Surf Scoter (*Melanitta perspicillata*) ecology on spring staging grounds and during the flightless period

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the requirements of the degree of Master of Science

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ABSTRACT

The behaviour of Surf Scoters (*Melanitta perspicillata*) was studied on staging grounds in spring of 2006 and compared to behaviour on moulting grounds later that summer. Moulting Surf Scoters have a distinct activity pattern in comparison to those on spring staging grounds. During moult, foraging occurs mainly in the morning and evening, whereas during the spring a similar proportion of birds foraged at all periods of the day. Birds having recently initiated moult foraged significantly less that on staging grounds. However, as moult progressed, this discrepancy disappeared.

In addition, we tracked the movements of flightless Surf Scoters using satellite telemetry during the 2006 wing-moult period. Despite their reduced mobility, Surf Scoters are able to swim long distances while flightless. However, the majority of their activities are carried out within small core areas. This study also indicates that satellite telemetry can be used effectively to track the daily movements of wildlife.

RÉSUMÉ

Le comportement des macreuses à front blanc (*Melanitta perspicillata*) tel qu'étudié sur leurs aire de repos au printemps 2006 a été comparé au comportement observé pendant la mue des ailes ce même été. Lors de la mue, les macreuses s'alimentent suivant une routine journalière qui n'est pas présente sur l'aire de repos printanière. De plus, elles se nourrissent principalement en matinée et en soirée, tandis qu'au printemps, la proportion de macreuses se nourrissant reste stable tout au cours de la journée. Les macreuses venant d'initier la mue se nourrissent moins que sur l'aire printanière, quoique cette différence disparaît dans les stades avancés de la mue.

Nous avons aussi suivi les mouvements des macreuses à l'aide de la télémétrie par satellite au cours de la mue de 2006. Malgré leur inhabileté à voler, les macreuses en mue sont aptes à se déplacer, en nageant, sur de longues distances. Cependant, l'aire utilisée pour entreprendre la plupart de leurs activités est restreinte, indiquant qu'elles sont relativement sédentaires durant cette période. Nous avons aussi conclu que la télémétrie par satellite est une méthode efficace pour documenter les déplacements journaliers des animaux.

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ACKNOWLEDGEMENTS

Studying the behaviours and movements of moulting Surf Scoters would not have been possible without the financial and logistical support provided by the Canadian Wildlife Service (CWS), Atlantic Region. Components of the study carried out on spring staging grounds were funded by the CWS and Science and Technology, Quebec Region. In addition funding, during both years of field work, was granted by the Northern Scientific Training Program (NSTP) of Indian and Northern Affairs Canada and by the Sea Duck Joint Venture. Field assistance provided by Joannie Lussier, Rachel Théoret-Gosselin and Michael Ross, in addition to support from Scott Gilliland and Pierre Ryan (CWS) and members of the Sikumiut Environmental Management team, especially Gus Dicker, was greatly appreciated. In addition, I am very grateful to community of Nain, Labrador whose citizens greeted us with open arms each time we arrived. The professors and graduate students of McGill University's Macdonald Campus, especially those involved with the Avian Science and Conservation Center, provided useful input throughout the course of this study. I particularly thank Shawn Craik for his help and advice during all stages of the study and Scott Gilliland for the time he devoted to the project. Finally, I am very grateful to my supervisors Dr. Rodger Titman and Dr. Jean-Pierre Savard for the advice provided and the time invested into this project.

PREFACE

Contribution of Authors - The following manuscript, as well as completion of field work and data analysis was written by the author of this thesis. In addition, Scott Gilliland assisted in the design and analysis of the portion of this study dealing with satellite tracking of Surf Scoters and provided assistance during the study of moult behaviour. Dr. Jean-Pierre Savard was instrumental in planning observations during spring staging and provided useful advice throughout the project. Dr. Rodger Titman provided useful input throughout the course of this study, in regard to both methodology used for behavioural analyses and the current thesis.

This thesis is presented in the form of two papers to be submitted for publication. The first (Chapter Two) will be submitted with Dr. Jean-Pierre Savard, Dr. Rodger Titman and Scott Gilliland as the second, third and fourth authors respectively. The second paper (Chapter Three) will be submitted with Scott Gilliland as the second author, and Dr. Jean-Pierre Savard and Dr. Rodger Titman as the third and fourth authors respectively.

CHAPTER ONE

INTRODUCTION AND LITERATURE REVIEW

Introduction

One of the key periods during the annual cycle of waterfowl is the time during which they become flightless. From an ancestral pattern of gradual wing moult, modern waterfowl have evolved a strategy whereby all flight feathers are shed simultaneously (King 1974). This pattern is thought to have evolved in ducks and geese because of the habitats they live in. The aquatic environments they inhabit make them most apt to overcome the difficulties associated with finding sufficient food and escaping predation while flightless (Hohman et al. 1992). That many species undergo a moult migration to secure, isolated areas with abundant food and optimal habitat parameters provides support for this claim (Salomonsen 1968). In addition, it has been hypothesized that the heavy wing-loading observed in waterfowl, especially sea ducks, significantly reduces their ability to fly after loss of even a single primary feather. Hence, simultaneous shedding of all flight feathers is believed to minimize the duration of the flightless period (Hohman et al. 1992, Baldassarre and Bolen 2006).

A number of strategies have evolved to compensate for the high energetic requirements of moult (King 1974, Hohman et al. 1992). While it does not appear that ducks and geese are nutritionally stressed during the flightless period (Ankney 1979, Hohman 1993, Thompson and Drobney 1996, Hohman et al. 1997, Fox and Kahlert 2005), the use of endogenous nutrient reserves appears to accelerate the process (Pehrsson 1987, Panek and Majewski 1990, Moorman et al. 1993, Van de Wetering and Cooke 2000). In fact some species seem to rely almost exclusively on endogenous reserves to fuel feather growth (Adams et al. 2000). Recent moult literature has focused mainly on energetics (Brown and Saunders 1998, Van de Wetering and Cooke 2000, Fox and Kalhert 2005) and only a handful of researchers have examined the behaviour of moulting waterfowl (Frimer 1994, Thompson and Drobney 1996, Adams et al. 2000). Scan-sampling is one of the most effective methods to determine the behaviour of animals in large groups (Altmann 1974). Since behaviour between species varies at all times of the year (Danell and Sjöberg 1982, Gammonley and Heitmeyer 1990, Arzel and Elmberg 2004), it is best to compare the behaviour of the focal species at different stages of its annual cycle to determine how it is affected by a particularly stressful period.

Little attention has been paid to the movements of waterfowl during the flightless period. Despite their inability to fly, it appears that moulting ducks and geese are capable of relatively long distance movements (Flint et al. 2004). If such is the case, then understanding the extent of such movements is important for management purposes. Satellite telemetry allows wildlife to be tracked over large distances without causing disturbances that might affect their behaviour (Mate et al. 1998, Flint et al. 2000, Fox et al. 2003, Miller et al. 2005). While the spatial accuracy of satellite transmitters is restricted (Keating et al. 1991, Britten et al. 1999, Hays et al. 2001), they can identify any long distance movements occurring during the moult and could prove useful to track daily movement patterns.

Determining the behaviours and movements of moulting waterfowl is particularly important in species for which little information is available at this and other stages of the annual cycle. Declining populations and lack of knowledge about sea ducks (Tribe Mergini) in general, and Surf Scoters (*Melanitta perspicillata*) in particular (Bellrose 1980, Savard et al. 1998a), make them ideal candidates for this type of research. Aspects of feeding ecology (Vermeer and Levings 1977, Schenkeveld and Ydenberg 1985, Beauchamp 1992, Lacroix et al. 2005, Lewis et al. 2005, 2007), breeding (Savard and Lamothe 1991, Reed et al. 1994, Henny et al. 1995, Lesage et al. 1997, Morrier et al. 1997), and wintering and staging (Stott and Olsen 1973, Savard et al. 1998a, Iverson et al. 2004, Zydelis et al. 2006) have been studied for Surf Scoters, but the moulting period remains the most understudied period of their annual cycle (Savard et al. 1998b).

Research Objectives

Considering the knowledge gaps highlighted above, the first objective of this study is to document the behaviour of flightless Surf Scoters and to determine whether changes occur in comparison to another time of year, the spring staging period. The second aim of the study is to use satellite telemetry to track the movements of individual Surf Scoters throughout the moulting period and to evaluate the accuracy of this tracking method.

Surf Scoter Ecology

The Surf Scoter is endemic to North America and is separated into populations along the East and West coasts. In the East, wintering grounds occur from Newfoundland as far south as South Carolina; however, major aggregations have long been known to occur along the New England coast (Mackay 1891, Palmer 1976, Johnsgard 1978, Savard et al. 1998b). During spring migration many birds use the north shore of the St-Lawrence estuary as a stopover site on their way to breeding grounds throughout the boreal forest (Savard and Lamothe 1991, Savard et al. 1998a). Subsequently, males aggregate in large numbers at coastal moulting sites, especially along the northern coast of Labrador, prior to their fall migration southward (Palmer 1976, Lock 1980). One of the major moulting sites along the Labrador coast is situated in the waters surrounding the community of Nain, Labrador (Gilliland et al. in prep).

Throughout their range, Surf Scoters are known to feed almost exclusively on bivalve molluscs that are associated with the coastal areas they inhabit. Blue mussels (*Mytilus edulis*) are usually the commonest prey consumed by scoters, but clams are also an important component of their diets (Stott and Olson 1973, Vermeer and Levings 1977, Vermeer 1981). In addition to foraging on molluscs, Surf Scoters are known to aggregate in areas with ephemerally abundant food sources (Lacroix et al. 2005, Lewis et al. 2007). As is the case for most diving ducks relying on their eyesight to detect benthic organisms, Surf Scoters do not appear to forage nocturnally (Guillemette 1998, Lewis et al. 2005).

Consequently, all activities related to energy acquisition are likely to occur during daylight hours when the birds are more easily observed.

Like most other ducks, Surf Scoters have two distinct plumages during their annual cycle (Dwight 1914, Palmer 1976, Savard et al. 1998b). Surf Scoters do not obtain their adult plumage until their 3rd year and age classes of males can be distinguished by differences in their plumages (Iverson et al. 2003). In adult birds, the definitive alternate plumage is obtained starting in late August and continuing throughout the fall and winter while basic plumages are obtained with the pre-basic moult occurring during summer (Dwight 1916, Palmer 1976, Savard et al. 1998b, Pyle 2005). In the pre-basic moult, all flight feathers are shed and replaced simultaneously (Palmer 1976).

Wing Moult

Males in most species of Anatinae do not take part in incubation or brood-rearing and as such generally abandon females once incubation has begun, to congregate in isolated moulting areas (Salomonsen 1968, Palmer 1976, Savard et al. 2007). On moulting grounds, flight feathers are shed simultaneously, as is the case in most other waterfowl species (King 1974, Hohman et al. 1992). Shedding all primaries means waterfowl lose their ability to fly for an extended period of time and become vulnerable to predation. Estimates for the duration of wing moult vary widely among species, but most are thought to remain flightless for a period of three to four weeks (Hohman et al. 1992). Complete remigial growth is not required before flight is possible. In fact, most birds regain flight once remiges attain 70-80% of their mature length (Panek and Majewski 1990, Hohman et al. 1992, Thompson and Drobney 1996, Brown and Saunders 1998, Van de Wetering and Cooke 2000).

It has been proposed that weight loss during remigial moult is an adaptive strategy to reduce wing loading and permit the earliest possible return to flight (Owen and Ogilvie 1979, Pehrsson 1987, Brown and Saunders 1998) rather than an indicator of nutritional stress (Hanson 1962). While a significant amount of energy is required for the moult (King 1974), most species do not appear to be nutritionally stressed by the process (Ankney 1979, Murphy and King 1984, Panek and Majewski 1990, Fox and Kalhert 2005). Instead, energetic demands are usually met exogenously and fluctuations in muscle mass seem to be due to their respective use and disuse relative to the moult (Ankney 1979, Bailey 1985, Gaunt et al. 1990, Hohman 1993, Thompson and Drobney 1996). However, endogenous proteins may be used to fuel remigial moult in some species.

The increase in time spent resting and decreased foraging by moulting Harlequin Ducks (*Histrionicus histrionicus*) suggests that they offset energetic requirements with endogenous reserves (Adams et al. 2000). Furthermore, the rate of feather growth in captive Mallards (*Anas platyrhynchos*; Pehrsson 1987), in wild Ring-necked Ducks (*Aythya collaris*; Hohman and Crawford 1995) and in Barrow's Goldeneyes (*Bucephala islandica*; Van de Wetering and Cooke 2000) was positively related to body condition. These findings suggest that endogenous reserves are likely important to assure optimal remigial growth and to fuel changes in behaviour.

Behaviour

Behaviour During Moult – While the study of behaviour can provide useful insights towards energy acquisition and use, little effort has been devoted to studying the activities of moulting waterfowl (Hohman et al. 1992). Time budgets on both wintering (Goudie and Ankney 1986, Laubhan and Metzner 1999, Fischer and Griffin 2000, Lewis et al. 2005, Michot et al. 2006) and breeding (Dwyer 1975, Afton 1979, Brown and Fredrickson 1987, Savard and Lamothe 1991, Tome 1991, Afton and Paulus 1992) grounds have been estimated for a number of species. Conversely only a few behavioural studies have been conducted on waterfowl during the flightless period. Oring (1964) observed the general behaviour of 13 species of waterfowl and laid out the changes in waterfowl activity associated with various stages of the moult, including the timing of moult migration. While his behavioural observations focused mainly on predator avoidance, he also noted changes in foraging and resting time for dabbling ducks (Oring 1964). Similarly, Redheads (*A. Americana*; Bailey 1985) were found to rest more while moulting than during the breeding and post-moult periods. Male Lesser Scaup (*A. affinis*; Austin 1987) were engaged in comfort activities more during the flightless period than at other times of the year.

Behaviour During Spring Staging – Discrepancies in behaviour are expected between the moulting and staging periods since priorities and energetic requirements vary between the two. Migrants travelling to spring staging grounds generally undergo significant weight loss after departing from wintering grounds (Bromley and Jarvis 1993, Ebbinge and Spaans 1995). Staging grounds thus serve as important refuelling stations prior to the breeding season and allow birds to maximize their reproductive output upon arrival to breeding grounds (Hohman et al. 1988, Barzen and Serie 1990, Gammonley and Heitmeyer 1990, LaMontagne et al. 2001, Clausen et al. 2003, Drent et al. 2003, Arzel et al. 2006, Badzinski and Petrie 2006). Because the males of most species do not contribute to incubation, they are generally less energetically constrained than females who rely, at least partly, on endogenous reserves for egg production and incubation (Ankney and Alisauskas 1991, Alisauskas and Ankney 1992, Gloutney and Clark 1991, Afton and Paulus 1992, Baldassarre and Bolen 2006). Considering this, males are likely able to refuel without foraging more intensely than they would under normal circumstances. Furthermore, while most pair-bonds are formed during winter, some courtship activities continue onto the staging grounds, especially in younger individuals (Spurr and Milne 1976, Rohwer and Anderson 1988, Lovvorn 1990, Robertson et al. 1998). Hence courtship and aggressive displays are expected to be more frequent than during moult. Despite the expected differences in behaviour between the two periods, a comparison between them will be useful to determine whether Surf Scoters modify their behaviour at different stages of the annual cycle.

Factors Affecting Behaviour – In addition to the increased energetic demand during moulting and staging, several other factors can modify the behaviour of waterfowl. For instance, decreasing temperatures are associated with increased foraging which helps to maintain thermal regulation (Owen 1970, Nilsson 1970, Jorde et al 1984, Turnbull and Baldassarre 1987, McKnight 1998). Similarly, diurnal foragers must intensify feeding activities as daylength decreases to balance their energy requirements (Guillemette 1998, Fischer and Griffin 2000, Systad et al 2000, Lewis et al 2005). Feeding behaviour is also affected by prey type and density, which influence search times and handling time as well as foraging efficiency (Schoener 1971, Tome 1988, Guillemette et al. 1992, Kohlmann and Risenhoover 1998, McKnight 1998, Rodway and Cooke 2001).

Aside from the constraints outlined above, the behaviour of waterfowl is shaped by the type and frequency of disturbances within the areas they use. Response to disturbance, similarly to predator avoidance, is driven by an optimal balance between the perceived risk of predation and the cost of ceasing activities ongoing prior to the disturbance event (Sih 1980, Ydenberg and Dill 1986, Lima and Dill 1990, Frid and Dill 2002, Beale and Monaghan 2004). This indicates that factors such as body condition (Lima 1988), nutritional state or food abundance (Milinski and Heller 1978, Godin and Crossman 1994, Beale and Monaghan 2004) and availability/quality of alternate sites (Madsen 1998, Gill et al. 2001, Kahlert 2003) influence the decision making process. Additionally, the ability of an individual to escape and its vulnerability to predation (Rand 1964, McLean and Godin 1989, Dill 1990, Bonenfant and Kramer 1996) play an important role in its susceptibility to disturbance. The reduced mobility of moulting waterfowl explains their strong reaction toward any source of disturbance (Bailey 1981, Derksen et al. 1982, Madsen and Mortensen 1987, Mosbech and Boertmann 1999).

Potential sources of disturbance in the remote moulting grounds used by sea ducks are mainly watercraft and aircraft since there are relatively few potential predators or anthropogenic pressures in these areas (Salomonsen 1968). Disturbance stemming from both sources is well documented for a number of wildlife species (Korschgen et al 1985, Burger 1998, Carney and Sydeman 1999, Rodgers and Schwikert 2002, Bright et al. 2003). Despite the ability of some waterfowl to habituate to aircraft disturbance (Harms et al. 1997, Conomy et al. 1998), reaction to the sound of engines is probable by Surf Scoters since they are hunted during moult and likely associate engines sounds with hunting pressure (Mosbech and Boertmann 1999).

Studying Behaviour – Focal and scan sampling are two basic techniques used for collecting behavioural samples from waterfowl (Altmann 1974). Focal samples tend to yield more detailed results and their use is generally favoured over other techniques (Dunbar 1975, Martin and Bateson 2007). However, it becomes impossible to track single unmarked individuals when a group is sufficiently large, or in species where diving is common (Mann 1999, Mitlöhner et al. 2001, Michot et al. 2006). In such cases, the use of scan sampling (Altmann 1974) becomes the technique of choice. Although this method is well-suited for gathering behavioural data on groups of moderate size, it also fails when high concentrations of individuals are present (Hepworth and Hamilton 2001). As such, modified scan samples, whereby only a sub-sample of the entire flock is observed (Davis et al. 1989, Squires and Anderson 1997, Hamilton et al. 2002) are most useful when studying wildlife in large aggregations. While sub-samples can provide useful estimates of flock behaviour, it is important to maintain randomness when deciding which individuals are sampled (Milinski 1997, Hepworth and Hamilton 2001).

Movements

Small-scale Movements – Regular patterns of diurnal movement have been observed in moulting ducks (Frimer 1994, Flint et al. 2004) but the extent of these movements by individuals has rarely been quantified. Radio-telemetry has shown that despite the constant presence of Long-tailed Ducks (*Clangula hyemalis*) at certain sites, there was significant turnover of the individuals present (Flint et al. 2004). The long distances travelled by Long-tailed Ducks (Flint et al. 2004) are in contrast to observations made by Bowman and Longcore (1989) who suggested that American Black Ducks (*A. rubripes*) are relatively sedentary during the flightless period. Similarly, several flightless Mallards were found to remain relatively sedentary yet the scale of movements varies between individuals since others cover large distances while moulting (Gilmer et al. 1977).

Large-scale Movements – While information on the small-scale movements of moulting waterfowl is lacking, large-scale studies are more common. Most focus on the timing and direction of movements towards and away from moulting grounds (Oring 1964, Johnson and Richardson 1982, Herter et al. 1989, Yarris et al. 1994, Phillips et al. 2006, Glahder et al. 2007). There is growing support for the claim that waterfowl exhibit moulting site fidelity. Bowman and Brown (1992) showed that 52% of moulting Black Ducks marked returned to the same moulting grounds the following year. Similarly, over 75% of Harlequin Ducks banded while moulting returned to the same site the following year (Cooke et al. 1997). More recently, studies by Flint et al. (2000) and Phillips and Powell (2006) have shown, respectively, that both Steller's Eiders (*Somateria fischeri*) and King Eiders (*S. mollissima*) exhibit high moulting site fidelity, suggesting this habit is common among sea ducks.

Studying Movements – Recent technological advances have made it easier to follow the movements of wildlife. Radio-telemetry has been used for several decades (LeMunyan et al. 1959, Cochran and Lord 1963) in a variety of wildlife research dealing with foraging behaviour (Trivelpiece et al. 1986, Custer et al. 1996, Lewis et al. 2005), dispersal (Hawkins and Montgomery 1969, Forsman et al. 2002, Pons and Pausas 2007), migration (Johnson et al. 1997, Gerlier and Roche 1998, Boyd et al. 2000) and habitat utilization (Trent and Rongstad 1974, Samuel et al. 1985, North and Reynolds 1996). While results are accurate, this method requires animals to be tracked from relatively close proximity. Considering the reaction of moulting waterfowl to disturbance events, it is unlikely that this technique can be used effectively without disturbing birds during searches.

Satellite telemetry has been in use for over two decades, but miniaturization of the technology has recently made it possible to use the transmitters with birds and small mammals (Hamer et al. 2000, Gillespie 2001, Green et al. 2002, Fox et al. 2003). Although the spatial resolution of satellite transmitters is lower than other techniques, advantages include the fact that animals can be tracked remotely and that the devices need not be recuperated (Rempel et al. 1995, Britten et al. 1999, Javed et al. 2003). Because of its lack of spatial accuracy, satellite telemetry is especially useful to track long distance movements in migrant species (Morreale et al. 1996, Eckert and Stewart 2001, Miller et al. 2005). However, given a sufficient number of locations it is likely possible to document areas of core utilization and movements at a finer scale (De Solla et al. 1999, McConnell et al. 1999, Girard et al. 2002, Merkel et al. 2006). While this technology has rarely been used to document local movement patterns, we suspect that the spatial resolution will, at worst, restrict observations to movements between moulting sites.

Summary

The high energetic demand and decreased mobility associated with the simultaneous regeneration of flight feathers in waterfowl leads them to remote environments that are free from predation and have abundant food supplies. Despite the impact of this period on the annual cycle of waterfowl, little attention has been paid to the strategies employed to ensure successful moults. Furthermore, the strong reaction of moulting waterfowl to disturbance has made it difficult to track their fine-scale movements. As such our use of satellite telemetry will provide one of the first accounts of the movements of sea ducks within their moulting area. Additionally, this is one of the first accounts of Surf Scoter behaviour during either the wing moult or spring staging periods.

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CONNECTING TEXT

Although the underlying principles of wing moult are understood for waterfowl, detailed accounts of ecology and behaviour during the flightless period are available for only a handful of species. The proposed research will fill many of the knowledge voids highlighted in this review. In the next chapter, we provide the first detailed description of the behaviour of Surf Scoters during both the spring staging and wing moult periods. Doing so will provide additional insight about the process of wing moult in waterfowl and how it is successfully achieved.

CHAPTER TWO

BEHAVIOURAL ECOLOGY OF SURF SCOTERS (*MELANITTA PERSPICILLATA*) DURING THE SPRING STAGING AND WING MOULT PERIODS

Abstract

This study describes, and compares, the behaviour of Surf Scoters during spring staging in the St-Lawrence Estuary and during the wing moult period in northern Labrador. On staging grounds, activities varied little throughout the day and foraging dominated the time-activity budget (45-49%) throughout the day. In contrast, flightless Surf Scoters exhibited a strong diurnal pattern of activity. Foraging was most intense during morning (64%) and evening (69%) hours, and rarely occurred during afternoons (8%). Furthermore, foraging occurred less frequently (27%) during the early stages of moult in comparison to the later stages (47-51%). Considering this, it is possible that endogenous reserves are used to fuel initial feather growth when birds are most vulnerable to predation. Proportion of time spent foraging on moulting grounds was inversely related to daylength, suggesting that energy budgets are at, or near, equilibrium and that nocturnal foraging does not occur. The strong reaction of flightless scoters to disturbance could render them more susceptible to the effects of increased human activity near moulting grounds.

Introduction

The replacement of primary feathers in waterfowl occurs simultaneously, leaving birds flightless for a period of several weeks (Hohman et al. 1992). Not only does replacing all flight-feathers at once require a significant amount of energy (King 1974, Lovvorn and Barzen 1988, Hohman et al. 1992), but the reduced mobility incurred makes it difficult for birds to find food and to escape predation. This vulnerability has led to the evolution of a moult migration that is especially well-developed in sea ducks (Salomonsen 1968). By moulting at sites with few predators and abundant food supplies, waterfowl are able to allocate an optimal amount of energy to the moulting process. In fact, it is their ability to forage and escape predation while flightless, combined with heavy wing-loading, which led to the evolution of a synchronous wing moult in most ducks and geese (Hohman et al. 1992).

There remains debate about how synchronous moulting is achieved energetically, as various species seem to adjust differently to the moulting period. For example Harlequin Ducks (*Histrionicus histrionicus*) reduce the amount of time spent active (including foraging) thereby maximizing the endogenous energy available for moulting (Adams et al. 2000). Van de Wetering and Cooke (2000) found a positive correlation between weight lost by male Barrow's Goldeneyes (*Bucephala islandica*) and corresponding remigial growth rates, also suggesting that endogenous reserves can be used to fuel the moult. In contrast, the dissection of Canvasback (*Aythya valisineria*) carcasses showed that their moult is fueled exogenously throughout remigial moult (Thompson and Drobney 1996).

While it is generally accepted that weight lost during the moult can be associated with nutrients made available for feather regeneration it is unlikely, although it has been suggested (Hanson 1962), that the loss occurs because of nutritional stress (Ankney 1979, Lovvorn and Barzen 1988, Panek and Majewski 1990, Fox and Kalhert 2005). Some have suggested that a decrease in body mass is an adaptive method that permits an earlier return to flight than would otherwise be possible (Owen and Ogilvie 1979, Pehrsson 1987, Brown and Saunders 1998).

Fluctuations in weight during the moult are generally attributed to the atrophy of flight muscles and subsequent hypertrophy of leg muscles induced by an increase in walking and swimming (Hanson 1962, Ankney 1979, Gaunt et al. 1990, Brown and Saunders 1998). Interestingly, Hohman (1993) showed that the leg muscles of Ruddy Ducks (*Oxyura jamaicensis*) incurred no signs of hypertrophy during the flightless period and suggested that this occurred because they did not swim or dive more than at other times of the year. This prediction should hold for other diving ducks that are behaviourally flightless throughout the year, suggesting that endogenous reserves may be more readily available for these species than for other waterfowl. Having selected a moulting site with abundant nutritional reserves, birds could use depleting breast muscle to supplement the exogenous reserves they acquire (Bailey 1985).

It was shown that Tufted Ducks (*A. fuligula*) use 3.5 times more energy for diving than for resting (Butler 2000) and that maintaining unnecessary energy stores can be detrimental to waterfowl (Witter and Cuthill 1993). In view of this, the degenerating breast muscle may allow birds to decrease foraging time and increase time spent in areas with lower risks of predation (Thornburg 1973, Reed and Flint 2007). Determining the time-activity budgets of moulting sea ducks could provide useful insight as to whether this is the case. While activity budgets are available for few species, they have proved useful in elucidating moult strategies used (Bailey 1981, Austin 1987, Frimer 1994, Adams et al. 2000). Furthermore, any observed departure from behaviour at other times of the year should provide evidence of adaptation for moulting. In particular, analysis of foraging behaviour (Pyke et al. 1977, Bautista et al. 1998) can provide insight into the energetics and ecology of moulting.

Interspecific variation in waterfowl activity makes it impossible to detect differences across species, even closely related ones (Danell and Sjöberg 1982, Gammonley and Heitmeyer 1990, Arzel and Elmberg 2004). As such, we compared the behaviour of Surf Scoters (*Melanitta perspicillata*) during remigial moult to their behaviour on spring staging grounds. The moulting ecology of Surf

Scoters has yet to be documented and little work has been conducted during spring staging (Savard et al. 1998).

Differences in behaviour between the two periods are expected because spring staging birds are recuperating from migration and pair-formation is ongoing (McLandress and Raveling 1981, Oring and Sayler 1992, Ebbinge and Spaans 1995, Lyons and Haig 1995, Arzel et al. 2006). Furthermore, since birds are preparing for reproduction, they are also expected to forage more than normal to build up energy stores (Ankney and Afton 1988, Krapu and Reinecke 1992). However, since there is little parental investment by male sea ducks, their need to store large nutrient reserves is less than for females (Ricklefs 1974, Afton and Paulus 1992). Considering this, it is likely that, aside from courtship, activities while staging should be representative of 'normal' behaviours. The purpose of this study was to compare the behaviour of Surf Scoters during the spring staging period to their activities while undergoing wing moult. We hypothesized that the vulnerability of moulting birds would cause a shift in their behaviour, thereby causing them to become less active.

Methods

Study Areas – Male Surf Scoters (hereafter scoters) were observed over a three week period during spring staging (May) and a six week period during the wing moult (July and August) of 2006. Staging observations were conducted along the north shore of the St-Lawrence River between Godbout and Port-Cartier, Quebec, Canada, where concentrations of staging scoters are known to occur (Falardeau and Savard 2003, Rail and Savard 2003). The majority of observations were carried out at Pointe-des-Monts, QC (N 49°19', W 67°22'). Shoreline structure varied between sites, but water was relatively shallow (<5m) at all sites and most had rocky shorelines. Observations conducted at Godbout and Pointe-aux-anglais, QC were along sandy beaches. Birds were observed from within 500m at most sites and observation posts were generally a short distance from roadsides and easily attainable.

Birds undergoing wing moult were observed at Iglosiatik Island (N 56°14', W 61°06') approximately 50 km southeast of Nain, Labrador. The island is approximately 10 km long, but observations were concentrated at the eastern tip because of the number of birds present, site accessibility and logistics. Numerous shoals and several smaller islands (including the Seniarlit complex as well as several unnamed islands) are situated around the eastern tip of Iglosiatik, but since no bathymetry studies have been conducted, water depths are unknown. The island rises to an elevation of 300m, providing elevated vantage points for observation. However, the rocky habitat, comprised mostly of tundra, with some small shrubs, provided little camouflage from the easily disturbed birds. As a result observations were rarely carried out at distances less than 500 m.

Observations – Four observation periods were considered for analyses. A single period was used for spring staging, while wing moult was divided into three roughly equivalent time frames considered to represent the early, mid- and late moult. Observations were also separated into three periods of the day: morning (sunrise-10:00), mid-day (10:01-15:00) and evening (15:01-sunset). Birds were generally observed from high vantage points (150-300 m) at distances ranging from 50 m – 3 km using either a 45x (staging) or 60x (moulting) spotting telescope. Behaviours were recorded using a modified scan-sampling technique (Altmann 1974) where scans were conducted in 30 minute observation blocks, each with 5 minute intervals between scans. Since individual birds could not be tracked, observation of large flocks (up to 2000 birds) was made manageable by dividing them into sections (*n* ≥250 birds; Figure 2.1). The behaviour of 50 birds, chosen at random from each section, at each scan (every 5 minutes), was noted. When ≥2 flocks were present, scanning sections were distributed among them (# of sections per flock relative to number of birds) to minimize potential for bias because of flock synchrony. Flocks of 150 birds or less were not divided. This method of sub-sampling allowed up to 5 groups (i.e. 250 individuals) to be sampled consecutively every 5 minutes.

Behaviours were assigned to one of six categories: foraging (diving and inter-dive pauses), locomotion (swimming and flying), maintenance (preening, scratching, splash bathing and stretching), resting (loafing and sleeping), alert (head-up scanning of the area and scooting) and social (courtship and agonistic; Goudie and Ankney 1986, Paulus 1988, Adams et al. 2000). Birds tended to move offshore (2-3 km) during afternoon hours making sampling more difficult as behaviours could not be clearly distinguished at such distances. Instead, observations were classed only as foraging or not-foraging since this provides important information about energy acquisition (Pyke et al. 1977, Bautista et al. 1998).

Prior to the start of each observation period wind strength (light, moderate, strong), cloud cover (0-25, 26-50, 51-75, 76-100%), and precipitation (none, fog patches, light rain, moderate rain) were recorded (Goudie 1999). Observations were rarely possible when strong wind or moderate rain was present since the behaviour of individual birds could not be determined. Daylength records (16-17, 17-18, ≥18 hrs) and tide level (high, ebb, low, flood) for each observation period were obtained after the study period (National Research Council of Canada 2007).

Statistical Analyses – For each 30 minute scan, we calculated the proportion of birds engaged in each activity. Since neither data (staging or moulting) could be normalized, non-parametric (Kruskal-Wallis and Mann-Whitney U) tests were used to identify differences in the proportion of time allocated to each activity between observation periods and periods of the day; significance was inferred at $P < 0.05$ (Zar 1974, Siegel and Castellan 1988).

Because complete activity-budgets could not be constructed during afternoon periods, data from scans containing all behavioural categories were converted to foraging or non-foraging for all periods of the day. Foraging included diving and pausing, while all other behaviours were considered to be non-foraging. The resulting dataset was analysed with regression trees, which do not make any assumptions about normality or linearity (De'ath and Fabricius 2000), to determine which factors influence the proportion of time spent foraging. Staging data were similarly converted and analysed for comparison. Regression trees were constructed using CART EX v.6.2 (Breiman et al. 1984, Steinberg and Colla 1997). The proportion of birds foraging per 30 minute scan was used as the dependent factor. Predictor variables were time of day, stage of moult (staging was considered separately), tide, cloud cover and daylength. Values for wind strength and precipitation were excluded from analysis because of bias (observations were not possible during periods of strong wind or heavy rain). The only restrictions specified for tree splitting were that parent nodes must contain at least 120 data points to be split and that all end nodes resulting from a split must contain a minimum of 60 cases (Figure 2.2) in order for that split to occur. Regression trees were evaluated using 10-fold cross-validation (Breiman et al 1984). Optimal trees were selected using the program's pruning function which uses a combination of relative error and a complexity score to select the best trees.

Results

Spring Staging Grounds

Flock Composition – Surf Scoters on their spring staging grounds were generally the second most abundant species within multi-species flocks. Black Scoters (*M. nigra*) were most numerous at a majority of sites. Common Eiders (*Somateria mollissima*) and Long-tailed Ducks (*Clangula hyemalis*) were generally present within the flocks, but several other species were observed occasionally. The proportion of Surf Scoters within flocks was greatest near the start of the staging period and declined progressively as the season advanced. The difference was due to lower numbers of Surf Scoters, not to more members of other species. At the locations sampled, the highest numbers of Surf Scoters were observed in the bays at Pointe-des-Monts, while a relatively large concentration was also observed near the shipwreck at Port-Cartier, QC. Male Surf Scoters outnumbered females by a ratio of more than 2:1 (Table 2.1). Scoters at this time of year were loosely aggregated in small groups and were dispersed throughout the observation area. However, when foraging they formed cohesive flocks of 30-100 individuals that tended to dive synchronously.

Time-activity Budgets – Time-activity budgets for staging scoters were constructed using data from 317 observation bouts, over a total of 158.5 hours, from 3-16 May 2006. Of the behaviours observed, foraging (45-49%) was the most prevalent activity at all periods of the day (Figure 2.3). Locomotion (19-24%) and loafing (16-18%) were the next most common activities. Comfort movements (7-9%) occurred regularly, but social behaviours (agonistic and courtship displays) were also relatively common (3-6%).

In contrast, alert behaviour was rarely observed (0-1%) and was usually a response to potential avian predators such as Great Black-backed Gulls (*Larus marinus*), Herring Gulls (*L. argentatus*) and eagles. Even Great Blue Herons (*Ardea herodias*) elicited a response from scoters when they glided overhead. Anthropogenic sources of disturbance were rare, with birds ignoring ships, trawlers and aircraft. The only human-induced disturbance observed was when we approached the shoreline too closely (<50m). Any disturbance event affected most birds in the immediate vicinity as they reacted to one another. When disturbed, flocks tended to rush offshore to group in dense rafts; some birds flew short distances, but they rarely left the area entirely. Disturbances were usually short-lived and normal activities resumed within a few minutes once the threat had passed.

The time-activity budget of spring staging scoters was consistent throughout the day and a similar proportion of birds was engaged in each activity during every sampling period. Only the social behaviours changed significantly between periods (Kruskal-Wallis $P<0.001$). These behaviours occurred more in the morning than at other times of the day (Mann-Whitney $P<0.005$), while the afternoon and evening periods were not different from one another ($P=0.277$).

Because most birds were concentrated around Pointe-des-Monts, the majority of observations were conducted there. It was impossible to compare behaviours between sites since few observations (n = 65) were carried out at the other localities. Also, Surf Scoters were only observed along sandy beaches (where clams dominate the diet) on two occasions (n = 30). Given this, foraging behaviour at these sites and those with rocky shorelines (n = 287) could not be compared due to the discrepancy in sample size.

Moulting Areas

Flock Composition – Surf Scoters rarely associated with other species during the moulting period. White-winged Scoters (*M. fusca*) and Black Scoters were occasionally observed within a flock of Surf Scoters, but they usually represented <1% of flock composition. Black Guillemots (*Cepphus grylle*) also foraged alongside scoters on occasion. Despite the presence of large numbers of Common Eiders and moulting Red-breasted Mergansers (*Mergus serrator*), clear segregation was always maintained. Few females were present within flocks of moulting scoters. In fact females represented only ~2% of birds present on moulting grounds (Table 2.1). Also in contrast to spring staging, Surf Scoters formed dense rafts during all hours of the day, regardless of activities undertaken. Rafts generally ranged in size from 150-300 individuals, but observing >500 Surf Scoters in a flock was not rare.

Daily Patterns – Behaviour on the moulting grounds was noticeably different from that observed during the staging period. While 475 scans, totalling 237.5h of observation, were conducted from 22 July – 19 August 2006, it is not possible to determine which behaviour dominated the time budget because of the drastic shift in afternoon behaviour mentioned previously. Considering all daylight hours, resting (as defined following amalgamation of behaviours) was the predominant activity (62%). Foraging was dominant during both morning (64%) and evening (69%) observation periods, while it comprised only 8% of the afternoon time budget. Time spent foraging was different for all periods of the day (Figure 2.5). During morning and evening foraging bouts, comfort movements (11-15%) and locomotion (11-14%) were the next most common activities. Alert behaviour made up no more than 5% of the time budget, but the prolonged effect of disturbance, compared to staging grounds, suggests that reaction to disturbance may be more significant during the moult.

Disturbance elicited a response at greater distances and was triggered by a wider range of causes during the moult (Appx. 2) than during spring staging. Aside from the same sources of disturbance as occurred on the staging grounds, moulting birds reacted to the sound of any engine as soon as, or before, it became audible to the observers, usually several kilometres away. Our presence atop the island, even from a distance as great as 1 km, was a source of disturbance if great care was not taken to remain hidden. As was the case on staging grounds, scoters scooted offshore in dense rafts when disturbed. While moulting however, ongoing activities were rarely resumed and birds continued swimming until they had moved far (2-3km) offshore. The duration of disturbance was not quantified, but birds were rarely observed at foraging sites until the next afternoon/morning (birds disturbed during morning foraging returned that evening, while birds disturbed later in the day were observed the following morning). It was not possible to determine whether nocturnal foraging may have been used to balance energy requirements.

Behaviour across moulting periods – During early stages of wing moult, foraging made up a relatively small proportion (27%) of the time budget (Figure 2.4). Scoters fed for a significantly larger proportion (47% and 51% respectively) of the time during both the mid-moult ($P < 0.001$) and late-moult ($P < 0.001$) periods. Foraging was not different ($P = 0.467$) between the latter moulting periods. The opposite trend was observed for resting because it represented all other activities. Interestingly, scoters in mid-moult ($P = 0.774$) and late moult ($P = 0.402$) phases did not forage less than those staging, despite the afternoon period of inactivity.

Regression Tree Analysis – The model selected by the CART algorithm as best explaining the data had a cross-validated relative error of 0.580 ± 0.04, but was also the most complex of all possible models. To avoid overfitting, we favoured selection of the next best model (Figure 2.6) which had a similar relative error (0.583 ± 0.04) but with a single terminal node pruned, making it more parsimonious. When considering only variables that were primary splitters in the tree selected, the root node was first split according to time of day, indicating that most of the variation within the foraging data was due to afternoon inactivity (Terminal Node 1). For foraging scoters (Node 2), the next most influential factor was daylength (variable importance = 9.45). The last split indicates that cloud cover (variable importance = 5.80) takes on a more important role as days become shorter. However, the true effect of either variable is probably minimal given their low variable importance scores relative to time of day. Regression tree analysis of the staging data provided little insight into foraging behaviour at that time of year. The optimal model had a cross-validated relative error of 1.023 ± 0.019, indicating that the model showed no predictive value. The tree's only split occurred because of differences in cloud cover.

Discussion

Flock Composition – The male-skew observed in the adult sex ratio of spring staging Surf Scoters is slightly elevated compared to other waterfowl species (Baldassarre and Bolen 2006). The observed sex ratio is likely the result of higher female mortality and could be one of the factors associated with recent population decline (Donald 2007). The change in sex ratio observed between spring staging and moulting grounds confirms that only a small number of females, likely non-breeders and failed-breeders, accompany males to their moulting grounds (Salomonsen 1968). Similarly, the change in species composition between the two areas may reflect the specificity of waterfowl moulting strategies and the need for efficient foraging during this time (Haramis et al. 1994).

Diurnal Activity Budgets – The diurnal pattern of activity was markedly different between seasons for Surf Scoters. In contrast to the spring staging period, when time allocated to various behaviours was distributed evenly throughout the day, flightless scoters displayed a distinct pattern of activity. Foraging occurred mostly in the morning and evenings while afternoons were spent resting. Proportion of time allocated to foraging during moulting and staging was higher than has been documented for brood-rearing females (32.1%; Savard et al. 1999). Considering the high energetic requirements of incubation for most diving ducks

(Ricklefs 1974, Afton and Paulus 1992) it is unlikely that staging or moulting males foraged more than did brood-rearing females to meet their elevated energetic requirements. Instead, time devoted to brood care (hens were vigilant over 37% of the time; Savard et al. 1999), probably resulted in females having less time to forage.

The lack of a diurnal foraging pattern while staging differs from the peaks in foraging intensity shown for other waterfowl, especially dabbling ducks (Bergan et al. 1989, Hamilton et al. 2002). Peaks in dabbling duck foraging have been related to daily peaks in prey abundance (Sjöberg and Danell 1982). However, since the prey of most diving ducks are sessile and abundance is constant throughout the day, foraging intensity should not vary throughout the day. In addition to the current study, Hardheads (*A. australis*; Hamilton et al. 2002), Lesser Scaup (*A. affinis*), Ring-necked Ducks (*A. collaris*; Bergan et al. 1989) and Common Eiders (Guillemette 1998) have been observed foraging steadily throughout the day. Considering this, we can assume that prey abundance is not driving the diurnal shift in foraging behaviour observed during the moulting period.

Time-activity budgets and regression tree analysis showed that feeding during the flightless period was concentrated in the morning and evening hours (Figures 2.6). A similar pattern was observed in moulting King Eiders (*S. spectabilis*; Frimer 1994). Given the potential vulnerability of moulting birds to predation (Salomonsen 1968) it is possible that a decrease in time spent foraging is advantageous. Risk of predation while foraging (Tamisier 1976, Panek and Majewski 1990) can be influenced by the foraging method employed (Randler 2006, Guillemain et al. 2007), so it is likely that diving has the greatest impact since visual contact with the surface is interrupted for the duration of the dive. However this cannot explain the diurnal routine observed in moulting scoters, especially during mid-moult and late moult when foraging time is similar to staging birds. Since equal amounts of diving take place during these periods, the pattern is likely better explained by the risks associated with time spent in near-shore habitat where scoters are more vulnerable to predation.

As many potential predators nest on island habitat (Good 1998, Gilchrist 2001, Kochert et al. 2002), it is possible that an elevated risk of predation and disturbance is associated with these habitats. While only one instance of predation was observed (by a Great Black-backed Gull) during the study, disturbance caused by the presence of avian predators suggests that the threat cannot be disregarded. Offshore resting bouts have been observed in flightless King Eiders (Frimer 1994), and in wintering Steller's Eiders (*Polysticta stelleri*) and Harlequin Ducks (Reed and Flint 2007) suggesting that the pattern is widespread among waterfowl. That ducks foraging in near-shore habitats were at a greater risk of predation by Bald Eagles (*Haliaeetus leucocephalus*) than they were after having moved offshore suggests that this type of movement increases chances of survival (Reed and Flint 2007). Adjustments to disturbance were also observed in diving ducks on fall staging grounds, in Mississippi where they shifted the timing of daily foraging patterns and habitats used, in response to hunting-induced disturbance (Thornburg 1973). Rafting, known to be an antipredator defence mechanism in waterfowl (Fox et al. 1994), was observed throughout daylight hours during the flightless period, while staging scoters only formed dense groups while foraging. The increase in rafting during wing moult lends further support to the claim that the vulnerability induced by flightlessness (Salomonsen 1968) has led to changes in the allocation of time by Surf Scoters.

Seasonal Allocation of Time – While vulnerability of moulting scoters appears to have altered their time budgets, proportion of time spent foraging differed significantly from that on staging grounds only during the earliest stage of moult (Figure 2.4). This supports similar findings for Lesser Scaup (Austin 1987) and King Eiders (Frimer 1994). Because waterfowl often respond to elevated energetic requirements by increasing foraging times (Pyke et al. 1977, Bautista et al. 1998, Rodway 1998), the parity in time spent foraging between spring staging and the latter stages of the moult suggests that scoters were not nutritionally stressed (Ankney 1979) during this period. In fact, total time spent foraging, based on number of daylight hours, varied little between staging and moulting grounds.

Reduced foraging observed during the early stages of moult is a possible indicator that scoters relied partially on endogenous reserves to fuel feather growth. While the flightless period is not nutritionally stressful for Barrow's Goldeneyes, the use of endogenous reserves by healthy males permitted an increased rate of remigial growth and an earlier return to flight (Van de Wetering and Cooke 2000). In addition, a decrease in overall body mass while flightless may be an adaptation for early return to flight (Hohman et al. 1992, Brown and Saunders 1998). The flightless period leads to atrophy of pectoral muscles in most waterfowl and is generally associated with hypertrophy of the leg muscles (Ankney 1984, Hohman et al. 1992, Thompson and Drobney 1996) resulting from their respective disuse and use. However Hohman (1993) suggested that hypertrophy of leg muscles is minimal in diving ducks because they tend to be behaviourally flightless and use their legs to power dives throughout the year. Given that Surf Scoters fit this mould, reduced foraging at the start of the moult is potentially a result of energy and nutrients made available by the depleting pectoral muscles. Scoters may rely on endogenous reserves more at the start of the moult until energy stores are depleted. This can allow them to spend more time in safer, offshore, environments when they are less able to escape predators (considering that any remigial growth will allow them to scoot faster as they flee from a disturbance). Alternatively, the disparity observed might result from a change in prey biomass on moulting grounds. If prey depletion occurs over the course of the moult, more time would be required to find and ingest an equivalent amount of prey at the end of the moult than at the start (Tome 1988, Lewis et al. 2007).

Regression Tree Analysis –Foraging patterns of moulting Surf Scoters were most influenced by time of day, as discussed previously. Tide levels had little impact on the distribution of foraging times as these were always concentrated in the morning or evening. This finding is not surprising considering the small tidal amplitude (~1 m) in the area and that scoters usually foraged in subtidal habitats. Frimer (1994) found that tides had little effect on the foraging patterns of King Eiders since they too tended to associate with deeper waters. Common Eiders on the other hand use intertidal zones and their feeding behaviour is consequently affected by the tides (Petersen 1980).

The effect of daylength on scoter activity is similar to that affecting King Eiders which foraged more intensely as days became shorter (Frimer 1994). Daylight diminished by more than two hours over the course of the moulting period. It appears that this is sufficient to affect foraging behaviour. A negative relationship between daylength and time spent foraging also lends support to the claim that Surf Scoters do not forage nocturnally (Lewis et al. 2005). Based on these findings we suspect that the allocation of time to foraging and resting by flightless Surf Scoters is optimal and that any changes affecting the proportion of each needs to be balanced, as is the case with decreasing daylength (Systad et al. 2000). Consequently it is important to determine how increased anthropogenic disturbance can affect foraging times and whether this can induce nocturnal foraging (Frimer 1994).

Conclusion

Surf Scoters allocated a large portion of their time to foraging and most of this activity was restricted to morning and evening hours. Because of their strong aversion to disturbance and high energetic requirements, disturbance should be minimized during wing moult. Consequently, this should be considered when planning any management activities. Since moulting sites are generally far from the coastline, changes in path and volume of traffic on shipping lanes are most likely to cause disturbance. Flightless scoters stop feeding when disturbed, thus it is imperative that shipping be minimized during the early morning and late afternoon periods. Hence, any boat traffic that must pass through moulting grounds should do so at midday. Similarly, while the nocturnal behaviour of flightless Surf Scoters is unknown, shipping is likely to have reduced impacts at this time since foraging is not believed to occur.

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Sampling design

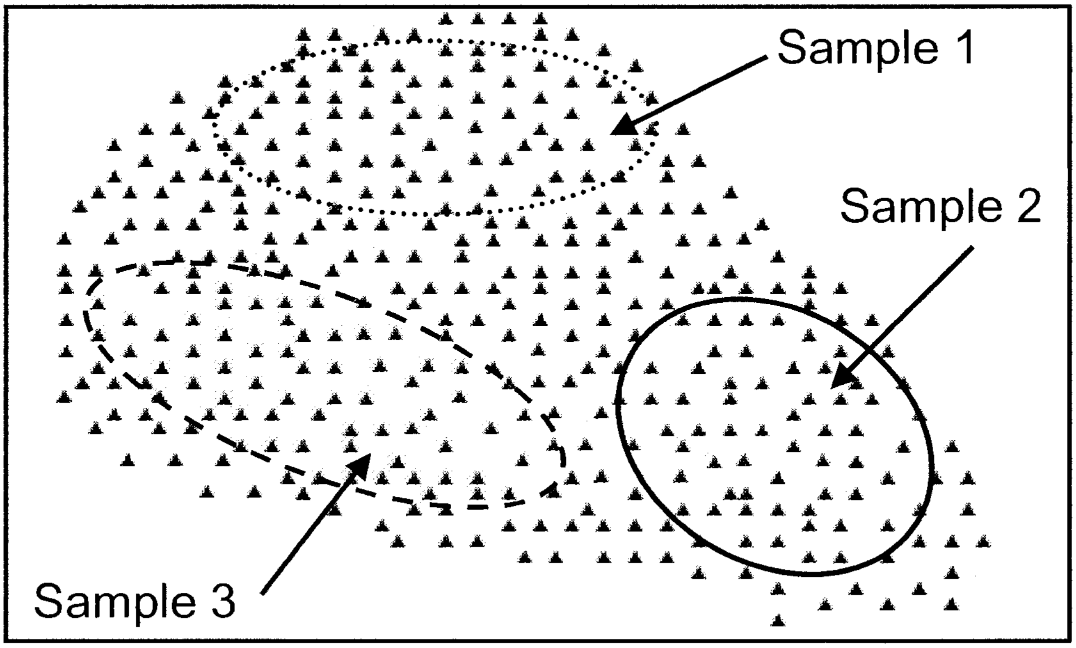
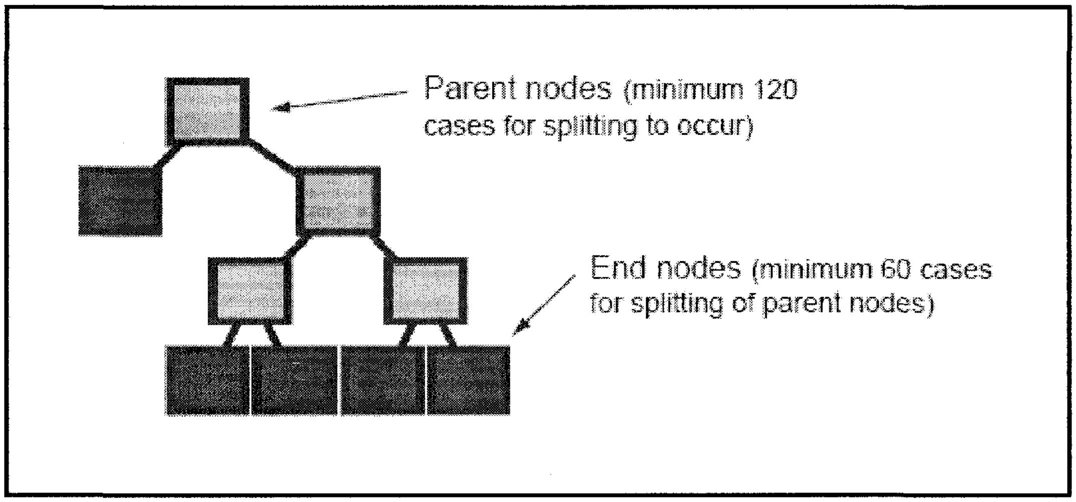


Figure 2.1 – Sub-sampling within a flock of Surf Scoters. Flocks are divided into sections and the behaviour of 50 birds, chosen at random, from each section is recorded.

Regression tree structure



Parent nodes (minimum 120 cases for splitting to occur)

End nodes (minimum 60 cases for splitting of parent nodes)

Figure 2.2 - Structure of a regression tree showing splitting restrictions on parent and end nodes.

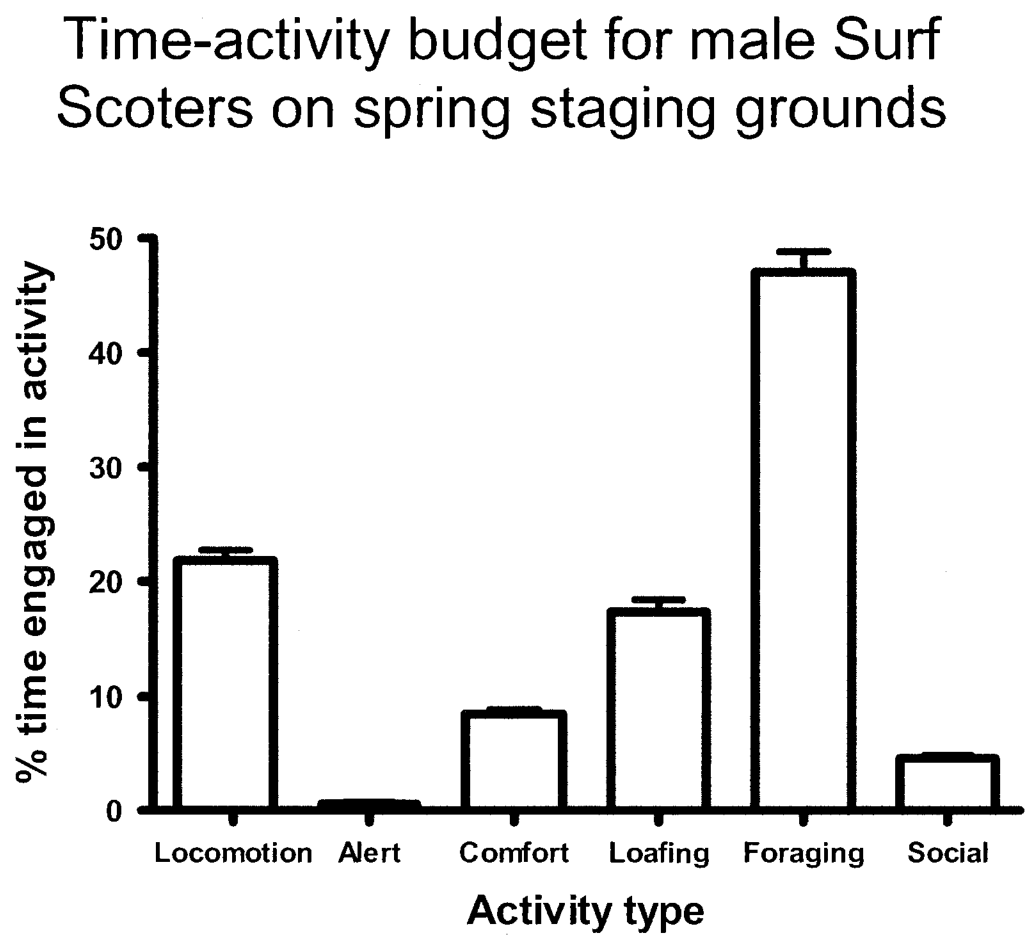


Figure 2.3 – Time-activity budget for Surf Scoters on their spring staging grounds. Column height indicates proportion of time engaged in each activity (±SE). Social interactions include both aggression and courtship displays.

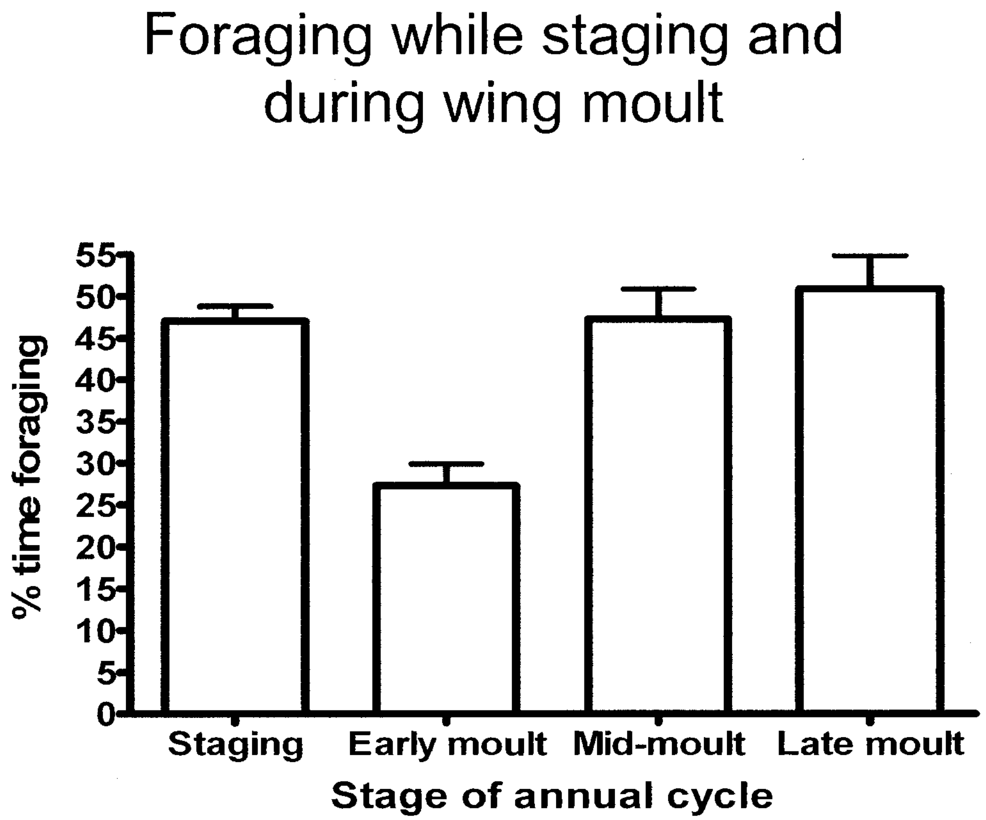


Figure 2.4 - Proportion of time (±SE) spent foraging by Surf Scoters during different stages of their annual cycle. The spring staging period is not divided, while wing moult is separated into three roughly equivalent periods.

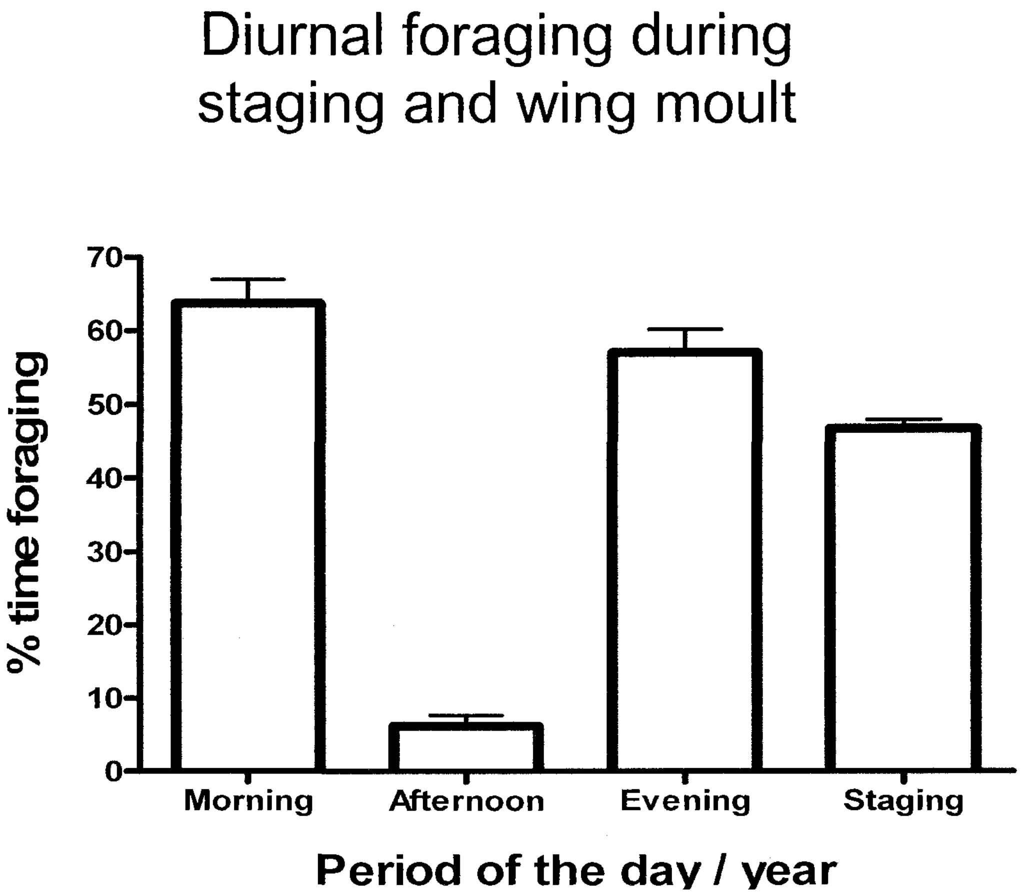


Figure 2.5 - Proportion of time spent foraging (±SE) during three separate periods of the day throughout the wing moult. No differences in proportion of time spent foraging exist between periods of the day during spring staging. Consequently, mean proportion of time spent foraging (±SE) for an entire day is displayed for comparison to moult.

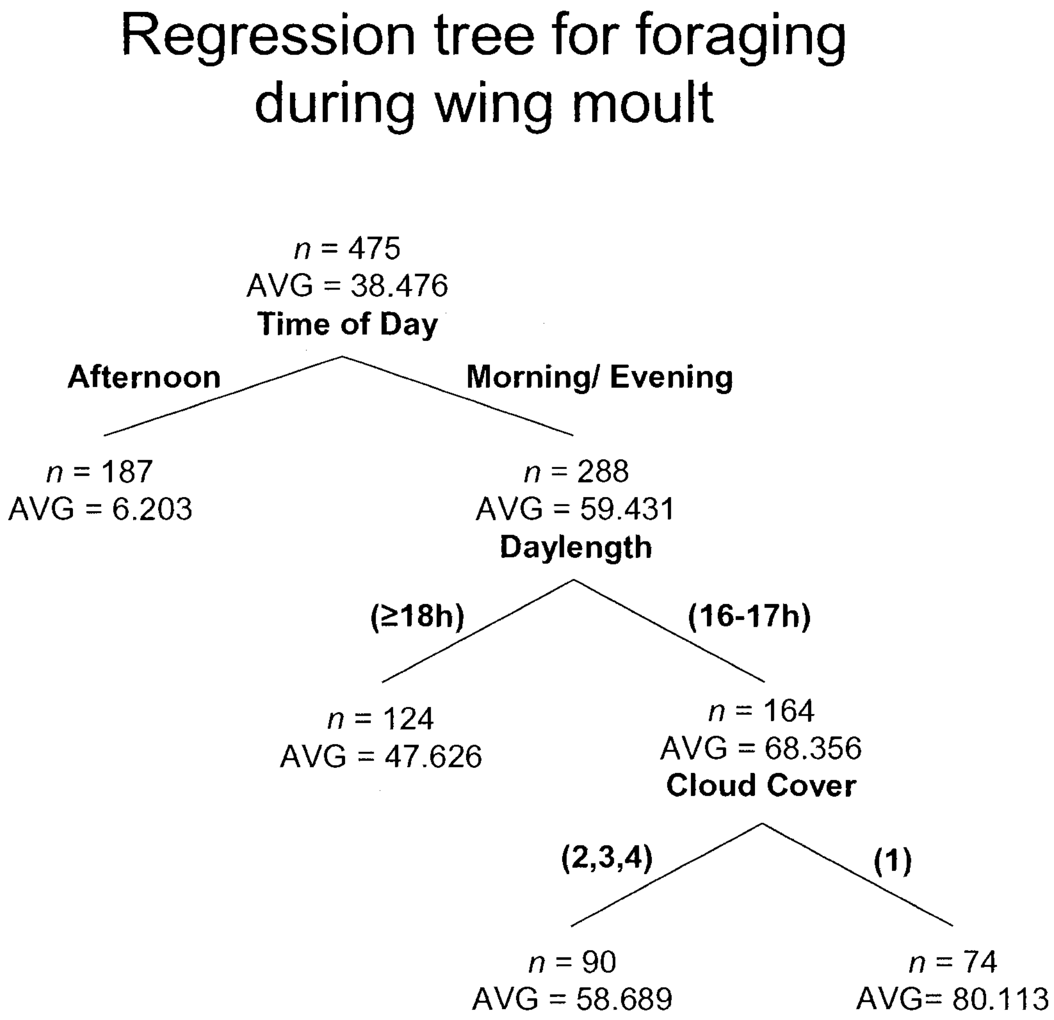


Figure 2.6 - Regression tree analysis of foraging data for wing moult period. The first line of each node indicates the number of observations included in that node. AVG is the average proportion of foraging time in the given sample. In non-terminal nodes, the third line indicates the splitting variable, used to produce new child-nodes. Values on diagonals indicate the categories included in the next node. Branching to the left indicates less foraging.

Sex ratio during wing moult

Table 2.1 –Sex ratio of Surf Scoters (proportion male) as estimated during spring staging and moulting.

Date of Scan	Males Observed	Females observed	Sex Ratio	Total Ratio (F/M)
5-May	400	203	0.66	0.67
7-May	400	188	0.68	
28-Jul	1000	10	0.99	0.98
1-Aug	560	13	0.98	
10-Aug	1000	26	0.97	

CONNECTING TEXT

The preceding chapter compared the behaviour of Surf Scoters at two periods of the year. During the spring staging period, behaviours were found to be relatively constant throughout the day. In contrast, moulting scoters expressed a distinct diurnal pattern which was likely related to their vulnerability and energy demand during this time.

The energetic constraints faced by moulting scoters suggest that they should reduce their movements while flightless. In addition, if optimal moulting habitats are selected, then movements should be restricted around areas with abundant resources that are free from predation. Considering this, Chapter Three investigates the extent and patterns of movement observed during wing moult. In addition, the accuracy of the satellite telemetry methods used in this study are evaluated.

CHAPTER THREE

HOME RANGE AND MOVEMENTS OF FLIGHTLESS SURF SCOTERS (*MELANITTA PERSPICILLATA*) AS DOCUMENTED BY SATELLITE TELEMETRY

Abstract

We used satellite telemetry to follow the movements of seven Surf Scoters (*Melanitta perspicillata*) during their wing moult in northern Labrador. Core areas used during the wing moult were small (3.3 ± 1.3 km^2), suggesting that the birds were quite sedentary throughout this period. However, long range movements (as much as 17 km per day) by some individuals reveal the high mobility of Surf Scoters, even while flightless. Considering that birds used different foraging and resting sites on a daily basis also suggests that despite the constant presence of birds at a study site, there was likely significant turnover of individuals. Finally, we showed that given a duty cycle sufficiently short to receive several high quality locations per day, satellite telemetry can be a useful tool for studying daily movements of wildlife.

Introduction

In most waterfowl, the prebasic moult occurs during the summer months and is characterized by a complete and simultaneous replacement of primary feathers (Humphrey and Parkes 1959, Palmer 1976, Pyle 2005). A 3-4 week period is required before birds regain their ability to fly, rendering them very vulnerable to predation (Hohman et al. 1992). As such, weight loss during wing moult is thought to be an adaptive strategy by which birds can reduce wing-loading and speed their return to flight (Owen and Ogilvie 1979, Brown and Saunders 1998). Moulting waterfowl also face high energetic demands associated with feather replacement (King 1974, Ankney 1979, Fox and Kahlert 2005). Given these constraints, they tend to seek optimal refuges where food is abundant and predation pressure or disturbances are minimal (Salomonsen 1968, Hohman et al. 1992). Such refuges tend to occur in northern, coastal waters where sea ducks aggregate in large flocks (Salomonsen 1968). The flocks are dominated by males since their lack of parental investment allows them to leave breeding grounds earlier than females (Afton and Paulus 1992, Baldassarre and Bolen 2006).

Due to their secretive nature, and the remoteness of areas used, most studies pertaining to the movement of moulting waterfowl have been restricted to identifying large scale patterns. In many cases, only the timing and direction of movement towards and away from moulting grounds have been documented (Oring 1964, Yarris et al. 1994, Phillips et al. 2006, Savard et al. 2007). While the mobility of flightless ducks is obviously limited during moult, little is known about the extent of their movements at this time of year. Mallard (*Anas platyrhynchos*) and Wood Duck (*Aix sponsa*) hens appear to be relatively sedentary while moulting, but this varies for some individuals depending on the habitats they use (Gilmer et al. 1977). Similarly, flightless Black Ducks (*A. rubripes*) that were not displaced during the study by Bowman and Longcore (1989) were relatively sedentary, and travelled less than 1 km from the initial capture site over the course of the moult. More recently, it was shown that while the number of birds present in aggregations of moulting Long-tailed Ducks (*Clangula hyemalis*) remains relatively stable, there is significant turnover of the individuals present. The extent of this turnover appears to depend upon the contiguity of the moult site, with birds less likely to move when forced to cross open water (Flint et al. 2004). Discrepancies in site fidelity observed between dabbling and sea ducks are potentially related to differences in the moulting habitats they select. The open water habitat provided by coastal refuges allows sea ducks to cover large distances more effortlessly than other waterfowl that must cross expanses of land to change watersheds (Schmidt-Nielsen 1972, Biewener and Corning 2001). In fact, Long-tailed Ducks were observed travelling >15 km while flightless (Flint et al. 2004) and a moulting Surf Scoter marked with a nasal tag was observed >30 km from its original capture location (S. Gilliland, pers. comm.).

Considering the potential for long-distance movements by moulting sea ducks, and the lack of knowledge associated with local movements, it is important to gain a better understanding of the area required by moulting sea ducks. This will help in designing effective marine protected areas for important moulting sites. The miniaturization and improved accuracy of satellite transmitters makes this technology appropriate for tracking waterfowl (Keating et al. 1991, Gillespie 2001, Green et al. 2002, Fox et al. 2003). While satellite telemetry is most frequently used to track large-scale patterns, local movements have been studied in a number of species (McConnell et al. 1999, Merkel et al. 2006, Soutullo et al. 2006). In the current study, satellite telemetry is used to document the local movements and overall area used by flightless Surf Scoters (*Melanitta perspicillata*). In doing so, we also address the accuracy of the satellite telemetry system used and assess its ability to track small scale movements.

Methods

Study Area – During the summer of 2006, 15 Surf Scoters having recently initiated wing moult were captured at one of several major moulting sites (Iglosiatik Island; N 56°14', W 61°06') off the coast of Nain, Labrador and fitted with satellite transmitters. Iglosiatik Island is large and relatively isolated from other islands, which likely minimizes the potential for long distance movements.

During banding efforts, Surf Scoter flocks were encountered in numerous locations along the shores of Iglosiatik. Bathymetry studies have not been conducted, thus it is impossible to identify all potential foraging habitats. However, the waters immediately surrounding most islands are relatively shallow and likely provide suitable habitat for the growth of molluscs.

Capture and Marking – Capture and marking of moulting Surf Scoters was accomplished by the Canadian Wildlife Service and U.S. Fish and Wildlife Service. Birds were captured by driving flocks into 150 x 4 m gill nets (89 mm mesh size) using 3 small boats and hazing devices (Gilliland et al. 2005). All birds had 40g Platform Transmitter Terminals (PTT; Microwave Telemetry Inc., Columbia, MD, USA) surgically implanted into their abdomen (Olsen et al. 1992, Korschgen et al. 1996). Each transmitter was programmed with a continuous transmission cycle of 3 hours ON followed by 4 hours OFF, for a period of 39 days, to assure detailed coverage of the moulting period while preserving battery life to document subsequent migratory activities (Merkel et al. 2006). Temperature sensors in each unit helped differentiate between bird mortality and transmitter malfunction (Malecki et al. 2001, Miller et al. 2005).

Analysis of Area Used – Locations were downloaded from the Argos satellite system (Service Argos Inc., Landover, MD, USA). Each location was assigned to a location class (LC) based on its estimated accuracy and the number of transmissions received during a satellite overpass. The best locations (LC = 3, 2, 1) have an estimated error of 250, 500 and 1500 m radius respectively. Auxiliary location classes (0, A, B, Z) result from too few transmissions during a satellite overpass to predict accuracy, which consequently is highly variable (Argos 1996). To ensure that only valid positions were selected, location data were filtered using the Douglas Argos-Filter Algorithm v7.03 (Douglas 2006). To make confident estimates, we retained all positions with the highest accuracy (LC = 3) and, using the minimum-redundant-distance (MRD) filter, all successive LC = 2 locations within 1 km of another point. We estimated the end of the flightless period to coincide with a 75% regrowth of the 9th primary based on a 2.6% day^{-1} growth rate (Van de Wetering and Cooke 2000) and known mean length of fully developed feathers (D. Esler, unpubl. data). All locations during flightlessness, as well as during a 5-day grace period following return to flight, were included in analyses.

Tests to detect autocorrelation were not conducted since, based on the duration of duty cycles, it is known that data are autocorrelated. Using auto-correlated data can negatively bias estimates of home range size in long term studies (Swihart and Slade 1985), but the effect is minimal when an animal has sufficient time to delineate the boundaries of its home range (Reynolds and Laundre 1990, Otis and White 1999). Because scoters were tracked throughout the flightless period, they inevitably crossed the entire area used. In addition, maximizing the number of valid positions improves the precision of most home range estimators (Rooney et al. 1998, Girard et al. 2002).

The area occupied by moulting Surf Scoters was found using the adaptive kernel home range estimator in the Home Range Extension (Rodgers and Carr 1998) of ArcView GIS (v2.04). Smoothing parameters used were chosen using least squares cross-validation (Seaman and Powell 1996). Unlike other estimators, the kernel method shows little bias when autocorrelated data are used (Worton 1989, Swihart and Slade 1997, de Solla et al. 1999). In general, this method provides a better estimate of home range than do others such as minimum convex polygon (MCP) or harmonic mean (Kernohan et al. 2001). For each individual, area used was estimated using both 50% (core areas) and 95% probabilistic home ranges. In addition, all 50 % home ranges were superposed, and the area of overlap was measured to identify sites important to moulting scoters.

Movement analysis – Daily distance travelled was calculated as the sum of the distances between all consecutive locations, separated by ≥1 h, and obtained during a 24 h period. Additionally, for each period of the day (morning, afternoon, evening, night), the arithmetic center of all locations obtained (ACP) was computed. Successive distance between each period also yields an estimate of the distance travelled in a given day. Fidelity to foraging and resting sites was determined by calculating successive distance between ACPs obtained for each day of the moulting period. A change in the location from day to day suggests that birds do not use specific foraging or resting sites. Differences in the mean distance travelled between birds were evaluated using ANOVA with significance attained at $P < 0.05$.

Location accuracy – Of the scoters that succumbed after satellite transmitters were implanted, four continued transmitting from a sessile location. While the exact location of these birds remains unknown, it was estimated, for each individual, as the mean center of all LC = 3 locations obtained during the moult. The locations obtained were centered on this location without any indication of directional bias. Considering this, the distance of each observation from the theoretical centre can be calculated using $D_i = \sqrt{(x_i - \mu_X)^2 + (y_i - \mu_Y)^2}$, with x-coordinates representing the longitude and y-coordinates representing the latitude of each position. Subsequently, a 95% CI representing the maximum distance between the true location and the position received for each location class can be estimated based on the sample variance (B. Collins pers. comm.). Since signals received from sessile transmitters can overestimate location accuracy (Blouin et al. 1999) the current estimate represents ideal transmitting conditions at our study site. Considering this, it is possible that the accuracy of locations was slightly overestimated.

Results

Mortality and transmission – Seven Surf Scoters (53%) did not survive past the first week following PTT attachment, as indicated by a decrease in transmitter temperature. Six individuals succumbed within two days following post-operative release, and the last before the end of the first week. Four PTTs continued to emit signals, post-mortem, from a fixed location, indicating they either drifted onto a beach, or were carried there by an aerial scavenger. Among the eight remaining transmitters, seven emitted signals until the end of the moult while one ceased transmitting (temperature sensor indicated the bird was alive) after 16 days following deployment. Only individuals for whom locations were obtained until the end of moult were considered during analysis. The number of transmissions from the surviving birds, including data from all location classes and all auxiliary locations, was 5844 ($\bar{n}$ = 820.6 per transmitter; SD= 63.8). Greatest number of locations were obtained for LC = 2 (n = 1241) and LC = 3 (n = 1785) categories. The Douglas Argos-Filter succeeded in removing nearly 20% of all locations, including over 23% of LC =1 and nearly 9% of LC = 2 data.

Area use – One individual (SUSC5) used two distinct sites over the course of moult; their areas were measured separately for the current analysis. Number of locations (LC = 2 and LC = 3) used per individual per day during home range analysis (Table 3.1) was 10.59 ± 1.29. Mean 95% home range size was 25.37 ± 2.82 km^2 and the mean core area used (50% home range) was 3.17 ± 0.46 km^2 (Table 3.2). A zone of overlap occurred in the 50% home range of four individuals; its area was 1.02 km^2. The area in question is situated near the south-eastern tip of Iglosiatik Island, where one of the largest Surf Scoter assemblages (up to 2,500 individuals) was observed throughout the course of the study.

Daily Movements – Mean distance travelled per day (Table 3.3) varied between individuals for both the ACP (P = *0.040*) and summation methods (P = *0.041*). Values obtained using the ACP method averaged 2.3 ± 0.54 km less than those obtained from the summation method. Mean daily displacement was 5.36 ± 1.18 km (90% < 10 km) for the ACP method and 7.67 ± 1.19 km (80% < 10 km) for the summation method. In both cases, long distance movements were usually the result of birds moving several kilometres offshore and returning to forage in near-shore habitats later the same day. In some cases, birds spent the day travelling towards another island, or archipelago where they generally remained for at least 1 day prior to returning to Iglosiatik. Permanent displacement to new moulting grounds was observed by two individuals. One scoter (SUSC2) moved into Voisey's Bay (18 km NW of Iglosiatik) immediately upon release while the other (SUSC5) remained at Iglosiatik for 7 days before moving 14 km south to Tunungayualok Island, then another 10 km east to moult along the coastline near Gibraltar Island (approx. 23 km total displacement).

Site fidelity – Site fidelity was assessed based on the distance between the locations of individuals during each time period, on consecutive days (Table 3.4). Distances travelled between consecutive morning foraging sites did not differ between individuals (P = 0.514). Mean distance between consecutive foraging sites for the morning period was 2.21 km (n = 142, SD = 2.19, range = 1.52 – 2.74). Similarly, distances between afternoon resting areas did not differ between individuals (P = 0.110), as each shifted by an average of 2.09 km (n = 133, SD = 1.92, range = 1.47 – 2.99). The degree of fidelity differed between individual scoters for both the evening (P = 0.08) and night (P = 0.046) periods; during the evening, daily locations shifted by an average of 2.02 km (n = 127, SD = 2.11, range = 0.86 – 2.97) and nighttime resting sites differed by an average of 1.77 km (n = 124, SD = 1.68, range = 0.91 – 2.52) per day. Of particular interest is that birds often spent the night at inshore areas that were commonly used for foraging during the day.

Location Accuracy – Transmitter accuracy (Table 3.5; LC = 1, 2, 3) was lower than predicted by Service Argos (Argos 1996) for all location qualities. The CI calculated for each location quality represents a radius within which 95% of all points for that location class are found. The highest quality signals (LC = 3), which provided locations within a radius (95% CI) of 659 m were closest to the theoretical true location. Data obtained from LC = 2 signals were accurate to within approximately 1 km. For LC = 1 data, the accuracy was again reduced as this type of signal could only locate birds to within ≥1.7 km despite the fact that all data were filtered following the same process as described for live birds.

Discussion

The current results suggest that satellite telemetry can be used effectively to monitor local movements of waterfowl, or any other organism that cannot be fitted with more accurate tracking devices (Hays et al. 2001, Hulbert and French 2001). While detailed movements cannot be tracked with certainty, the resolution provided by LC = 3 and LC = 2 locations provides a thorough account of the general movement patterns that occur. Using a short duty cycle allows several locations per day to be obtained and facilitates tracking of individuals across their habitats (Arthur and Schwartz 1999, Merkel et al. 2006). Of particular concern is the high mortality rate endured by Surf Scoters during this study. Recent improvement of the surgical techniques has reduced mortality rates associated with implanting transmitters (Olsen et al. 1992, Korschgen et al. 1996, Mulcahy and Esler 1999). Given the high mortality rates observed in this study, implanting transmitters at another period of the annual cycle and planning a change in duty cycle for the moulting period might reduce the disturbance associated with the procedure.

The rarity of long range movements in moulting Surf Scoters is expected. However, as is the case for moulting Long-tailed Ducks, it is possible for a flightless scoter to travel well over 10 km in a single day (Flint et al. 2004). Unfortunately, sufficient data are lacking to determine the cause of such long distance movements. However, they appear to occur independently of disturbance events. The low frequency of disturbance events at these moulting grounds is likely insufficient to permanently displace Surf Scoters from the areas they are using (Kenow et al. 2003). With over 2,000 individuals present on some days there is a strong possibility that prey items were depleted over the course of the moult. Long distance exploratory movements away from the moulting site would thus be expected, but the hasty return of most individuals to the south-eastern tip of Iglosiatik Island suggests that surrounding areas are prey deficient (Tome 1988, 1989).

The discrepancy between daily movements as estimated by the two methods used reflects the detail considered by each. Because the ACP method uses the mean position for each period, it neglects all movements with opposing polarities and as such, likely underestimates the actual distance travelled. In contrast, the summation method accounts for all back and forth movements within a given period. However, the uncertainty associated with data accuracy is compounded for each additional location in a given period. Consequently, the summation of all locations separated by > 1 h likely overestimates the distance travelled. Hence, the range provided by the two estimates likely better reflects the extent of daily movement by moulting Surf Scoters.

Surf Scoters used several foraging and resting areas while flightless. Throughout the study period, large aggregations of foraging birds were generally observed at two separate sites near the south-eastern tip of Iglosiatik Island. These were separated by nearly 2 km and likely reflect much of the variation between feeding sites used. In addition, satellite tracking showed that some birds travel to entirely different foraging grounds for short periods of time. More importantly, the use of different foraging and resting locations indicates that while the number of birds present within aggregations may remain relatively constant there is significant turnover of the individuals present, as is the case with Long-tailed Ducks (Flint et al. 2004).

The presence, at night, of Surf Scoters in areas that are used for foraging during the day could indicate that nocturnal foraging occurs during the wing moult. If such is the case, then moulting scoters forage substantially longer than they do on spring staging grounds. Alternatively, their presence at inshore locations could be the result of reduced disturbance at night. Safety provided by the cover of darkness might prevent birds from expending the energy needed to move offshore as they do during the afternoon hours (Thibault and McNeil 1994).

The 95% and core (50%) home ranges of flightless Surf Scoters indicate that despite some lengthy movements, they are relatively sedentary overall. A 1.02 km^2 overlap in the core area of four out of five scoters that completed moult at Iglosiatik, and the sedentary nature of these ducks, suggests that the Eastern tip of Iglosiatik Island is a particularly important moulting area. Core areas of approximately 3.2 km^2 and 95% home ranges of just over 25 km^2 are intermediate between those of wintering Common Eiders (95% = 67.8 km^2, 50% = 8.1 km^2; Merkel et al. 2006) and Lesser Scaups (*Aythya affinis*; 95% = 15.1 km^2, 50% = 2.8 km^2; Herring and Collazo 2005). Reduced mobility, since wintering ducks are able to fly, probably accounts for much of the reduction in home range size, especially at the 95% home range level, compared with Common Eiders (Merkel et al. 2006). Despite the flightlessness of Surf Scoters, their home ranges may be slightly larger than those documented of Lesser Scaup simply because the frequency of monitoring in this study accounts for temporary movements outside the home range (Herring and Collazo 2005). In addition, the ability to cover large distances by swimming provides Surf Scoters more flexibility in the areas they occupy than is possible for most dabbling ducks during moult (Gilmer et al. 1977, Bowman and Longcore 1989). Despite this, their inability to fly restricts scoters in their choice of habitats. Fidelity to moulting sites has been shown for several waterfowl species (Szymczak and Rexstad 1991, Bowman and Brown 1992, Bollinger and Derksen 1996, Flint et al. 2000) and likely reflects the importance of selecting sites with predictable resources (Hohman et al. 1992). Only two birds tagged in this study survived until the next wing moult. One returned to moult in proximity to Iglosiatik Island, but the other moulted on the southern end of Hudson Bay, some 1,000 km away. The former did not breed and the second nested closer to Hudson Bay than to the Labrador coast. This raises questions about how ties to moulting areas are formed.

The discrepancy between the accuracy of the current tracking system and what has been described previously (Keating et al. 1991, Argos 1996, Britten et al. 1999, Hays et al. 2001) suggests that satellite tracking systems (data filter included) should be evaluated independently for all studies whose conclusions depend upon their resolution. Filtering data prior to conducting any analyses improves the system by removing positions that are not plausible based on successive locations, considering the reduced mobility of moulting scoters. Despite this improvement, the accuracy of LC = 1 signals was just under 2 km which renders them inappropriate for small-scale studies. The accuracy of LC = 3 locations makes them appropriate for tracking local movement patterns over a short period of time. While LC = 2 locations are less accurate, they nonetheless permit daily movements to be followed with relative confidence. Consequently they are useful for small-scale studies, especially during periods when LC = 3 locations are not available.

Conclusion

The successful use of satellite telemetry in this study highlights its usefulness in tracking the daily movements of wildlife. More importantly species that are easily distressed by the presence of humans can be followed remotely without creating any disturbance during tracking. The overall movement patterns observed, suggest that despite their flightlessness, moulting scoters can potentially make large movements (≥ 10 km). Most of their activities are however concentrated within a few square kilometres. As such, localized management of moulting Surf Scoter flocks is possible, but protection of large areas may be needed. However, before more concrete management conclusions can be drawn a more complete understanding of habitat availability and selection during moult is necessary.

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Core areas used during wing moult

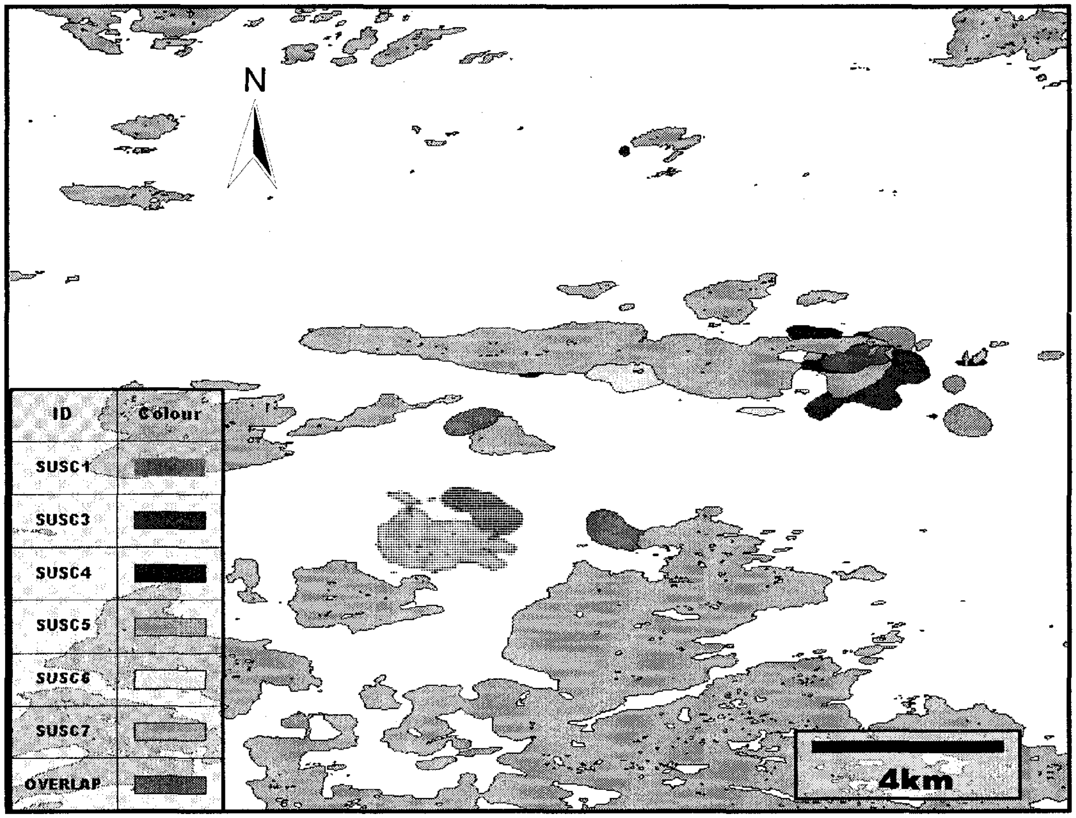

Figure 3.1 – Core areas used by Surf Scoters moulting in proximity to Iglosiatik Island, Labrador, Canada. The red polygon represents a 1.02 km^2 overlap in the core area of four scoters (SUSC3, SUSC4, SUSC5 and SUSC7). SUSC2 is not shown in this diagram because it moulted in another area following PTT attachment.

Surf Scoter locations during moult

Table 3.1 – Positions (± SD) obtained per day per location class (only LC = 3 and LC = 2 locations were retained) for Surf Scoters tracked by satellite telemetry during moult.

ID	Days[a]	Total LC3	LC3 day^{-1}	Total LC2[b]	LC2 day^{-1}	Total LC2+3	LC2+3 day^{-1}
SUSC1	8 (30J-7A)	59	7.38	30	3.75	89	11.13
SUSC2	30 (30J-24A)	140	4.67	127	4.23	267	8.90
SUSC3	20 (3A-19A)	127	6.35	95	4.75	222	11.10
SUSC4	20 (3A-19A)	156	7.80	102	5.10	258	12.90
SUSC5	20 (3A-19A)	134	6.70	75	3.75	209	10.45
SUSC6	31 (30J-31A)	200	6.45	110	3.55	310	10.00
SUSC7	21 (2A-19A)	107	5.35	86	4.30	193	9.65
Mean (± SE)			**6.38 ± 0.41**		**4.20 ± 0.22**		**10.59 ± 0.49**

a Number of days tracked includes estimated flightless period plus a 5-day grace period (J = July; A = August)

b Number of LC = 2 locations represents only those that were not filtered

Area use by moulting Surf Scoters

Table 3.2 – Area used (km^2) by moulting Surf Scoters during the moulting period shown as 95% (overall) and 50% (core) areas.

ID	95% (km^2)	50% (km^2)
SUSC1	20.28	3.70
SUSC2	18.93	4.20
SUSC3	29.69	4.09
SUSC4	33.70	2.33
SUSC5	33.36	4.43
SUSC6	26.90	1.33
SUSC7	14.73	2.08
Mean (± SE)	**25.37 ± 2.82**	**3.17 ± 0.46**

Mean distance travelled by moulting Surf Scoters

Table 3.3 – Mean distance travelled per day (km) by Surf Scoters during the moulting period as calculated using average position for each period of the day (ACP) and summation of all positions ≥1 h apart (SUM).

ID	ACP	Range	SUM	Range
SUSC1	4.20	1.69 - 6.17	7.45	5.00 - 10.82
SUSC2	4.87	0.73 - 12.25	7.39	2.23 - 14.43
SUSC3	6.50	0.98 - 10.98	9.04	2.08 - 12.57
SUSC4	7.09	1.75 - 17.24	9.11	3.93 - 26.25
SUSC5	6.14	1.14 - 16.69	8.18	3.21 - 17.94
SUSC6	4.35	0.65 - 16.65	6.57	1.74 - 15.60
SUSC7	4.41	0.73 - 17.24	5.94	2.19 - 12.48
Mean (± SE)	**5.36 ± 0.45**	**0.73 – 17.24**	**7.67 ± 0.45**	**1.74 - 26.25**

Table 3.4 – Mean distance (km) between consecutive daily locations by Surf Scoters at four periods of the day (morning, afternoon, evening, night) during wing moult.

ID	Morning	Afternoon	Evening	Night
SUSC1	2.62	2.10	1.06	1.52
SUSC2	2.14	1.63	1.34	1.77
SUSC3	2.71	2.99	2.97[ab]	2.52[a]
SUSC4	2.21	2.30	2.83[a]	2.11[a]
SUSC5	2.74	2.65	2.68[a]	2.26[a]
SUSC6	1.52	1.47	0.86[a]	0.91[a]
SUSC7	1.92	1.90	1.51[b]	1.47
Mean (± SE)	**2.27 ± 0.17**	**2.15 ± 0.21**	**1.89 ± 0.34**	**1.79 ± 0.21**

a Mean distance between consecutive evening (P = 0.08) and night (P = 0.046) positions is lower for SUSC6 than for SUSC3,4,5.

b Mean distance between consecutive evening positions is lower for SUSC7 than for SUSC3 (P = 0.008).

Accuracy of the satellite tracking system

Table 3.5 – Accuracy (m) of the satellite telemetry system used to track the movements of moulting Surf Scoters. Transmitters are listed as T-1 to T-4.

Transmitter	LC = 3	LC = 2*	LC = 1*
T-1	781.48	1269.69	2555.90
T-2	664.24	1079.14	1794.03
T-3	464.00	680.96	1149.12
T-4	726.54	971.72	1536.11
Total (± SE)	**659.07 ± 69.29**	**1000.38 ± 123.01**	**1758.79 ± 296.92**

* Locations from LC = 2 and LC = 1 were first filtered using the Douglas Argo-Filter (Douglas 2006) prior to estimating accuracy.

SUMMARY AND CONCLUSIONS

The wing moult period is particularly energy demanding compared to other periods of the year for waterfowl. Because of this, and due to the increased vulnerability caused by flightlessness, adaptations are expected that allow ducks and geese to cope more easily with the added pressures of this period of their annual cycle. For example, weight loss while moulting is thought to speed the return to flight; thereby minimizing the vulnerability to predation. Comparing the behaviour of Surf Scoters on their moulting grounds to the way they conducted themselves during a spring stopover on the north shore of the Saint-Lawrence Estuary identified potential behavioural adaptations present in this species. First, as is the case with most moulting waterfowl, they became more wary of human presence and fled from greater distances than while staging. The second major change in behaviour, and the most interesting, was a complete shift in foraging and resting behaviour compared to the spring period. Instead of foraging throughout the day as they did during staging, moulting scoters foraged in the morning and evening and rested far offshore during the afternoon hours. Additionally, during the earliest stage of the flightless period, less foraging was observed than during the later stages. Interestingly, proportion of time spent foraging during the later stages was similar to that observed during spring staging. While energetic analyses are necessary to better understand this pattern, it is probable that it allows the ducks to balance their energy requirements while minimizing their chances of being preyed upon. This is based on reduced predation risk in offshore habitats where resting took place, and a potential reduction in energy expenditure during the early stages of the moult when endogenous reserves may have been used to fuel feather growth.

The change in energetic requirements, combined with reduced mobility during the wing moult period suggests that waterfowl should remain relatively sedentary during this period. In fact, many dabbling ducks that moult on small ponds remain in the same location throughout the moult. However, in the case of sea ducks it appears that their ability to swim to new habitats makes long range movements more energetically affordable. In fact, Surf Scoters marked with PTTs were observed moving to new moult sites (14 km; 23 km) on two occasions and it was not uncommon for individuals to temporarily undertake long movements. This indicates that large areas are required by moulting Surf Scoters. However, since the majority of activities are carried out in relatively small areas, these may be more appropriate for management purposes.

Together, these findings suggest that while they are subject to a high energy demand, Surf Scoters can moult successfully in waters of the Labrador coast. Despite their potential for long range movements, the reduced mobility of moulting ducks makes it unlikely that they will be displaced by low levels of disturbance, despite their strong adverse reaction towards human activity. Considering this, it is important that when human activities must be carried out in proximity to moulting grounds, they be planned to minimize their impacts on the birds present.

APPENDIX I

DIVE DURATION IN MOULTING SURF SCOTERS

Dive	2005 dive duration (s)	2006 dive duration (s)
1	58	63
2	48	58
3	55	58
4	55	63
5	57	61
6	59	42
7	58	64
8	57	57
9	56	58
10	48	48
11	47	58
12	58	56
13	50	50
14	56	58
15	56	56
16	60	65
17	47	58
18	43	
19	55	
20	53	
21	47	
22	55	
23	50	
24	49	
25	44	
26	44	
27	48	
28	40	
29	42	
30	39	
31	41	
32	39	
33	48	
34	44	
35	46	
36	52	
37	41	
38	48	
Mean (± SD)	49.82 ± 6.32	57.24 ± 5.93

Dive times were calculated from the time the first bird dove until the first bird resurfaced. Since flock synchrony was very high, this estimate should be representative of individual dive lengths.

APPENDIX II

DISTURBANCE EVENTS DOCUMENTED DURING MOULT

Date	Time	Source	Reaction	Duration	Considerations
July 25	10:00	Plane engine	All disturbed, moved offshore	Displaced	
	12:10	Seals surfacing	All scattered	10 min	
	17:40	Plane engine	All disturbed, moved offshore	30 min	
July 26	15:15	Cargo ship	All disturbed, moved offshore	Displaced	
July 28	10:00	Motor boat	All disturbed, moved offshore	Displaced	Birds driven for banding purposes
	17:15	Plane engine	All disturbed, ceased foraging	5 min	
August 1	14:20	Motor boat	All disturbed, moved offshore	Displaced	
August 2	10:05	Cargo ship	S of Iglosiatik - moderate reaction	5 min	Strong winds, ship passes closer to N
			N of Iglosiatik - all disturbed, offshore	Displaced	
August 3	12:05	Oil tanker	S of Iglosiatik - all disturbed, offshore	Displaced	Birds on N only reacted after ship passed tip of island (sound barrier)
			N of Iglosiatik - all disturbed,offshore	Displaced	
August 6	17:05	Hunters	All disturbed, moved offshore	Displaced	Birds shot at, dispersed, regrouped offshore
August 8	15:45	Military vessel	S side of Iglosiatik - No reaction	No change	Vessel audible from N only due to proximity and wind
			N side of Iglosiatik- all disturbed, offshore	Displaced	
August 17	17:15	Oil tanker	Most disturbed, offshore	Displaced	Birds behind Seniarlit did not react (furthest)