest desertion is a major component of the nesting ecology of Red-breasted Mergansers on Tern Islands. Between 40 and 45% of nests were abandoned in each year of my study, and >30% of nests were abandoned annually on Tern Islands in 2007 (32%) and 2008 (36%; R. D. Titman, unpubl. data). My observational study was unsuccessful at identifying the precise cause of nest desertion for most nests, although intraspecific nest parasitism, female harassment by conspecifics and Common Terns, and investigator disturbance were likely responsible for some abandonment. An experimental investigator disturbance approach (e.g., Bolduc and Guillemette 2003) would be a first step in examining the cause-and-effect relationships among abandoned merganser nests on Tern Islands because nests deserted from natural causes would be isolated. The relatively low success of the earliest dump nests suggests that a heavily parasitized nest plays an important role on a female's decision to desert her nest.

The combination of favorable nesting conditions on Tern Islands (e.g., extreme tern densities, controlled human access) are unlikely to be encountered by Red-breasted Mergansers breeding elsewhere in the Gulf of St. Lawrence. Vital rates and factors influencing nest success and nest-site selection for Red-breasted Mergansers outside of Kouchibouguac National Park, such as in the Miramichi River Estuary and Neguac region (Erskine 1992), are needed to better understand the nesting ecology of mergansers in the Gulf of St. Lawrence.

BROOD ECOLOGY

Selection of continental estuarine intertidal flats and tidal streams by Red-breasted Merganser broods at Kouchibouguac National Park presumably evolved through survival and fitness benefits associated with these habitats. My efforts to determine merganser duckling and brood survival at Kouchibouguac National Park, however, were unsuccessful because of poor retention of duckling markers (e.g., nape tags applied on eight broods in 2003 and 2004). Given the importance of variation in duckling survival rates to duck population growth (Hoekman et al. 2002), understanding the factors potentially affecting duckling and brood survival, including choice of habitat, predation, weather, and post-hatch brood amalgamation, should be kept a priority for future merganser research. Accordingly, a novel duckling marker technique will be necessary to examine survival throughout the rearing period.

Tidal stream and saltmarsh habitats were more important for age class I broods than for age classes II and III, which often frequented more exposed habitat types. It is unclear whether these age-related shifts were driven by nutritional or behavioral requirements, the distribution of food resources, or by a combination of factors. However, I suspect that newly hatched merganser ducklings benefited by loafing among the protective features associated continental estuarine intertidal, tidal stream, and saltmarsh habitats, particularly stands of saltwater cordgrass (*Spartina alterniflora*). Time-activity budgets would be particularly useful for identifying important activities performed in each habitat type for different brood age classes, and under various environmental conditions.

ECOLOGY OF FLIGHTLESS INDIVIDUALS

I complemented information on microhabitat characteristics at sites used by flightless male Red-breasted Mergansers at Anticosti Island with time-activity and stomach content data, which resulted in a much clearer interpretation of habitat requirements than if I had relied solely on information from microhabitat measurements. Time-activity information identified conditions at foraging habitats (time of day, tidal stage), and confirmed merganser use of intertidal and shallow subtidal habitats. By considering the ecology of merganser food items, I was able to hypothesize that the relatively intense foraging around sunrise and sunset was influenced by peaks in shallow-water activity of some prey species. Accordingly, I encourage waterfowl biologists to consider multiple sources of data, including time budget and diet, when studying habitat requirements. Nevertheless, we know little about patterns of macrohabitat use among flightless male Red-breasted Mergansers. Habitat requirements at multiple spatial scales should be understood before the suitability of coastal sites for molting mergansers is evaluated.

I provide evidence that male Red-breasted Mergansers gain body mass while flightless, suggesting that some sea ducks (Mergini) using open water habitats may have little difficulty in meeting the energetic and nutrient demands of molt (Fox et al. 2008) because these birds use habitats with little predation pressure and abundant food resources (Thompson and Drobney 1996). Furthermore, human disturbance along the shorelines of my study sites was rare, so natural activity patterns of male Red-breasted Mergansers were generally unaltered throughout wing molt. Human disturbance (e.g., large boats), however, may impose constraints on feeding times of flightless male sea ducks (M. A. J. O'Connor, pers. comm.). Thus, time-activity budgets and nutrient reserve dynamics should be compared among flightless sea ducks at sites with varying levels of human disturbance.

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STATEMENT OF ORIGINALITY

This thesis provides the following original contributions to the scientific literature:

1) My research advances our knowledge of the ecology of nesting ducks. I am the first to show that, despite extremely low pressure from terrestrial and avian egg predators, Anatinae will select macro- and microhabitat features that maximize overhead and lateral concealment at nest sites. Also, this is among the first studies to demonstrate that female abandonment can be a major factor governing nest success within a population of ground-nesting Anatinae. To the best of my knowledge, I report the highest rates of nest abandonment among ground-nesting ducks in North America.

2) This study provides original insight into the ecology of brood-rearing Anatinae. I am the first to show that piscivorous duck broods undertake extensive movements to preferred habitat throughout the rearing period, although I caution that variation in movements between broods may be extensive. My study is the first to provide evidence that Red-breasted Merganser broods foraging in coastal lagoon habitats have little impact on commercially- and recreationally important fish populations, including those of Atlantic salmon (*Salmo salar*).

3) This study advances our understanding of molt among Anatinae as it is the first to indicate that sea ducks undergo portions of two body molts (prealternate and prebasic) while flightless, and that bright feathers of the basic plumage are replaced with cryptic feathers (e.g., on breeding grounds) prior to wing molt.

4) My research is the first to show that some Anatinae increase foraging activity and body mass during the later stages of the flightless period, and that this may have implications on the length of the period of flightlessness. Also, I am the first to show that habitat requirements of foraging sea ducks in wing molt may vary from those of flightless, resting individuals.

5) This is the first study of habitat selection by nearctic Red-breasted Mergansers. I am the first to examine nest-site selection, brood habitat selection, and habitat use of molting Red-breasted Mergansers. Collectively, my research provides a much better understanding of the factors shaping life-history characteristics and the ecological strategies underlying fitness of Red-breasted Mergansers, and identifies future research that should help to better understand correlates of survival for this species.

6) Overall, my work has contributed to improving application of the avian habitat concept as I examined habitat use and selection, considered habitat selection at multiple spatial scales, inferred habitat use at population and individual levels, and determined habitat requirements with various sources of data.

APPENDIX I

BREEDING PHILOPATRY AMONG FEMALE RED-BREASTED MERGANSERS AT KOUCHIBOUGUAC NATIONAL PARK, NEW BRUNSWICK

Abstract. I report evidence of breeding philopatry and adaptive nest-site placement among adult female Red-breasted Mergansers (*Mergus serrator*) nesting on Tern Islands at Kouchibouguac National Park, New Brunswick, Canada. Nineteen (26%) of 72 females marked between 2002 and 2007 were recaptured, but as many as 50% marked in one year were recaptured. Of seven females captured over two consecutive breeding seasons, five returned to nest successfully on the island where they were successful during the previous year.

INTRODUCTION

Breeding experience influences patterns of nest-site selection (Anderson et al. 1992). Successfully-nesting hens are more likely to return to a breeding site the following year than are unsuccessful individuals, which may disperse to other nesting areas (Lokemoen et al. 1990). Accordingly, fidelity to breeding sites or nesting habitat where fitness was previously high reflects adaptive nest-site placement (Clark and Shutler 1999). Female breeding philopatry has been reported among numerous duck (Anatinae) populations (reviewed in Anderson et al. 1992), including Red-breasted Mergansers (*Mergus serrator*) nesting on Tern Islands at Kouchibouguac National Park, New Brunswick, Canada (Titman 1997). In this paper, I report rates of breeding philopatry among female Red-breasted

Mergansers at Kouchibouguac National Park by examining 1) the proportion of banded birds recaptured through the study period and 2) annual return rates (Johnson et al. 1992). Finally, I provide evidence for adaptive nest-site placement by describing the propensity of hens to nest successfully on the island where they were successful during the previous year.

METHODS

From 2002 to 2008, I captured adult female Red-breasted Mergansers on their nest during the later stages of incubation with a dip net or automatic trap (Weller 1957) on the three Tern Islands (46°46' N, 64°52' W; Chapter 3). Females were issued standard leg bands, or previous band numbers were recorded. The fate of each nest was either 1) successful, 2) abandoned, or 3) depredated (Chapter 2). Descriptive statistics were performed with SPSS 11.5 (SPSS Inc., Chicago, IL), and we present values as means ± 95% confidence intervals (CI).

RESULTS

I banded 72 adult female Red-breasted Mergansers on Tern Islands between 2002 and 2007 ($\bar{x}$ = 12 females year^{-1}, 95% CI: 3-21; Table 1). Nineteen females (26%) were recaptured between 2003 and 2008, but as many as 50% banded in one year were recaptured (Table 1). Eleven females were recaptured once and eight were recaptured twice. Return rates averaged 15% (95% CI: 2-28%). Of seven females captured over two consecutive seasons, five returned to nest successfully on the island where they nested successfully during the previous breeding season. One female was captured over three consecutive seasons; she abandoned a nest on

Tern Island 1 in 2006, abandoned a nest on Tern Island 2 in 2007, and was successful on Tern Island 2 in 2008.

DISCUSSION

Female Red-breasted Mergansers return to breed on Tern Islands at Kouchibouguac National Park. The proportion of female mergansers recaptured between 2003 and 2008 (26%) was similar to that on Tern Islands from 1992 to 1995 (28%; Titman 1997). However, these estimates are likely biased low; in most years, I captured females at <30% of the nesting attempts on Tern Islands. This suggests strong breeding-site philopatry among Red-breasted Mergansers on Tern Islands (Anderson et al. 1992).

Female Red-breasted Mergansers nested successfully on the island where they were successful during the previous year, indicating fidelity is adaptive on Tern Islands (Clark and Shutler 1999). Probability of return, however, may be unrelated to experience in areas where nest success is relatively high (Anderson et al. 1992). Given the high success and extremely low rates of depredation at Red-breasted Merganser nests on Tern Islands (Young and Titman 1986, Chapter 2), I suspect that at least some failed nesters return to breed on the island complex in the following year.

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TABLE 1. Numbers banded, percent recaptured, and return rates among female Red-breasted Mergansers (*Mergus serrator*) breeding on Tern Islands, Kouchibouguac National Park, New Brunswick, 2002-2008. Sample sizes are in parentheses.

Year	Number banded	Recaptured (%)[a]	Return rate (%)[b]
2002	9	44 (4)	33 (3)
2003	8	38 (3)	25 (2)
2004	11	45 (5)	9 (1)
2005	9	33 (3)	0 (0)
2006	6	50 (3)	17 (1)
2007	29	7 (2)	7 (2)

[a] Recaptured between 2003 and 2008.

[b] Proportion of marked birds captured in year *t* and recaptured in year *t* + 1.