THE REPRODUCTIVE BEHAVIOUR AND ECOLOGY OF SABINE'S GULLS (Xema sabini) IN THE EASTERN CANADIAN ARCTIC

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THE REPRODUCTIVE BEHAVIOUR AND ECOLOGY OF SABINE'S GULLS (*Xema sabini*) IN THE EASTERN CANADIAN ARCTIC

by

A thesis submitted to the
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ABSTRACT

Life history theory focuses on how phenotypic traits interact to determine an organism's fitness, which is generally measured in terms of survival and reproduction. An animal's behaviour is a critical component in its ability to survive and reproduce, because natural selection promotes individuals that are behaviourally efficient.

Like many avian species breeding at high latitudes, the reproductive behaviour and ecology of Sabine's Gull (*Xema sabini*) has been rarely studied. This species nests in coastal wetland tundra across the Arctic, and winters at cold-water upwelling zones in the Tropics and Subtropics. It is considered an atypical gull, both morphologically and behaviourally, and is recognized as phylogenetically distinct.

At East Bay, Southampton Island, Nunavut, Sabine's Gulls nested on mossy edges of freshwater ponds, and were non-randomly distributed across the study area and within nesting habitat. Compared with other gulls, they exhibit several distinct ecological traits. They had relatively short incubation and fledging periods, and, within 24 hours of hatching, families relocated to post-hatching territories at the shoreline. These aspects of their reproductive ecology, which differ from other gulls, are likely adaptive traits that have evolved in response to specific characteristics of their Arctic breeding areas.

Sabine's Gulls also exhibit a number of behavioural traits that are typical of gulls. Pairs showed strong site-tenacity and mate-fidelity from year to year. Throughout incubation and early brooding, males and females showed high reproductive investment. Overall, they shared parental duties equally, although there was considerable variation among pairs. Sabine's Gulls distinguished between threatening and non-threatening species close to their nests, and both members of a pair were aggressive towards predators. Although the relative intensity of response did not change over time, it did differ among predator types. Reproductive success was variable among years, and indirectly influenced by availability of microtine rodents, via their shared predators. The local annual survival rate, estimated at 0.89 ± 0.04, was close to those of other gull and tern species.

Overall, the evolution of Sabine's Gull life history traits appears to have been influenced by both their phylogeny and the particular ecological conditions of their breeding environment, and/or interactions between these.

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1.0 Introduction and Overview

The theory of evolution by natural selection is founded on the existence of phenotypic variation among individuals of a particular species (Darwin 1859). In other words, within a given population, each characteristic of the species varies between individuals. Many studies have shown that aspects of phenotypic variation that exist among and within natural populations are inherited and, therefore, genetic in origin (Merilä & Sheldon 2001). However, full siblings reared in contrasting environments often develop different phenotypic traits, despite their shared genetic background (Merilä 1997), indicating that phenotypic variation is also under the influence of particular ecological conditions (Nager *et al.* 2000). Thus, the process of natural selection results in organisms that exhibit life history traits that reflect both their phylogeny, or evolutionary history, and their adaptive responses to their recent environment (Ligon 1993).

In *The Origin of Species*, Darwin (1859) recognized that descent from common ancestry often results in similarities between species, while differences between closely related species are more likely due to evolutionary adaptation to different environments. Comparing closely related species living in different habitats can often reveal aspects of life history and behaviour which are particularly important in adapting an animal to its specific environment (McFarland 1999). Thus, the comparative approach is an important element in behavioural and ecological studies.

Generally, life history theory focuses on how phenotypic traits interact to determine fitness (Nager *et al.* 2000). An organism's fitness, a function of its genotype and its particular ecological setting, is generally measured in terms of survival and reproduction (Roff 1992).

Clearly, an individual's overall fitness is best measured in terms of lifetime reproductive success, which can only be achieved through long-term studies of individual life histories. There is still, however, a great need to investigate the consequences of particular reproductive decisions, even over the short-term (Clutton-Brock 1988). Furthermore, although reproductive costs can be inferred from straightforward observational studies, manipulative field experiments are more likely to provide conclusive evidence (Harvey *et al.* 1988).

An animal's behaviour is a critical component of its ability to survive and reproduce, because natural selection tends to promote individuals that are efficient at foraging, caring for offspring, avoiding predators, etc. (Krebs & Davies 1993). The constraints of limited resources, however, prevent natural selection from maximizing all life history traits simultaneously, thus, inevitably, individuals face trade-offs between competing priorities (Stearns 1992). The most appropriate action an animal can take at any particular moment in time will depend on the behavioural alternatives available, and the costs and benefits of each of those alternatives (McFarland 1999).

An individual's reproductive decisions may be influenced by both intrinsic factors, such as its ability to recognize and select suitable nesting habitat and the resources it has available to contribute to parental activities, and extrinsic factors, such as inter-annual variation in phenology and predation pressure. Ultimately, the dynamic interactions between and among these factors may have considerable effect on demographic patterns and processes.

The reproductive success of birds is influenced by many factors, resulting in between-season as well as within-season differences (Lack 1966). Factors, such as the availability of suitable habitat, access to food resources, the extent of predation, and environmental conditions, generally affect populations (Lack 1968, Clutton-Brock 1988). Finer-scale factors, however, such as body size, age and experience, and mate quality, are also known to affect the reproductive success of individuals within populations (Lack 1968, Scott 1988). Thus, to understand the significance of adaptive traits, it is necessary to identify how specific variables affect different components of a species' reproductive behaviour and ecology (Clutton-Brock 1988).

1.1 STUDY SPECIES

The Sabine's Gull (*Xema sabini*) is a trans-equatorial migrant, which breeds at high latitudes in the Arctic and winters at cold-water upwellings zones in Tropical and Sub-tropical regions of the eastern Atlantic and Pacific oceans. The species was first described by Edward Sabine in 1818 at Melville Bay, Greenland (Sabine 1819). It is a small monomorphic gull (27-32 cm) with a forked tail, rare among gulls, and long narrow wings. It has a striking upper wing pattern of black, white and grey triangles, a black bill with yellow tip, a scarlet orbital ring, and a dark grey hood (in summer) or half collar on nape (in winter: Grant 1986). In North America, Sabine's Gulls breed in western and northern Alaska, and across northern Canada from the Mackenzie Delta, through the central Arctic islands, to the eastern Arctic islands in and north of Hudson Bay (Fig. 1; Day *et al.* 2001). Sabine's Gull also breeds in small numbers in northern and eastern Greenland (Boertmann 1994), and small colonies exist on Spitzbergen (Cramp & Simmons 1983). In the Russian Arctic, it breeds along the northern coasts of Siberia, mainly at major river deltas, from the Taimyr Peninsula to the Bering Sea coast, and on the Novosibirskii Islands and Wrangel Island (Ilyichev & Zubakin 1988).

Sabine's Gulls have been rarely studied and much remains to be learned about most aspects of their ecology (Day *et al.* 2001). Its remote breeding areas are rarely visited, and its wintering areas have only been discovered recently. Siberian and Alaskan breeders winter off the Pacific coast of South America (Chapman 1969) and Greenland and Canadian breeders winter in the South Atlantic off of southern Africa (Zoutendyk 1965, 1968), although a few birds may winter in the north near polynyas (Day *et al.* 2001). In addition, this species is considered aberrant within the gull family (*Laridae*) and is recognized as phylogenetically distinct (Chu 1998), as well as atypical in several aspects of morphology (Day *et al.* 2001), breeding behaviour (Brown *et al.* 1967) and reproductive biology (Stenhouse *et al.* 2001). For example, it is one of only two gulls that have a black bill with a yellow tip, it exhibits a distraction display similar to shorebirds, such as plovers and sandpipers, and it has relatively short incubation and fledging periods. It is precisely these unusual characteristics that make Sabine's Gull an interesting and useful subject for comparative behavioural and ecological studies.

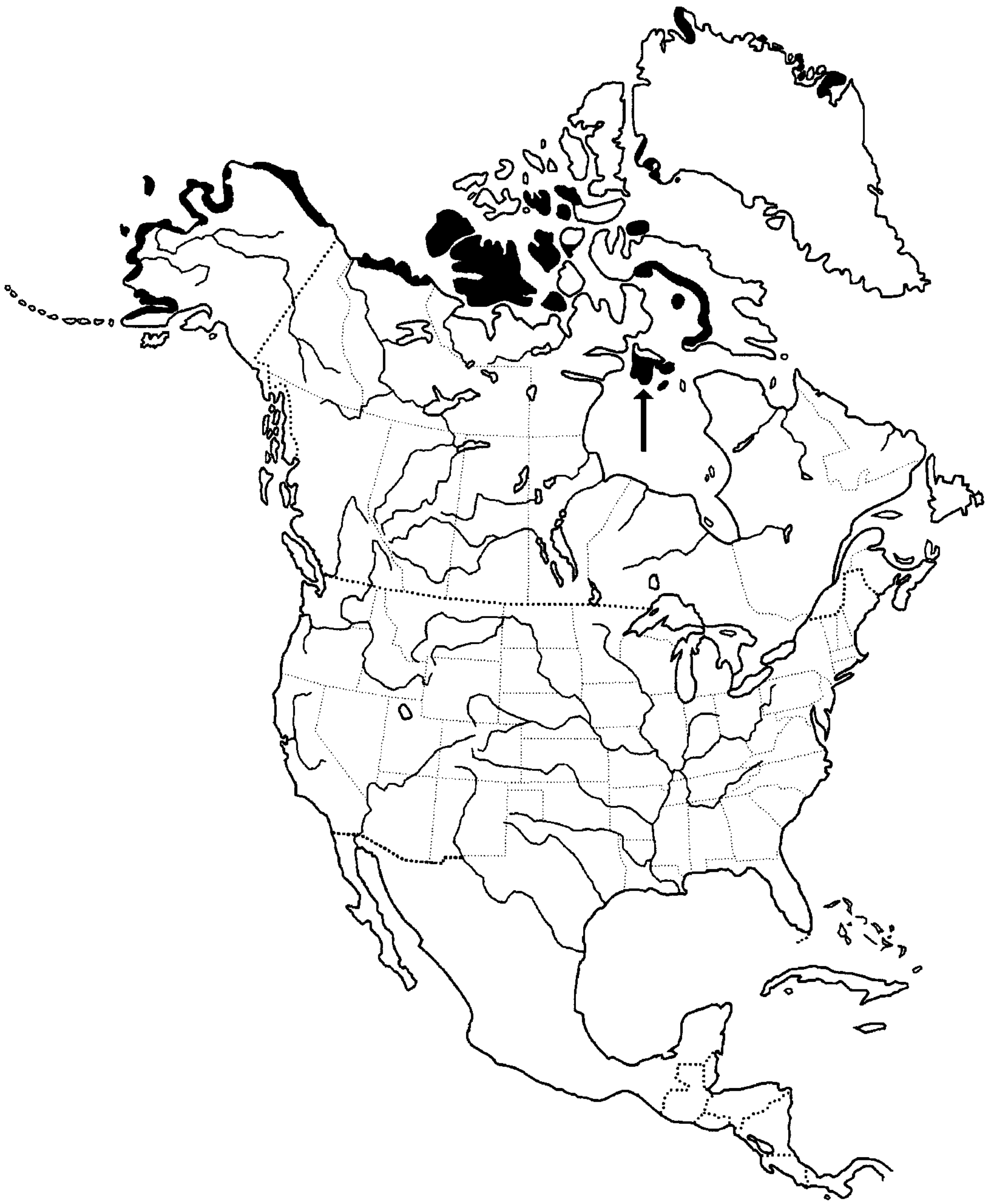

Fig. 1.1: Map of Sabine's Gull breeding range in North America and Greenland, with arrow indicating Southampton Island, Nunavut, Canada (after Day *et al.* 2001).

1.2 STUDY AREA

This study was carried out within the East Bay Migratory Bird Sanctuary (64°01'N, 81°47'W), an area of approximately 1,200 km^2 on Southampton Island, in the Canadian territory of Nunavut. Southampton Island has long been recognized as a breeding area for Sabine's Gulls (Bent 1921), and East Bay is currently the location of a long-term research programme on marine and terrestrial birds (Gilchrist & Heise 1997).

Despite being located within the Low Arctic region, East Bay is generally High Arctic in character, influenced in its ecological and physical characteristics by the deep, cold waters of the Foxe Channel. Land-fast sea ice can remain in East Bay well into July and daily minimum temperatures are usually close to freezing throughout the summer months.

The research camp is located on a raised gravel ridge, perpendicular to and approximately 2 km south of the southern shore of East Bay. The study plot is a 2.5 x 2 km block of low-lying, coastal wetland tundra, with a complex of brackish and freshwater ponds typical of the area. The study area lies immediately north of the camp, between the gravel ridge and the shore of East Bay. Within the study area, sub-habitats are few and distinct, with wetland areas characterized by mosses, sedges and grasses, and drier areas dominated by dwarf shrubs (*Salix* spp.) and Mountain Avens (*Dryas integrifolia*). As a product of the low relief, brackish ponds extend several hundred metres from the shoreline. Areas of high salinity along the shore are colonized by few plants, and are characterized by bare sandy or rocky substrate sparsely broken by small patches of vegetation.

A secondary study area, 8 km west of the main study area, is similar in character and was visited briefly in 1998 and 1999. This site was used by Abraham (1982, 1986, Abraham & Ankney 1984) in a one year study of the foraging interactions between Sabine's Gulls and Arctic Terns (*Sterna paradisaea*). Basic reproductive data from that study provided an opportunity for relatively long-term comparisons of the breeding biology of Sabine's Gulls at East Bay.

1.3 CHAPTER OUTLINES

1.3.1 CHAPTER 2

As little was previously known about Sabine's Gulls, it was critical to first establish basic breeding parameters and life history traits, such as clutch size, breeding phenology, and rate of reproductive success, and to assess the degree of annual variation in these characteristics. An earlier study of the foraging interactions between Sabine's Gulls and Arctic Terns in East Bay (Abraham 1982) provided information on some aspects of the breeding ecology of Sabine's Gulls and the first opportunity for long-term comparison in this species.

Establishing breeding parameters and life history traits also allowed a comparison of the characteristics of Sabine's Gulls with other gull and tern species. At the outset, the most recent reconstruction of phylogenetic relationships within the gulls was based on structural features (Chu 1998), and grouped the fork-tailed gulls (*Xema* and *Creagrus*) with kittiwakes (*Rissa* spp.), and the Ivory Gull (*Pagophila eburnea*). However, recent examination of the phylogenetic relationships among gulls has been based on molecular genetics (Crochet & Desmarais 2000, Crochet *et al.* 2000), and suggests that Sabine's Gull had been incorrectly positioned in previous phylogenetic trees. Crochet *et al.* (2000) grouped Sabine's Gull and Ivory Gull as sister taxa, and suggested that these species last shared a common ancestor around 2 million years ago. Thus, it seemed valuable to compare ecological characteristics of Sabine's Gulls with the species that it was thought to be phylogenetically related to, as well as other gull and tern species.

1.3.2 CHAPTER 3

By definition, annual reproductive success in a genetically monogamous species is equal for both members of a pair (Thomas & Coulson 1988). However, the optimal investment for each parent will depend on the contribution provided by its mate, and, even in biparental species, parental care is not always shared equally between the members of a pair (Houston & Davies 1985). In extreme environments with short breeding seasons, these dynamics may have considerable influence on annual reproductive success. In seabirds, survival of the offspring is highly dependent on extensive investment by both parents (Furness & Monaghan 1987). Studies of several colonially nesting seabird species have clearly shown sexual differences in the division of, and contributions to, parental activities (Montevecchi & Porter 1980, Burger 1981, Butler & Janes-Butler 1983, Morris 1987). In general, females invest more heavily than males (Trivers 1972, Clutton-Brock 1991), but, in at least one seabird species, the Black Skimmer (*Rynchops niger*), males have been shown to provide greater parental care than females (Burger 1981).

Individual differences in the performance of parental care by gulls (Laridae) may contribute to differential reproductive success (Southern 1987) and pairs displaying the greatest synchrony and equitability in parental care have been shown to produce most young (Burger 1981, Morris 1987). Where the benefits of parental care are similar for males and females, however, parental care activities are expected to be shared equally.

During this study, I established a colour-banded population of Sabine's Gulls (one of very few in the world). This enabled me to focus on the reproductive roles of individual parents, and the consequences of their respective contributions to parental care. In Chapter 3, I examine the breeding activity of male and female Sabine's Gulls throughout incubation and immediately post-hatch.

1.3.3 CHAPTER 4

It is generally expected that the majority of individuals in a species will select the habitat features that provide the optimal conditions for survival and reproduction (Buckley & Buckley 1980). Furthermore, it is generally assumed that natural selection for optimal habitat will result in non-random distributions (Southwood 1977).

The reproductive success of many avian species depends on breeding habitat selection (Cody 1985). Therefore, birds should have evolved to select features of their environment that maximize reproductive fitness, and, as a result, nesting distributions are likely to be non-random. Long-lived species with delayed maturity, such as seabirds, may have considerable opportunity to assess and compare habitats prior to initiating breeding (Cadiou *et al.* 1994). Furthermore, seabirds may experience their greatest exposure to natural selective forces during breeding, when they have their greatest ties to terrestrial habitats (Buckley & Buckley 1980). Thus, habitat selection can carry considerable evolutionary consequences.

Clark & Shutler (1999) recently reviewed the avian habitat selection literature and concluded that most studies focused on patterns of habitat use, rather than seeking to identify how the process of natural selection has shaped habitat selection. In Chapter 4, I examine both pattern and process in habitat selection. Specifically, I compare characteristics of nest sites and random sites (pattern), as well as comparing characteristics of successful nests with unsuccessful nests (process).

1.3.4 CHAPTER 5

Many species of Arctic-breeding birds exhibit variable annual breeding success (Freuchen & Salomonsen 1958, Larson 1960). These fluctuations were once considered random, and caused by variation in the rate of snow melt between years (Boyd 1987, Owen 1987). However, the Alternative Prey Hypothesis (APH; also known as prey switching or shared predator hypothesis; Roselaar 1979, Summers 1986, Bêty *et al.* 2002) predicts that cycles in avian productivity should also be positively related to small mammal abundance, which could dilute the impact of their common predators (Sutherland 1988). For example, some northern microtine rodent populations exhibit a three to five year fluctuation, with high spring densities prior to peak summers and extremely low spring densities combined with summer declines in crash years (Ylönen 1994). In the years of high abundance, predators such as Arctic foxes (*Alopex lagopus*), prey largely on rodents.

When rodents are scarce, however, predators typically switch their diet to focus on the eggs and young of ground-nesting birds.

Summers (1986) and Summers & Underhill (1987) showed that a three-year cycle in the breeding productivity of Dark-bellied Brent Geese (*Branta b. bernicla*) was positively correlated with the abundance of lemmings (*Dicrostonyx* spp., *Lemmus* spp.) on the Taimyr Peninsula, Siberia. Similar links with small mammal populations have been shown for other Arctic-breeding avian species, including ducks (Pehrsson 1986), grouse (Järvinen 1990), shorebirds (Underhill *et al.* 1989, Summers *et al.* 1998), jaegers (de Korte & Wattel 1988), and passerines (Järvinen 1990). However, most studies have focused on species with weaker nest defence behaviour than Sabine's Gulls.

As in many animals, parent birds often face a trade-off between the care and defence of their offspring, and their own survival (Montgomerie & Weatherhead 1988). Due to the vulnerability of eggs and small chicks, natural selection should favour any behaviour that diminishes their loss to predators. Many birds exhibit conspicuous anti-predator behaviour during reproduction (Redondo 1989). In defending offspring, parents increase the chances of survival of their young, and, in turn, increase their own reproductive fitness, assuming they survive the encounter (Clutton-Brock 1991). Defence behaviour is risky, however, due to the threat of being caught or injured by a predator (Myers 1978). In addition, defence of offspring reduces time and energy available for other essential activities, such as foraging (Walters 1982).

Nest defence has been well studied in altricial species, particularly species which breed in nest boxes, where nest predation is not severe (Brunton 1990). However, this has been studied less often in ground-nesting species, where the nest is easily accessible to predators, and anti-predator behaviour may be critically important in reproductive success (Gochfeld 1984). Anti-predator behaviour, such as calling, chasing, mobbing and distraction displays, has been examined in several shorebird species (Byrkjedal 1987, Brunton 1990, Kis *et al.* 2000). Sabine's Gulls also exhibit all of these of behaviours, some of which do not occur among other gulls. The distraction display of Sabine's Gulls is particularly notable, being more characteristic of shorebirds and jaegers than other gulls (Brown *et al.* 1967, Day *et al.* 2001), suggesting that they have evolved in an environment where predation pressures are particularly intense.

In Chapter 5, I examine the anti-predator behaviour of Sabine's Gulls through behavioural observation and experimental manipulation, and establish links between the breeding success of Sabine's Gulls, the extent of nest predation, and the abundance of lemmings, in a given year.

1.3.5 CHAPTER 6

Understanding features of life history, such as age of maturity, fecundity, longevity and mortality rates, is essential in assessing and predicting population trends (Stearns 1992). In doing so, it may be possible to calculate the strength of selection on life history traits (Stearns 1992), i.e. evolutionary responses of a population to its environment. Furthermore, it is important to establish baseline demographic information necessary to model population dynamics under different environmental stresses over time (Greenwood *et al.* 1993). This may be particularly important for species in the Arctic, where potential climate changes in that environment may be considerable (Maxwell 1992).

There is a lack of knowledge concerning demographic trends of most avian species breeding in the Arctic, including the Sabine's Gull. In Chapter 6, I present some of the first evidence of strong mate fidelity and nest-site tenacity, and the first information on natal philopatry, age of first breeding, and adult survival rates. This information is critical to population modelling, allows comparison of demographic traits with other species, and could allow comparisons between Sabine's Gull populations in future.

1.4 STATISTICAL ANALYSES

I recognize that there is a long-running and ongoing discussion within the ecological literature regarding an over-reliance on statistical hypothesis testing, particularly in reference to biological and behavioural data (Cohen 1990, 1994, Schrader-Frechette & McCoy 1992, Shaver 1993, Carver 1993, Thomas & Juanes 1996, Johnson 1999). However, I have chosen to follow current conventions throughout this thesis, but have attempted to highlight and discuss biological significance, as well as statistical significance, wherever possible.

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1.6 STATEMENT OF AUTHORSHIP

The elements of this project were planned in collaboration with my co-supervisors, Dr. H. Grant Gilchrist and Dr. William A. Montevecchi, with the support of my supervisory committee, Dr. Gregory J. Robertson and Dr. Ian L. Jones. However, I was solely responsible for the specific design of field studies, behavioural observations, and experiments. I was assisted in fieldwork and data collection by a co-worker, Karen Truman, in 1998 and 1999, and by a dedicated field assistant, Rachel Bryant, in 2000 and 2001. They carried out fieldwork under my supervision and followed my existing guidelines and protocols. I was solely responsible for catching and banding all Sabine's Gulls over the course of this study, under banding permit 10650 B. In 2000 and 2001, I collected blood samples from Sabine's Gulls, with the approval of Memorial University's Institutional Animal Care Committee (Protocol Numbers: 00-91-WM and 01-91-WM). Molecular sexing using these blood samples was carried out by Anne-Marie Gale of the Biology Department, Memorial University of Newfoundland.

I collated, entered and analysed all data. I carried out all statistical analyses, with advice from my supervisory committee, with the exception of the adult survival modeling, which was carried out by Dr. Gregory J. Robertson. I interpreted all results and wrote the manuscripts that constitute the chapters of this thesis. I have revised the manuscripts, however, based on the advice and comments of my co-supervisors, supervisory committee members, trusted colleagues, and journal reviewers.

Data on the breeding biology of Sabine's Gulls collected in 1998 and 1999, and analysis and interpretation thereof, included in Chapter 2, were first published in:-

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Chapter 5 - Predation, anti-predator behaviour, and the influence of alternative prey in Sabine's Gulls (*Xema sabini*) - was submitted to *Behavioural Ecology & Sociobiology* in July 2003, under the authorship of Stenhouse, I.J., Gilchrist, H.G. & Montevecchi, W.A., and is currently under review.

Chapter 6 – Philopatry, site tenacity, mate fidelity and adult survival in Sabine's Gulls – was submitted to *Ibis* in August 2003, under the authorship of Stenhouse, I.J. and Robertson, G.J., and is currently under review.

2.0 The reproductive biology of Sabine's Gull

2.1 ABSTRACT

The reproductive biology of Sabine's Gulls (*Xema sabini*) breeding on Southampton Island, in the eastern Canadian Arctic, was studied from May to August of 1998 to 2001. Results were compared with information collected from the same region in 1980 (Abraham 1982). Breeding phenology was 10 days earlier in 1998 and 2001, when compared to other years, and reflects an earlier onset of snow melt. Nests were generally well dispersed, with a density of 10.4 to 12.6 nests per km^2. Throughout this study, mean clutch size was lower than in 1980, but higher in 1998 and 2001 (early years) than in 1999 or 2000 (late years). Hatching success was also lower than in 1980, and lowest in 1999 (21%) due to increased predation, most likely by Arctic foxes (*Alopex lagopus*). Adults and chicks abandoned nest-sites within a few hours of the hatching of the last chick, and relocated to coastal ponds where adults continued to attend chicks. In comparison with closely related tern-like gull species and other 'black-headed' gulls, Sabine's Gulls showed a number of distinct ecological and behavioural differences and clearly represent an ecological outlier within the gulls (*Laridae*).

2.2 INTRODUCTION

The gulls (Laridae) are among the most widely studied of avian species. Research has been directed at a variety of behavioural, ecological and evolutionary issues. The large *Larus* species have received much of the research attention around the world, and their breeding ecology is generally well documented (Southern 1987). The reproductive biology of a number of small gull species, however, remains poorly understood.

A recent reconstruction of phylogenetic relationships within the gulls, based on structural characteristics, grouped kittiwakes (*Rissa* spp.), fork-tailed gulls (*Xema* and *Creagrus* spp.) and the Ivory Gull (*Pagophila eburnea*) in a distinct lineage (Chu 1998). The kittiwakes have been well-studied in both the Palearctic and the Nearctic (Byrd & Williams 1993, Baird 1994), however, little is known about the ecology of the other three 'tern-like' genera. These three genera are each represented by a single species. The Sabine's Gull (*Xema sabini*) and Ivory Gull have circumpolar distributions and breed at high latitudes, while the Swallow-tailed Gull (*Creagrus furcatus*) breeds on the Galápagos Islands.

Sabine's Gull has rarely been studied, largely due to its remote Arctic breeding locations. It is a trans-equatorial migrant which spends most of its life at sea, and its wintering areas have only been documented in the last few decades (Zoutendyk 1965, 1968). As well as being phylogenetically distinct, Sabine's Gull is considered highly atypical in many aspects of its behaviour compared to other gulls (Brown *et a*l. 1967). For example, the species has several foraging strategies characteristic of shorebirds, such as pattering on mud and picking at the substrate like plovers (Hersey in Bent 1921), and spinning on the surface of ponds and picking at the water surface like phalaropes (Brown *et al.* 1967). Sabine's Gulls also exhibit a distraction display when potential predators approach their eggs or chicks, more typical of many shorebirds and skuas, suggesting that they have evolved in environments where predation pressures are intense. Generally, in this display, they land immediately in front of predators and run along the ground in a hunched posture, occasionally with wings slightly lowered, and may fly up to dive on the predator a few times before returning to the ground display (Bent 1921, Brown *et al.* 1967, Parmelee *et al.* 1967, Abraham 1986).

Sabine's Gulls also have an unusual moult chronology compared to most other gulls. Young Sabine's Gulls retain their plumage through their first autumn, and do not start a post-juvenile head and body moult to first-winter plumage until they reach their wintering areas (Grant 1986). Adult Sabine's Gulls also undergo a complete moult in spring, prior to their northward migration, and a partial moult in autumn, on arrival at their wintering area; the reverse pattern of most other gulls (Grant 1986). The timing of moult could provide insights into seasonal energetic constraints of this long-distance migrant.

In this study, I detail the reproductive biology of Sabine's Gulls in East Bay, on Southampton Island, Nunavut, in the eastern Canadian Arctic. A previous study of the foraging interactions between Arctic Terns (*Sterna paradisaea*) and Sabine's Gulls was carried out in East Bay in 1980 (Abraham 1982), and these data provide the first opportunity for long term comparisons in this species. Specifically, I compare reproductive parameters from 1998-2001, and with those from 1980 where comparable data exist. Finally, I compare aspects of the breeding ecology of Sabine's Gull with the other 'tern-like' gull species, believed to be closely related (Chu 1998), as well as small 'black-headed' gulls (Little Gull, *Larus minutus*; Common Black-headed Gull, *L. ridibundis*; Mediterranean Gull, *L. melanocephalus*), and other small Arctic breeders (Ross' Gull, *Rhodostethia rosea*; Arctic Tern) and explore ecological similarities and differences among these species.

2.2.1 STUDY AREA

This investigation of the reproductive biology of Sabine's Gull was carried out in the East Bay Migratory Bird Sanctuary (64°01'N, 81°47'W), Southampton Island, Nunavut, in the eastern Canadian Arctic. The sanctuary encompasses an area of approximately 1,200 km^2. Despite being located within the Low Arctic region, East Bay is generally High Arctic in character, influenced in its ecological and physical characteristics by the deep, cold waters of the Foxe Channel. Land-fast sea ice remains in East Bay well into July and daily minimum temperatures are close to freezing throughout the summer months. The study area is a 2 x 2.5 km plot of low-lying, coastal tundra, with a complex of brackish and freshwater ponds, typical of the area. Within the plot, sub-habitats are few and distinct, with wetland areas characterized by mosses, sedges and grasses, and drier areas dominated by dwarf shrubs (*Salix* spp.) and Mountain Avens (*Dryas integrifolia*). As a product of the low relief, brackish ponds extend several hundred metres from the shoreline, well into the study plot.

A secondary study area, 8 km west of the main study area, is similar in character. This area was the site of a one-year study of foraging interactions between Sabine's Gulls and Arctic Terns in 1980 (Abraham 1982, 1986, Abraham & Ankney 1984). Basic reproductive data from that study provides a unique opportunity for decadal comparisons in the breeding biology of Sabine's Gulls at East Bay.

2.3 METHODS

2.3.1 DATA COLLECTION

Fieldwork was conducted from late May to early August 1998-2001. Reproductive success was followed in all nests located within the primary study area on the southern shore of East Bay. In addition, a single visit was made to the secondary study area in 1998 and 1999. In both areas, nests were located by searching on foot. In the primary study area, during favourable weather conditions, nests were visited either daily or every second day until the clutch was complete, on average every three days during incubation, and daily during the hatching period. In the secondary study area, nests were visited only once during incubation.

Basic nest characteristics were recorded for each nest when first found. The latitude and longitude were recorded to the nearest 0.1 s with a hand-held GPS unit (Garmin GPS II Plus, Garmin Corp., KS). Co-ordinates were entered into MapInfo (MapInfo Pro, v. 5.0, MapInfo Corp., NY) as decimal degrees. Mean internest distances were calculated in MapInfo using a MapBasic programme, called 'CalcDist'.

When first found, eggs were measured to the nearest 0.1 mm with vernier calipers and weighed to the nearest 0.5 g with a 60 g Pesola scale. A total of 27 eggs were measured within 48 hrs of laying, and considered freshly-laid. From linear measurements of these freshly-laid eggs, an egg volume index was calculated using the formula V = length*breadth^2. To estimate fresh mass of eggs found later in incubation (>48 hrs post-laying), mass of freshly-laid eggs was regressed against volume index, to determine the linear relationship between these variables. Statistical inspection showed that the relationship between mass and volume index was the same for first-, second- and third-laid eggs.

Clutch initiation dates were established by direct observation of the appearance of the first egg, or calculated from the earliest hatch date in a clutch minus 21 days (see Results). Hatching success was considered the number of eggs hatched divided by the number of eggs laid, and an egg was considered depredated if it disappeared from a nest cup prior to hatch or was found broken or punctured.

Adults were captured at the nest during incubation with a simple wire mesh fall trap (Bub 1991). If their partners had not already replaced them, banded birds usually returned to incubate within minutes of release, and no nest desertion occurred as a direct result of trapping. Adults were marked with a numbered metal band and a unique combination of three coloured plastic bands. Chicks were marked at the nest immediately after hatching, with a numbered metal band and a single coloured plastic band (identifying year of hatch), as their tarsus was too short to use individual combinations. Metal bands placed on chicks were lined with plasticine to reduce loss during the first few days. In some cases, however, small chicks did lose metal bands, but usually retained their single colour band. During the first few days after leaving the nest, chicks were captured by hand, usually when swimming across shallow ponds. Later, chicks were caught whenever possible in the same manner, or with a dipnet. Chicks were rarely caught repeatedly, however, due to their mobility and/or crypticity. For both adults and chicks, the length of the tarsus and exposed culmen was measured to the nearest 0.1 mm using vernier calipers, and mass was measured to the nearest 1 g with a Pesola scale (300 g scale for adults, 100 g scale for chicks). Wing length was measured to the nearest 1 mm in adults and in chicks of 5 days and older, when primaries had broken through feather sheaths.

2.3.2 STATISTICAL ANALYSIS

Goodness of fit was examined using the *G*-test of independence, employing the Williams' correction for C x R contingency tables (Sokal and Rohlf 1995). Relationships between variables and between years were examined using ANOVA (DataDesk v. 6.0 , Data Description Inc., Ithaca, NY), and the Kruskal-Wallis test (Minitab v. 13.3, Minitab Inc., State College, PA). Statistical significance was recognized at $P \leq 0.05$, and, wherever possible, error distributions were examined for homogeneity, normality, and independence of residuals. The residuals from the regression of weight on tarsus were used as an index of condition in breeding adults. Values reported are means ± SD, unless otherwise stated.

2.4 RESULTS

2.4.1 PHENOLOGY

Previous studies suggest that arrival at the breeding ground and the general timing of breeding in Sabine's Gulls is highly dependent on environmental conditions, particularly ice and snow melt (Sutton 1932, Abraham 1986). In this study, nest building and egg laying were highly variable and dependent on the timing of snow melt. In general, breeding commenced as soon as conditions allowed after a pair bonded or were reunited (i.e. once freshwater ponds formed and tundra was exposed on the breeding territory).

In comparison to the other years, 1998 and 2001 were early years, in that the onset of snow melt occurred 10-14 days earlier than in 1999 and 2000 (Fig. 2.1). Over the years of this study, adults were first observed in the breeding areas at East Bay from 3 to 11 June, with the first eggs being laid from 14 to 28 June (Table 2.1). The median date of clutch initiation varied considerably, with a 12-day difference between the earliest (15 June 1998) and the latest (27 June 2000) year, and was significantly different among years (Kruskal-Wallis test, $H_{3,\,67} = 53.5$, $P < 0.001$; Table 2.2). However, despite earlier arrival of birds in the study area, and the earlier onset of snow melt and exposure of tundra in 2001, than in 1998, clutch initiation began on the same date (Jun 14) in both these early years. The median date of hatch was also significantly different between years (Kruskal-Wallis test, $H_{3,\,126} = 103.3$, $P < 0.001$; Table 2.3).

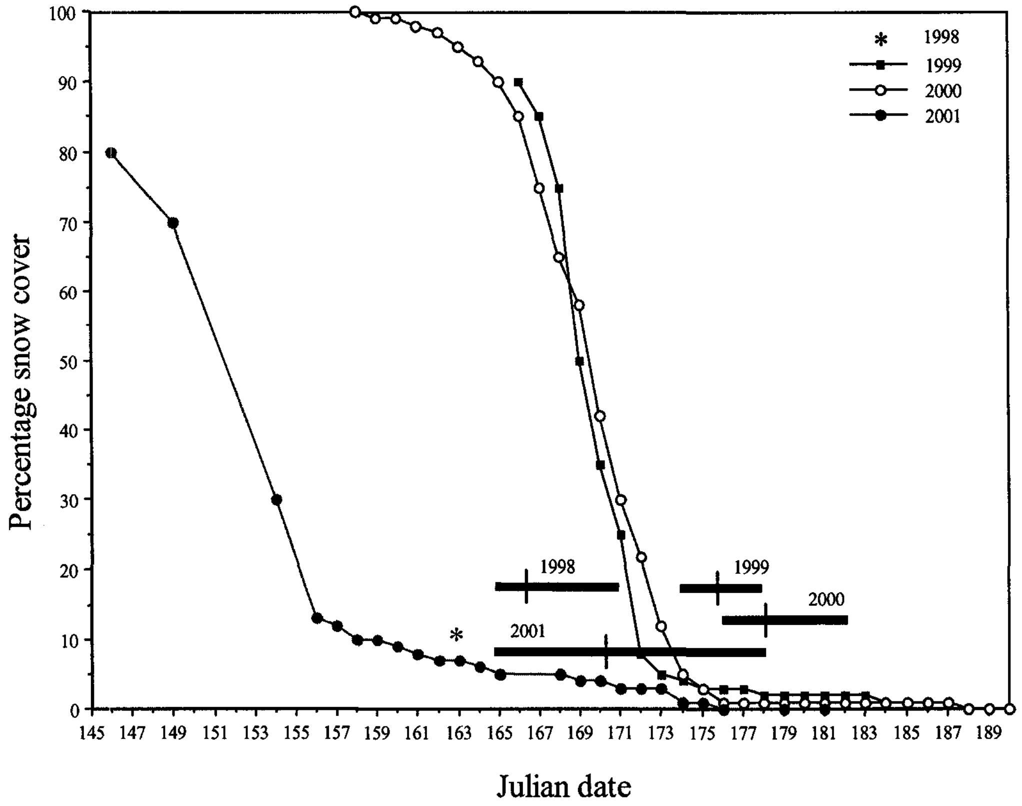

Fig. 2.1: The onset and progress of snow melt at East Bay, Southampton Island, Nunavut, and the period of clutch initiation in Sabine's Gulls in each year (horizontal bars = range, vertical bars = median). *NB*: daily changes in snow melt were not followed in 1998, although it was noted when snow cover was reduced to 10 %.

Table 2.1: The breeding phenology of Sabine's Gulls at East Bay, Southampton Island, Nunavut, in 1980 and 1998 - 2001.

	First gulls in study area	Onset of snowmelt	Exposure of tundra (90%)	Clutch initiation	Hatching dates
1980[1]	12 June	18 June	24 June	23 June - 3 July	14 - 22 July
1998	7 June	4 June	12 June	14 - 20 June	5 - 12 July
1999	11 June	14 June	21 June	23 - 27 June	15 - 19 July
2000	10 June	12 June	23 June	25 June - 1 July	16 - 23 July
2001	3 June	~1 June	7 June	14 - 28 June	6 - 19 July

[1] from Abraham (1986)

Table 2.2: Median clutch initiation dates and clutch initiation period for Sabine's Gulls at East Bay, Southampton Island, Nunavut, in 1980 and 1998 - 2001.

Year	*n*	Median date	Range	Clutch initiation period
1980[1]	19	26 June	23 June-3 July	11 days
1998	18	15 June	14-20 June	7 days
1999	13	25 June	23-27 June	5 days
2000	20	27 June	25 June-1 July	7 days
2001	18	19 June	14-28 June	15 days

[1] from Abraham (1986)

Table 2.3: Median hatching dates and hatching period for Sabine's Gull eggs at East Bay, Southampton Island, Nunavut, in 1980 and 1998 - 2001.

Year	*n*	Median date	Range	Hatching period
1980[1]	18	17 July	14-22 July	9 days
1998	40	7 July	5-12 July	8 days
1999	13	17 July	15-19 July	5 days
2000	35	19 July	16-23 July	8 days
2001	39	11 July	6-19 July	14 days

[1] from Abraham (1986)

2.4.2 NESTING DENSITY AND NEST-SITES

At East Bay, Sabine's Gulls restricted nesting to a specific habitat band that ran parallel to the shoreline. The band started around 200 m from shore and reached inland to approximately 1100 m from shore (see Chapter 4). Within this band, a subunit of the larger study area and measured as 2.65 x 0.83 km, nesting density ranged from 10.4 to 12.6 nests per km^2. The mean distance to nearest neighbouring conspecific nest was 87 m (range = 24 - 251 m, $n = 23$) in 1998, 102 m (range = 18 - 439 m, $n = 24$) in 1999, 101 m (range = 27 – 279 m, $n = 25$) in 2000, and 82 m (range = 12 – 675 m, $n = 28$) in 2001, and did not differ among years ($F_{3,\,99} = 0.32$, $P = 0.81$). Generally, nests were widely and evenly distributed at East Bay. However, in one location, at the secondary study area, a few pairs nested very close together on a small mossy island; three pairs in 1998 (mean internest distance = 5.9 m) and two pairs in 1999 (internest distance = 3.5 m). Sabine's Gulls also displayed strong fidelity to their breeding area, with most pairs breeding within a few hundred metres of their previous nest sites (see Chapter 6). In 1999, two pairs returned to the same nest cup they had used in 1998.

At East Bay, Sabine's Gulls generally formed their nest cup in soft, damp moss on the edges of ponds or on small islands within ponds. The study area is extremely flat and all nests were completely exposed i.e. were not associated with any type of cover or particular aspect (see Chapter 4). The nest cup was usually bare but sometimes lined with a few goose feather quills, dried plant stems or pieces of dried seaweed. Nests were always located close to water and some remained visibly damp throughout much of the breeding season. Nest cups were occasionally found on a slightly raised hummock of moss, perhaps providing improved drainage. During periods of flooding, however, Sabine's Gulls often lined their nest cups with a layer of grasses and sedges. At one site, in 1998, after several days of heavy rain, eggs appeared (and presumably were rolled) approximately 15 cm from a nest cup, which was submerged at the edge of an encroaching pond. A new nest cup was constructed where the eggs lay, incubation continued uninterrupted and the eggs eventually hatched.

2.4.3 EGGS, CLUTCH SIZE AND INCUBATION

Overall, the mean mass of freshly-laid eggs was 24.1 ± 2.2 g, and did not differ among years ($F_{3, 26} = 0.7$, $P = 0.5$) or laying order ($F_{2, 26} = 0.01$, $P = 0.9$), and there was no interaction between year and laying order ($F_{3, 26} = 0.6$, $P = 0.6$). Mean estimated fresh mass of all eggs of unknown age combined was 23.9 ± 1.6 g, and did not differ among years ($F_{3, 241} = 0.7$, $P = 0.6$). Overall, the mean length of freshly-laid eggs was 45.5 ± 1.8 mm, and did not differ among years ($F_{3, 28} = 0.2$, $P = 0.9$) or laying order ($F_{2, 28} = 0.1$, $P = 0.9$), and there was no interaction between year and laying order ($F_{3, 28} = 0.8$, $P = 0.5$). Mean length of all eggs of unknown age combined was 45.2 ± 1.9 mm, ($n = 242$), and did not differ between years ($F_{3, 241} = 0.9$, $P = 0.4$). Overall, mean breadth of freshly-laid eggs was 32.5 ± 1.1 mm, and did not differ among years ($F_{3, 28} = 1.0$, $P = 0.4$) or laying order ($F_{2, 28} = 0.2$, $P = 0.8$), and there was no interaction between year and laying order ($F_{3, 28} = 0.3$, $P = 0.8$). Mean breadth of all eggs of unknown age combined was 32.5 ± 0.9 mm, and did not differ among years ($F_{3, 242} = 0.7$, $P = 0.5$; Table 2.4).

Table 2.4: Mean clutch size (± SD) and morphometrics of freshly-laid (<48 hrs) Sabine's Gull eggs and eggs of unknown age at East Bay, Southampton Island, Nunavut, in 1980 and 1998 - 2001.

		Freshly-laid eggs			**Eggs of unknown age**		
Year	Clutch size	Egg length (mm)	Egg breadth (mm)	Egg mass (g)	Egg length (mm)	Egg breadth (mm)	Estimated fresh mass (g)
1980[1]	2.8 ± 0.1 (*n* = 19)	--	--	22.3 ± 0.4 (*n* = 25)	--	--	--
1998[2]	2.6 ± 0.6 (*n* = 27)	44.3 ± 3.3 (*n* = 3)	32.4 ± 0.5 (*n* = 3)	24.1 ± 3.1 (*n* = 2)	45.1 ± 1.6 (*n* = 55)	32.5 ± 0.8 (*n* = 55)	23.8 ± 1.2 (*n* = 55)
1999[2]	2.4 ± 0.6 (*n* = 37)	45.9 ± 2.1 (*n* = 10)	33.0 ± 0.9 (*n* = 10)	24.9 ± 2.3 (*n* = 10)	45.1 ± 1.7 (*n* = 76)	32.6 ± 0.8 (*n* = 76)	24.0 ± 1.5 (*n* = 76)
2000	2.4 ± 0.6 (*n* = 25)	45.5 ± 1.6 (*n* = 2)	32.1 ± 0.9 (*n* = 2)	22.0 ± --- (*n* = 1)	45.5 ± 1.9 (*n* = 54)	32.6 ± 0.8 (*n* = 55)	24.0 ± 1.4 (*n* = 54)
2001	2.7 ± (*n* = 28)	45.5 ± 1.1 (*n* = 14)	32.3 ± 1.1 (*n* = 14)	23.7 ± 2.0 (*n* = 14)	44.9 ± 2.3 (*n* = 57)	32.4 ± 1.2 (*n* = 57)	23.7 ± 2.1 (*n* = 57)

[1] from Abraham (1986) [2] includes clutches from secondary field site

Overall, mean clutch size was 2.5 ± 0.64 (n =101). Clutch size did not differ among years ($F_{3,\,100}$ = 2.2, P = 0.09), but was lower in all years of this study than in 1980 (Table 2.4). The proportions of 2- and 3-egg clutches were significantly different among years (χ^2_3 = 10.6, P = 0.014), however, with greater proportions of 3-egg clutches in 1998 and 2001 (65 and 75 %, respectively), of 2-egg clutches in 1999 and 2000 (56 and 48 %, respectively). The proportion of 1-egg clutches was similar in all years (<10%; Table 2.5).

Incubation began with the laying of the first egg, albeit intermittent (pers. obs.), and both members of a pair were observed to attend the nest and share incubation (see Chapter 3). Three brood patches, two lateral and one median, were observed in both sexes. Eggs were often exposed while adults foraged nearby, and occasionally eggs were found completely unattended with no adults in the vicinity. Over the years of the study, both laying and hatching dates were certain for a total of 14 eggs, of which 9 (64 %) hatched on day 21 of incubation and 5 (36 %) hatched on day 22 of incubation.

2.4.4 HATCHING SUCCESS AND EGG MORTALITY

There was a significant difference in the proportion of eggs hatched among years (G_3 = 28.4, $P < 0.001$; Table 2.6). Hatching success was lower in all years of this study than that found in 1980 (Table 2.6; Abraham 1986). The low hatching success observed in 1999, compared with all other years, reflects a marked increase in egg predation in 1999, most likely by Arctic foxes (*Alopex lagopus*) which were observed in the study area more frequently in that year (see Chapter 5). There was a significant

Table 2.5: Clutch sizes in Sabine's Gulls at East Bay, Southampton Island, Nunavut, 1998 – 2001.

	Clutch size			
	3 eggs	2 eggs	1 egg	Total
1998				
Number of nests	15	6	2	23
% of total nests	65 %	26 %	9 %	100 %
Number of eggs	45	12	2	59
1999				
Number of nests	9	14	2	25
% of total nests	36 %	56 %	8 %	100 %
Number of eggs	27	28	2	57
2000				
Number of nests	11	12	2	25
% of total nests	44 %	48 %	8 %	100 %
Number of eggs	33	24	2	59
2001				
Number of nests	21	5	2	28
% of total nests	75 %	18 %	7 %	100 %
Number of eggs	63	10	2	75

difference in the proportion of eggs depredated among years ($G_3 = 42.5$, $P < 0.001$; Table 2.6).

2.4.5 POSTNATAL DEVELOPMENT

Based on newly-hatched chicks (< 24 hrs post-hatch) measured in each year, there was no difference in mean tarsus length ($F_{3, 86} = 2.5$, $P = 0.06$), culmen length ($F_{3, 86} = 1.2$, $P = 0.29$), or mass ($F_{3, 86} = 0.9$, $P = 0.42$) among years (Table 2.7).

Chicks were downy at hatch, with pale pink legs and bill. Down was rusty red on upper parts (upper breast, head, back, rump, upper wing), with the typical dark striped pattern of gull chicks, and white below (belly and under wing). The down faded to a paler fawn colour and the bill tip and legs darkened at approximately three days post-hatch. The egg tooth was retained until day five or six post-hatch. Chicks were capable of leaving the nest as soon as their down was dry, and could walk and/or swim away from the nest when threatened. Small chicks often hid under rocks within a few metres of the nest, or along the mossy edges of nearby ponds.

Adults led their broods away from the nest site within 24-36 hrs of the last chick hatching. In East Bay, family groups moved to saltwater ponds along the edge of the bay, where they became extremely difficult to monitor. Family groups appeared to stay together, and all adults in the area came together to mob potential predators. Chicks were highly mobile at this stage. They could run, swim and hide from potential threats, and were easily lost in the confusion of mobbing. Chicks of at least one family, however, were found repeatedly in the same area and appeared to return to the same location after disturbances. This highly mobile chick stage away from the nest is

Table 2.6: Reproductive performance of Sabine's Gulls at East Bay, Southampton Island, Nunavut, in 1980 and 1998 - 2001.

	1980[1]	1998	1999	2000	2001
No. clutches followed	19	23	25	25	28
Total no. eggs laid	53	60	57	59	75
No. eggs depredated	3	16	43	16	21
No. eggs abandoned	6	6	2	6	3
No. eggs hatched	44	38	12	37	39
No. eggs hatched / egg laid	0.83	0.63	0.21	0.63	0.52
No. eggs hatched / clutch	2.31	1.65	0.48	1.48	1.39

[1] from Abraham (1986)

Table 2.7: Mean (± SD) morphometrics of newly-hatched (< 24 hrs) Sabine's Gull chicks at East Bay, Southampton Island, Nunavut, 1998 – 2001, and all years combined.

Year	*n*	Tarsus (mm)	Culmen (mm)	Mass (g)
1998	27	18.6 ± 0.57	9.3 ± 0.49	17 ± 2
1999	12	17.8 ± 0.63	9.7 ± 0.29	17 ± 1
2000	27	18.6 ± 1.38	9.5 ± 0.99	16 ± 1
2001	21	18.3 ± 0.77	9.6 ± 0.63	17 ± 1
Overall	87	18.4 ± 0.97	9.5 ± 0.70	17 ± 1

atypical for gulls, and prevents detailed study of chick growth and fledgling development, as well as preventing an accurate measure of fledging success.

Repeated measurements of chicks were recorded whenever possible in 1998 and 1999. Based on these measures, Sabine's Gull chicks exhibited typical sigmoidal patterns of growth (Fig. 2.2). Compared to measures of incubating adults breeding in East Bay in these same years, on average chicks attained 92 % of mean adult tarsus length by 12 days post-hatch, reaching 100 % between 17 to 21 days post-hatch; 75 % of mean adult culmen length by 12 days post-hatch, reaching around 85 % by 15–21 days post-hatch; and 89 % of mean adult mass by 12 days post-hatch, reaching 100% between 16 and 21 days post-hatch. Sabine's Gull chicks followed the pattern exhibited by most seabird species, in that they attained their peak mass, approximately 108 % of mean adult mass, several days prior to fledging. Growth of the 9th primary followed a typical linear development, and chicks attained 47 % of mean adult wing length by 12 days post-hatch, reaching 72 % of adult wing length by 22 days post-hatch (Fig. 2.2).

2.4.6 ADULT MORPHOMETRICS

Breeding adults were measured during incubation in 1998, 1999 and 2001. Structural measures did not differ among years (mean tarsus length, $F_{2,50} = 0.3$, $P = 0.77$; mean culmen length $F_{2,50} = 0.9$, $P = 0.43$). However, both mean mass ($F_{2,48} = 16.7$, $P < 0.001$) and wing length ($F_{2,48} = 3.5$, $P = 0.04$) differed among years (Table 2.8).

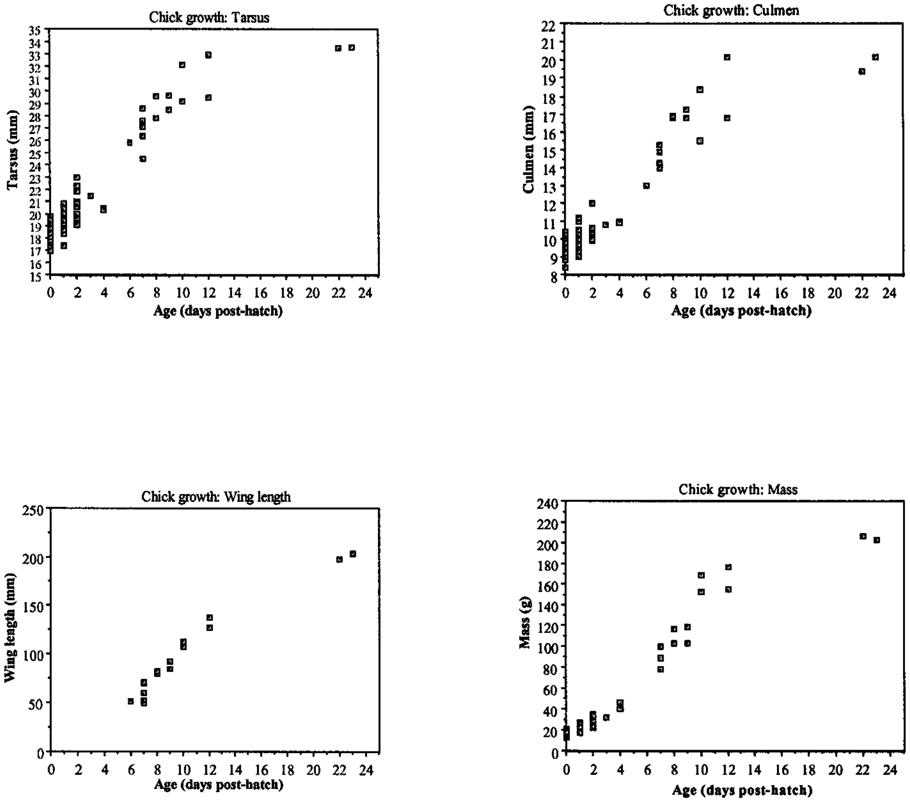

Fig. 2.2: Growth rates of Sabine's Gull chicks at East Bay, 1998 and 1999.

Table 2.8: Mean (± SD) morphometrics of incubating Sabine's Gulls at east Bay, Southampton Island, Nunavut, 1998 – 2001, and all years combined for measures that did not differ among years.

Year	*n*	Tarsus (mm)	Culmen (mm)	Wing (mm)	Mass (g)
1998	26	33.6 ± 1.4	25.4 ± 1.4	281± 7	198 ± 10
1999	19	33.4 ± 1.3	24.5 ± 1.1	274.2 ± 9	180 ± 10
2001	6	33.3 ± 1.4	24.6 ± 2.1	279 ± 7	186 ± 11
Overall	51	33.5 ± 1.3	24.8 ± 1.4	--	--

Controlling for body size, based on the regression of mass on tarsus measures, breeding adults were found to be in poorer condition during incubation ($F_{1,39} = 32.9, P < 0.001$) and exhibited lower body mass and shorter wing length in 1999 (a late breeding year) versus 1998 (an early breeding year).

2.4.7 COMPARISON WITH OTHER SMALL GULLS

Sabine's Gulls show distinct differences from gull species considered to be closely related, such as the Black-legged Kittiwake, Ivory Gull, and Swallow-tailed Gull (Chu 1998), and some similarities with other small 'black-headed' gulls, such as the Little Gull, Common Black-headed Gull, and Mediterranean Gull (Table 2.9). Sabine's Gull has a circumpolar distribution but is largely restricted to the Low Arctic during breeding. Of the species in the related grouping, only the Black-legged Kittiwake has a broad breeding distribution. Sabine's Gull is the only exclusively ground-nesting species in the group, and the only one that often nests solitarily. These characteristics are shared, however, with the other small 'black-headed' gulls, except the Mediterranean Gull that nests at high densities.

Compared to the other species in Chu's (1998) closely-related grouping, Sabine's Gull exhibits an earlier maturation, believed to initiate breeding at 2 years, another characteristic shared with the other small 'black-headed' gulls. Sabine's Gull is also a small bird, about 50 % lighter than the Black-legged Kittiwake. The ratio of egg mass to female body mass in Sabine's Gull is similar to the others in Chu's (1998) group, however, the larger clutch size in Sabine's Gull could be a greater drain on female nutrient reserves than in the other species (clutch mass up to 36 % of female body mass). Only the Little Gull and Common Black-headed Gull show a similar or higher egg to female body mass ratio and a similar mean clutch size to Sabine's Gull (Table 2.9). Sabine's Gull exhibits a relatively short breeding season with contracted incubation and fledging periods compared to the species in Chu's (1998) grouping, but, again, is similar to the other small 'black-headed' gulls. In addition, Sabine's Gull has a long migration, an annual round trip migration of approximately 25,000 km, similar to the Arctic Tern (Table 2.9).

2.5 DISCUSSION

At East Bay, breeding effort by Sabine's Gulls was comparable in all years of this study (1998-2001). They also showed little variation in density, nests were widely and evenly dispersed, except at one site where two to three pairs nested close together on a small island. Contrary to early reports on this species (Nelson in Bent 1921, Bray 1943, Salomonsen 1951, Larson 1960, Sutton in Bannerman 1962), Sabine's Gulls at East Bay were not colonial, nor did they appear to nest in close proximity to Arctic Terns. The existence of the small island group, however, suggests that this species is occasionally semi-colonial at this location.

Nests of Sabine's Gulls at East Bay were similar to those previously described for this species (Ilyichev & Zubakin 1988). Nest cups were placed on damp mossy areas at pond edges. In northeast Greenland, however, nests were found on small patches of vegetation on slopes of eroded bedrock and gravel banks (Forchhammer & Maagaard 1991). Inter-annual variation in climatic conditions in East Bay, particularly prevailing wind direction, could have some effect on the precise positioning of nests

Table 2.9: Comparison of Sabine's Gull life-history parameters with other small gull species and Arctic Tern.

Species	Breeding distribution	Coloniality & density	Nest location	Age at 1st breeding (yr)	Adult mass (g)	Mean clutch size (range)	Egg mass as a % of female mass	Incubation period (days)	Fledging period (days)	Migration distance
Sabine's Gull[a]	low arctic	solitary-low density	ground	≥ 2	180-210	2.8 (1-3)	10-13	21-23	25-30	v. long
Black-legged Kittiwake[b]	subarctic - high arctic	high density	cliff	3 - 5	382-423	1.7 (1-3)	11-18	25-27	34-36	medium
Ivory Gull[c]	high arctic	low-high density	cliff, ground	> 2	448-687	? (1-2)	10-14	24-26	30-35	medium
Swallow-tailed Gull[d]	tropics	low density	cliff, ground	4 - 5	610-780	1 (1-2)	10-13	29-38	58-84	v. short
Little Gull[e]	boreal	solitary-low density	ground	2 - 3	99-156	2.7 (1-3)	18-20	23-25	21-24	medium
Common Black-headed Gull[f]	boreal-subarctic	solitary-high density	ground	2 - 3	195-327	2.5 (1-4)	10-16	23-26	c. 35	medium-long

Species	Breeding distribution	Coloniality & density	Nest location	Age at 1st breeding (yr)	Adult mass (g)	Mean clutch size (range)	Egg mass as a % of female mass	Incubation period (days)	Fledging period (days)	Migration distance
Mediterranean Gull[g]	boreal	high density	ground	2 - 3	230-280	? (2-3)	14-18	23-25	35-40	medium
Ross' Gull[h]	subarctic-low arctic	low density	ground	≥ 2	120-200	3 (1-3)	?	19-22	c. 21	short
Arctic Tern[i]	boreal-high arctic	solitary-high density	ground	2 - 5	87-119	2.0 (1-3)	16-22	20-24	21-24	v. long

[a] this study, Abraham (1982, 1986)

[b] Baird (1994)

[c] Haney & MacDonald (1995)

[d] Harris (1970)

[e] Ewins & Weseloh (1999)

[f, g] Cramp & Simmons (1983)

[h] Cramp & Simmons (1983), del Hoyo *et al.* (1996)

[i] Cramp (1985), Snow & Perrins (1998)

in relation to the nearest water. This may reflect that nests at East Bay can be washed over by spray from pond edges or surrounded by foam blown from the surface of ponds in stormy conditions (pers. obs).

In 1999 and 2000, the general phenology of breeding at East Bay was similar to that observed in 1980. However, 1998 and 2001 were considerably earlier than other years in all respects, and, in these years, snow melt began 10-14 days earlier. In 1998 and 2001, Sabine's Gulls arrived at the breeding area earlier, and both nest initiation and hatch were approximately 10 days earlier than other years. This suggests that the onset of snow melt partly determined the initiation of breeding, as would be expected for ground-nesting birds in the Arctic.

The ability to initiate breeding almost immediately suggests that females arrive with the energetic resources required for egg laying, rather than building these resources on arrival at the breeding site. Although Sabine's Gulls can take advantage of earlier conditions in some years, they may be physiologically unable to initiate clutches prior to mid-June.

An association between clutch size and laying date has been observed in other species (Winkler & Allen 1996). In this study, a greater proportion of 3-egg clutches was observed in early years (1998 and 2001), and of 2-egg clutches in late years (1999 and 2000). This may be the result of an increased period between arrival and nesting in 1999 and 2000, due to the later onset of snow melt and exposure of tundra. In addition, incubating adults were in poorer condition in 1999 than in 1998. As has been suggested for Arctic-breeding geese (Ankney & McInnes 1978, Davies & Cooke 1983, Ebbinge & Spaans 1995), Sabine's Gulls may have to rely on their nutrient reserves while waiting to nest and, therefore, females have fewer reserve resources available for egg production in late years. However, even though breeding phenology in 1999 and 2000 was similar to 1980, clutch size and hatching success were higher in 1980 than in all years of this study (1998-2001). The extent of reserve resources available for egg production is likely the combined result of conditions experienced (1) prior to migration, (2) during migration, and (3) during the pre-laying period at the breeding ground.

The reverse moult pattern exhibited by Sabine's Gulls has interesting implications. The environmental conditions experienced during the complete moult in spring, prior to migration, could influence feather growth (i.e. wing length). Whereas, body mass may reflect the conditions experienced during migration or locally on arrival at the breeding site. Thus, wing length and body mass may represent different indices of condition, and in years of particularly poor conditions during late winter and early spring, both would be expected to be compromised. Interestingly, when controlled for size using a structural measure (tarsus), both wing length and body mass were indeed lower in 1999 than 1998, suggesting that 1999 was a poor year for Sabine's Gulls throughout.

The extended laying and hatching period observed in 2001 was driven by one nest where clutch initiation was notably late. When this outlier was removed from analyses, median laying and hatching dates did not change, but laying and hatching periods were similar to those of other years (10 and 9 days, respectively). This particularly late nest may have belonged to a young pair which started late, or an older, experienced pair which started early and laid a replacement clutch after the loss of their first egg(s) to predation or flooding. Although no evidence of replacement clutches existed in the other years of this study at East Bay, possible clutch replacement has been reported from Alaska (Brandt 1943) and Russia (Dement'ev & Gladkov 1951).

Due to egg-loss to predators, reproductive output was significantly reduced in 1999, compared with other years of this study. In 1999, the number of chicks hatched per clutch was roughly one third of that found in all other years. Few eggs were depredated in 1980, compared with the years of this study, and in 1980 abandoned eggs and dead chicks remained undisturbed on the study area despite the presence of avian and mammalian predators (Abraham 1986). This suggests that the predators and scavengers in the area were not food-stressed in 1980. The extraordinary level of egg predation in 1999 coincided with a considerable increase in Arctic fox activity within the study area. Predation rates on nesting birds can vary considerably in Arctic tundra environments (Summers and Underhill 1987). In some years Arctic foxes depend almost entirely on the eggs and young of nesting birds (Larson 1960, Sklepkovych & Montevecchi 1996). Occasional, extreme predation of this kind has been observed in several Arctic breeding bird species (Summers 1986, Underhill 1987, Underhill *et al.* 1989) and is generally related to annual variation in alternative prey populations (i.e. rodents; Summers & Underhill 1987, Sklepkovych & Montevecchi 1996, Summers *et al.* 1998). Sabine's Gulls in East Bay are also influenced by the availability of alternative prey for mammalian predators (see Chapter 5), which adds to increasing evidence linking the reproductive success of Arctic-breeding, ground-nesting birds to the microtine rodent cycle (Sutherland 1988, Newton 1998).

Although Abraham (1986) found that Sabine's Gulls in East Bay left their nests soon after hatch, she did not report their movements beyond this stage. Observations from this study, that families moved to large saltwater ponds along the edge of the bay immediately after hatch, and that chicks were found at the same location on several occasions, support Forchhammer & Maagaard's (1991) suggestion that Sabine's Gulls establish small post-hatching territories.

Some aspects of the reproductive biology of Sabine's Gulls are typical of larger gulls: 1) they have simple nest-site requirements, 2) they display a strong fidelity to their breeding area, and 3) they generally lay three eggs (except in Greenland; Forchhammer & Maagaard 1991). However, some aspects of the reproductive biology of Sabine's Gulls are clearly atypical of most gulls. The early abandonment of the nest, relocation of the entire family, and establishment of post-hatching territories are particularly notable. Thus, this study supports the conclusion that Sabine's Gull represents an ecological outlier within the gulls, even when compared to species considered closely-related.

Their relatively short incubation and fledging periods, their departure from nests immediately after hatch, and their establishment of post-hatching territories could be adaptations to the ephemeral nature of their aquatic and terrestrial invertebrate prey during the breeding season. However, Forchhammer & Maagaard (1991) did not observe adults foraging in post-hatching territories. Alternatively, congregating on larger coastal ponds could facilitate escape and/or concealment of chicks from predators and enhance the ability of Sabine's Gulls to collectively mob predators. Another possible explanation, which is not mutually exclusive, is that these behaviours may reflect intense pressure to leave the breeding area as soon as possible, and switch to marine prey in preparation for their migration to wintering areas in the southern hemisphere.

Based on its ecological differences, I support the retention of Sabine's Gull in a single genera (*Xema*). This could also be said, however, of the other genera in Chu's (1998) grouping (*Rissa*, *Creagrus*, *Pagophila*). The general similarities of Sabine's Gull with other small 'black-headed' gulls certainly calls into question gull groupings based on morphometrics alone. Clearly, the question of whether current groupings actually relate to phylogeny or to convergent evolution remains and can only be resolved with an exhaustive and comprehensive genetic analysis of the entire Laridae.

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3.0 Reproductive investment and parental roles in Sabine's Gulls

3.1 ABSTRACT

More than 90 % of avian species exhibit biparental care, though parental activities are often shared unequally between the members of a pair. Among gull species (Laridae), males and females generally share parental activities, although there appear to be considerable differences among species in the relative contribution of each sex. This study examined the behaviour of male and female Sabine's Gulls (*Xema sabini*) during the incubation period and immediately post-hatch; particularly the amount of time they each invested in breeding activities. Although considered an aberrant species in aspects of behaviour and biology, the Sabine's Gull showed a high reproductive investment by both sexes, as other gulls do. Males fed females prior to egg laying, and both sexes contributed equally to incubation, chick provisioning, and nest defence. Overall, there was no difference between the sexes in the extent of their contributions to parental care, although there was considerable individual variation within pairs. Sabine's Gulls are Arctic breeders and the extent of their contributions to parental activities could have been influenced by their unpredictable breeding environment and short breeding season.

3.2 INTRODUCTION

Birds are unique among vertebrates, in that social monogamy is the dominant mating system (>95 % of avian species; Gill 1994) and is strongly associated with biparental care (>90 % of avian species; Lack 1968). Ligon (1999) suggested that the most important factor driving the prevalence of monogamy in birds is the ability to maximize the number of young reared by sharing the costs of reproduction.

In the majority of avian species, males contribute directly to the welfare of their offspring through conspicuous parental activities, such as provisioning (Ligon 1999). Nevertheless, even in biparental species, parental care is not always shared equally. Based on the anisogamous nature of avian reproduction, it has generally been assumed that females make a greater contribution to the raising of offspring than males (Trivers 1972). However, where the benefits of parental care are similar for males and females, parental care activities are expected to be shared equally (Ligon 1983), although the optimal investment for each individual parent is likely influenced by the contribution provided by its mate (Houston & Davies 1985).

Silver *et al.* (1985) attempted to predict the extent of male involvement in parental activities in avian subfamilies based on their life-history traits. They found that the strongest predictors included the morphology, mating system and mode of chick development. Groups that are monomorphic, socially monogamous, and have altricial young, tend to show greater male contribution to parental care. However, Silver *et al.* (1985) did not take into account interactive environmental factors, such as seasonality, length of the breeding season, predictability of resources, and risk of predation. These factors are also considered to influence the extent of parental care and can vary widely across the breeding range of a single species (Clutton-Brock 1991).

In seabirds, offspring survival is usually highly dependent on care by both parents (Furness & Monaghan 1987). Studies of a range of colonially nesting seabirds have shown considerable investment by both parents, and often clear sex differences in parental roles (Nelson 1978, Montevecchi & Porter 1980, Burger 1981, Pierotti 1981, Southern 1981, Butler & Janes-Butler 1983, Dulude *et al.* 1987, Morris 1987). For example, gull species (Laridae) are generally monomorphic, socially monogamous, colonial breeders, with semi-precocial or precocial young. Among the gulls, it is generally accepted that males and females share parental activities, particularly incubation, chick provisioning, and territorial defence (Morris 1987). However, among gull species, there are differences in the relative contributions of each sex to parental care activities (Dulude *et al.* 1987).

Sabine's Gull (*Xema sabini*) is a relatively poorly known species and considered unusual within the gull family. It is recognized as phylogenetically distinct (Chu 1998), as well as being considered atypical in aspects of its morphology (Day *et al.* 2001), behaviour (Brown *et al.* 1967) and reproductive biology (Abraham 1986, Stenhouse *et al.* 2001). For much of the year they are almost entirely pelagic (Grant 1997), wintering mostly in subtropical and tropical coastal upwelling zones (Day *et al.* 2001). Their breeding distribution is circumpolar and ranges from sub-Arctic to Arctic regions between 55° N and 75° N, where members of this species nest in loose colonies, usually on small islands, or solitarily in open, marshy tundra areas (Day *et al.* 2001). They lay 1-3 eggs in rudimentary nests, usually simple depressions in moss at the edges of ponds (Stenhouse *et* *al.* 2001). Sabine's Gulls usually lay at daily intervals, and, although incubation begins with the first egg, it is often incomplete until the full clutch is laid (Day *et al.* 2001). The incubation period lasts for 21-23 days (Stenhouse *et al.* 2001). Once hatched, chicks grow rapidly, which is considered to be an adaptation to the short duration of their Arctic breeding season (Abraham 1986). In addition, they display several other behavioural traits that suggest the extent of reproductive investment could reflect their unpredictable breeding environment and short breeding season: 1) egg-laying is synchronous at East Bay, which reduces the likelihood of extra-pair copulation, encourages genetic monogamy, and potentially increases paternal investment, 2) terrestrial and aquatic prey are ephemeral and prey items are small and dispersed, thus provisioning chicks probably requires considerable input by both parents, 3) the entire family moves away from nest area within 24 hours of the last chick hatching and chicks are semi-precocial and nidifugous; Ilyichev & Zubakin 1988, Day *et al.* 2001), and 4) chicks attempt to feed themselves within a few hours of hatching and can feed independently by 2-3 days old (Abraham 1986, Ilyichev & Zubakin 1988).

Relatively little is known about the behaviour and breeding ecology of Sabine's Gulls (Day *et al.* 2001). However, high annual variation in breeding effort (Forchhammer & Maagaard 1991), in predation and reproductive success (see Chapter 5), the low opportunity for re-laying after egg loss (Day *et al.* 2001), and the short duration of their breeding window, all suggest that each breeding attempt is of considerable importance in an individual's lifetime reproductive success. Thus, each member of a pair is predicted to contribute to each stage of breeding, as well as contribute similar amounts of time to parental activities throughout the breeding period. In this study, I examined the behaviour of Sabine's Gulls during the incubation period and immediately after hatching, with a focus on the amount of time that males and females invested in critical breeding activities, and also the extent of their involvement in nest defence and chick provisioning.

3.3 METHODS

3.3.1 STUDY AREA

Field work was conducted from late May to mid-August of 2000-2001 in the East Bay Migratory Bird Sanctuary (64°01'N, 81°47'W), Southampton Island, Nunavut, in the eastern Canadian Arctic. The East Bay sanctuary encompasses an area of approximately 1,200 km^2, and, despite being located within the Low Arctic region, is generally High Arctic in character, influenced in its ecological and physical characteristics by the deep, cold waters of the Foxe Channel. Land-fast sea ice often remains in East Bay well into July and daily minimum temperatures are close to freezing throughout summer.

The study site is a 2 x 2.5 km area of coastal wetland tundra, with a complex of brackish and freshwater ponds, typical of the region. Within the study area, habitat types are few and distinct, with wet areas characterized by mosses, sedges and grasses, and drier areas dominated by dwarf shrubs (*Salix* spp.) and Mountain Avens (*Dryas integrefolia*). As a product of the low relief, brackish ponds extend several hundred metres from the shoreline. In summer, the area supports a diverse avian community characteristic of the region (Abraham & Ankney 1986). At East Bay, Sabine's Gulls nest solitarily on the damp, mossy edges of small, shallow ponds or on small islands within ponds, and are generally found nesting 200-1100 m from shore (Stenhouse *et al.* 2001).

3.3.2 NEST SEARCHING AND OBSERVATIONS

Within the study area, nest searches were carried out on foot during the pre-laying and laying stages, but most nests were found only after clutch completion. The breeding behaviour of individuals and the extent to which they contributed to parental activities were explored through behavioural observations. Casual observations of Sabine's Gulls in the study area were made during nest searches in the week prior to the initiation of egg laying. Once nests were established and clutches were complete, portable canvas blinds were placed ~100 m from nests, and the nesting pair (where at least one bird was banded and blood sampled for genetic sexing) were observed with the aid of a telescope and binoculars. Observations were carried out during 3-hr periods throughout the day (0800-1100, 1400-1700, and 1900-2200 hr). A total of 42 hr of observation was achieved for 2 pairs in 2000, and 170 hr for 8 different pairs in 2001. The bulk of the observation periods (n = 64, 191 hr) were carried out during the incubation phase, but some (n = 7, 21 hr) were also made at five nests during hatching and the first few days of chick-rearing, referred to as the brooding phase, prior to the family's departure from the nest at approximately 24 hr after hatch of the last chick. In each observation period, I recorded the time each member of the focal pair was 1) incubating (on the nest), 2) present at the nest (within 3 m), 3) nearby (>3 m from the nest, but within sight), and 4) absent (out of sight), as well as all instances of incubation exchange, aggressive interaction and chick provisioning. During some observation periods, complete incubation shifts were recorded and allowed a comparison of mean incubation shift length between the sexes. Anti-predator behaviour was defined as an incubating individual leaving the nest to attack a potential predator, and attack rate was calculated for each individual as the number of such interactions per hour in attendance at the nest. Provisioning rate was calculated as the number of times per hour each parent fed chicks, based on the total hours of observation. The sex of breeding Sabine's Gulls under observation was later determined from blood samples, based on the amplification of a portion of two sex-linked genes, following the procedure of Griffiths *et al.* (1998).

3.3.3 STATISTICAL ANALYSES

Behavioural activities, expressed as proportions of the total observation time at each nest, were compared between males and females and among pairs. Where data included repeated observations of the same birds, tests examined means or medians for each individual. There did not appear to be any difference in the breeding behaviour of Sabine's Gulls between years and data were lumped for analyses. When data did not meet the assumptions of parametric statistics, a non-parametric test, the Wilcoxon signed rank test, was used. All statistical tests were performed using DataDesk statistical software v. 6.1 (Data Description Inc., Ithaca, NY). Throughout, statistical significance was recognized at $P \leq 0.05$ and tests were two-tailed. Values reported are means ± SD, unless otherwise stated.

3.4 RESULTS

3.4.1 PRE-LAYING PHASE

Qualitative observations in the week prior to egg-laying showed that pairs spent increasing time associated with a particular area in which they eventually nested. Males were occasionally observed to feed females (courtship feeding) during this pre-laying period, but not during incubation.

3.4.2 INCUBATION PHASE

Overall, there were no significant differences between males and females in the percentage of time they spent in different behavioural activities during the incubation phase, although males appeared to show slightly more individual variation in their parental contributions than females. Females and males spent a similar percentage of time incubating (Table 3.1). However, the difference between individuals in the percentage of time they spent in incubation varied considerably and ranged up to 44 % among females (27-71 % of time) and 48 % among males (23-71 % of time). Two pairs showed equal effort (<5 % difference in the percentage of time males and females spent incubating) and eight pairs showed unequal effort (>5 % difference), with females incubating more in 5 pairs, and males more in 3 pairs. In the most extreme cases, in one pair the female incubated for 71 % and the male for 23 % of the time, while in another pair the female incubated for 27 % and the male for 71 % of the time. Time spent in incubation by both sexes remained similar throughout the day and there were no statistical differences between females and males in each time period (Table 3.2).

Table 3.1: Mean (±SD) percentage of total observation time spent in activities and attack rate (mean no. attacks/hr in attendance) for female (n = 10) and male (n = 10) Sabine's Gulls breeding at East Bay, Southampton Island, Nunavut, during the incubation period, and the results of tests comparing the sexes (T = Wilcoxon signed rank test, t = t-test).

Behaviour	**Female** Mean	SD	**Male** Mean	SD	Test	*P*
Incubation	51.1	16.1	45.8	16.6	*T*	0.85
At nest	0.2	0.2	0.7	1.5	*T*	0.94
Nearby	9.7	8.4	14.4	12.4	*T*	0.92
Absent	39.1	13.2	39.3	15.6	*T*	0.49
Attack rate	0.51	0.37	0.57	0.35	*t*	0.87

Table 3.2: Mean (± SD) % time spent in incubation throughout the day by female and male Sabine's Gulls breeding at East Bay, Southampton Island, Nunavut, and the results of Wilcoxon signed rank test comparing females and males for each time period.

	Female			**Male**				
Time period	*n*	Mean	SD	*n*	Mean	SD	*z*	*P*
0800-1100	22	49	31	22	46	32	0.36	0.72
1400-1700	33	49	26	33	45	28	0.33	0.73
1900-2200	16	56	22	16	41	21	0.96	0.34

The duration of incubation shifts were also similar for females (66 ± 13 min, $n = 7$) and males (51 ± 13 min, $n = 7$), and there was no difference in the mean length of incubation shifts between the sexes (2 sample t-test, $t = 1.74$, $P = 0.10$). On 9 occasions, birds were observed to incubate for a complete observation period (≥3 hours), 6 involving females and 3 involving males. Besides incubating, both females and males spent very little time at the nest, little time nearby, and a similar amount of time absent from the nest area (Table 3.1). However, the difference between individuals in the proportion of time they were absent varied considerably and ranged up to 39 % (23-62 % of time) among females and 45 % (21-66% of time) among males.

Anti-predator behaviour was similar in both sexes during the incubation period, as there was no difference between females and males in attack rate (Table 3.1). Overall, there was no association between the time spent in incubation and the number of times birds left the nest to attack ($r_s = 0.22$). Furthermore, there was no difference in the proportion of potential predatory threats (i.e. the presence of a predator in the area) that incubating females (0.81 ± 0.16, $n = 8$) and males (0.77 ± 0.26, $n = 10$) responded to (Wilcoxon signed rank test, $P = 0.84$).

Of the 10 pairs observed, only one was unsuccessful in hatching chicks, due to predation of the eggs at day 19 in incubation. This was similar to the success rate (0.8) at 10 randomly selected unobserved nests from the same years (2 in 2000, 8 in 2001), and suggests that the presence of observation blinds and movements of researchers had little negative influence on observed pairs. In the observed nests, the unsuccessful pair showed few behavioural differences when compared to successful pairs. However, the female of the unsuccessful pair spent the lowest percentage of time in incubation (27 %) and the greatest percentage absent (62 %) from the nest area. This was compensated by the percentage of time the male spent in incubation (71 %) and, overall, the eggs were incubated 97 % of the time observed, higher than some of the successful pairs (mean = 97 %, range = 94-98 %, $n = 9$).

3.4.3 BROODING PHASE

In general, there were no significant differences between females and males in the time they spent in different behavioural activities during the early brooding phase, although females appeared to show slightly more individual variation in their parental contributions than males.

Although the mean time spent brooding chicks was higher for males than females, there was no statistical difference (Table 3.3). The difference between individuals in time spent on the nest varied considerably, however, and ranged up to 34 % (19-53 % of time) among females and 52 % (24-76 % of time) among males.

During the brooding phase, gulls spent very little time at the nest. However, they spent more time nearby than during the incubation phase (Table 3.3), largely due to short-range foraging bouts around the nest to provision chicks. Females were absent from the nest area as much as they were during the incubation phase, and while males were absent for considerably less time than they were during the incubation phase, there was no statistical difference in male absence between phases (Table 3.3; Wilcoxon sign rank test,

Table 3.3: Mean (±SD) percentage of total observation time spent in activities, attack rate (mean no. attacks/hr in attendance) and chick provisioning rate (mean no. feedings/hr) for female (n = 5) and male (n = 5) Sabine's Gulls breeding at East Bay, Southampton Island, Nunavut, during the brooding period, and the results of tests comparing the sexes (T = Wilcoxon signed rank test, t = t-test).

Behaviour	**Female** Mean	SD	**Male** Mean	SD	Test	*P*
Brooding	37.0	22.7	50.4	21.9	*T*	0.44
At nest	2.3	1.7	4.9	4.9	*T*	0.38
Nearby	25.0	15.1	29.0	9.7	*T*	0.19
Absent	39.2	23.9	19.2	9.3	*T*	0.88
Attack rate	0.17	0.16	0.30	0.24	*t*	0.82
Provisioning rate	0.70	0.45	0.70	0.18	*t*	0.56

P = 0.12). There were also no differences in the mean attack or provisioning rates of females and males. Although the anti-predator behaviour of both females and males appeared lower during brooding than in the incubation phase, there were no significant differences between phases (females, t = -0.48, P = 0.65; males, t = 0.36, P = 0.73). There was also no apparent difference in the proportion of potential predatory threats responded to by brooding females (1.00 ± 0.0) and males (0.83 ± 0.33).

3.5 DISCUSSION

Despite being considered an aberrant species, based on several aspects of behaviour and ecology, Sabine's gull appears to exhibit a fairly typical gull pattern in its breeding behaviour (i.e. both sexes exhibit a high reproductive investment and share parental activities). Courtship feeding is recognized as an important contribution to the production of eggs and more than simply a behavioural indicator of pair bonding (Brown 1967, Nisbet 1973, Møller 1981, Pierotti 1981, Burger 1986). In this study, courtship feeding was observed prior to egg laying, but not during incubation. In courtship feeding, males always regurgitated food onto the ground in front of females (*cf.* Brown *et al.* 1967), as do other gulls. The behaviour of Sabine's Gulls during the incubation and brooding phases also appeared similar to that of other gulls, although there was considerable individual variation within pairs. Despite an unequal division of time spent in incubation in some pairs, nest attendance by at least one parent was very high at all nests (94-98 %) over the incubation phase, and hatching success at East Bay was relatively high in both years of this study. In some large gull species, males are often more involved in anti-predator interactions and nest defence than females (Southern 1981, Morris & Bidochka 1982, Hand 1986), however, this was not the case in Sabine's Gulls, as overall there were no statistical differences between the sexes in their contribution to parental activities.

Provisioning rates during the brooding phase were relatively low, but chicks were 1-3 days old and very small at that stage, and provisioning no doubt increased once the family departed the nest area. Their departure from the nest so soon after hatching is particularly notable and may reflect the high risk of nest predation in some years (see Chapter 5). Although Sabine's Gulls attend their chicks after leaving the nest (Day *et al.* 2001), the roles of parents and the division and durations of parental activities during this period remains unknown. In this species, both parents likely continue to contribute considerable time and energy to feeding and defence of the young until they are fully fledged (20-21 days; Abraham 1986).

It has been suggested that females carry a greater burden of reproduction (Trivers 1972). However, as is expected among monogamous, biparental care-givers, the males of most gull species invest heavily in the production of their young, contributing to the formation of the clutch and other critical parental activities (Pierotti 1981, Butler & Janes-Butler 1983, Dulude *et al.* 1987). In general, the ecological and breeding characteristics of gulls do not easily match with those identified by Silver *et al.* (1985) as being associated with a high degree of parental care in avian subfamilies. In their analysis, groups with precocial young were associated with male contributions to incubation and escorting of the young, but not with feeding females and chick provisioning. Monogamy was generally associated with males feeding their mates and young. Silver *et al.*'s (1985) analysis indicated that the most powerful predictors of male involvement in parental care included mode of development, mating system, and certain habitat characteristics. They did not, however, thoroughly examine the effects of environmental factors. The particularly high degree of parental care exhibited by both sexes of Sabine's Gulls in this study may have been influenced by the pressures of a short breeding season (Day *et al.* 2001) and the high risk of predation at the nest in some years (see Chapter 5).

Sample sizes were admittedly low throughout this study, particularly during the brooding phase, thus statistical power was likely also low. Increasing sample sizes would increase the power of statistical tests (Steidl *et al.* 1997), and could potentially lead to statistically significant results. Throughout, however, the differences between females and males in their contributions to breeding activities (i.e. the effect sizes) were slight and, even if found to be statistically significant with much increased sample sizes, may not be of great biological consequence.

The extent of individual variation in parental contributions within pairs of Sabine's Gulls is particularly intriguing. Individual differences in the performance of parental care by gulls may contribute to differential reproductive success (Southern 1987). Ideally, it would be enlightening to relate the variation in the division of parental activities within pairs to their reproductive success (see Morris 1987). However, hatching success in Sabine's Gulls was high in both years of this study, and sample sizes were low, precluding such investigation. A thorough examination of the influence of individual variation on fitness would require a considerably longer-term study, increased sample sizes, and inclusion of years of high reproductive failure (e.g. due to egg predation). It is during poor reproductive years that variation in the division of critical parental activities, such as incubation and nest defence, would be predicted to be most influential and evident. Further study based on a banded population of individuals of known age and experience would also be most interesting.

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4.0 Nesting habitat and nest-sites of Sabine's Gulls

4.1 ABSTRACT

The selection of breeding habitat is of prime importance in individual fitness, and natural selection should favour the evolution of the ability to recognize and select optimal habitat. This study compares the characteristics of Sabine's Gull (*Xema sabini*) nest sites with random points across the study area and within nesting habitat. The availability of terrestrial invertebrates was also examined among habitat types in the study area. Sabine's Gull nests were clearly non-randomly distributed, and selected sites with the greatest proportion of moss and standing water (i.e. they nested close to pond edges). However, there were no detectable differences in characteristics between successful and unsuccessful nests. The dynamics of terrestrial invertebrate communities varied between years, but the volume of invertebrates in Sabine's Gull nesting habitat was intermediate between the most and the least productive habitats in both years. However, habitat selection in Sabine's Gulls may also be influenced by the availability of aquatic invertebrates among habitats.

4.2 INTRODUCTION

It is generally expected that the majority of individuals of a species will select breeding habitat features that provide the optimal conditions for survival and reproduction (Cody 1985). Furthermore, it is when seabirds have their strongest ties to terrestrial habitats that they may experience their greatest exposure to selective forces, such as predation, disease, and competition for resources, including nest sites (Buckley & Buckley 1980). Thus, birds should have evolved to select features of their environment that will maximize their chances of successful reproduction.

The greatest influences on breeding habitat selection are considered to be safety from predators and access to food (Lack 1968). These factors are not mutually exclusive, however, and some trade-off between the two may come into play in the choice of a specific nest site (Martin 1992, 1995).

The selection of a breeding site that provides optimal conditions for successful reproduction and the survival of young is of critical importance to individual fitness (Buckley & Buckley 1980). In a flat landscape, such as the Arctic, with short vegetation and limited habitat structure, factors influencing nest-site selection may be extremely subtle. Micro-habitat features, such as characteristics of vegetation, substrate, micro-topography, micro-climate, and the presence or absence of conspecifics and/or other species, may have considerable influence on nest-site selection by birds (Cody 1985). Furthermore, the proximity and availability of prey, in relation to micro-habitat characteristics, may play an important role in nest-site selection (Buckley & Buckley 1980).

Across the Arctic, the Sabine's Gull (*Xema sabini*) nests in low-lying, coastal wetland tundra (Day *et al.* 2001). It is considered an unusual species within the gull family (Laridae) and is recognized as phylogenetically distinct (Chu 1998), as well as being considered atypical in several aspects of its reproductive biology and behaviour. For example, it has relatively short incubation and fledging periods (Stenhouse *et al.* 2001), and exhibits a distraction display, when potential predators approach the nest (Brown *et al.* 1967).

In the eastern Canadian Arctic, Sabine's Gulls generally nest on the edges of small freshwater or brackish ponds, or on small islands within larger ponds (Stenhouse *et al.* 2001). They primarily feed on terrestrial and freshwater aquatic invertebrates during the breeding season (Abraham 1984). This study attempts to identify characteristics of their breeding habitat and identify elements important to their selection of nest sites. Specifically, I 1) compare the characteristics of nest sites with random points both across the study area and within their nesting habitat, 2) compare characteristics of successful nests with unsuccessful nests, and 3) examine availability of terrestrial invertebrate prey, in relation to nest location.

4.3 METHODS

4.3.1 STUDY AREA

This study was carried out in the East Bay Migratory Bird Sanctuary (64°01'N, 81°47'W), Southampton Island, Nunavut, in the eastern Canadian Arctic, from May to August 1998-2001. The East Bay sanctuary encompasses an area of approximately 1,200

km^2, and, despite being located within the Low Arctic region, is generally High Arctic in character, influenced in its ecological and physical characteristics by the deep, cold waters of the Foxe Channel. Land-fast sea ice can remain in East Bay well into July and daily minimum temperatures often remain close to freezing throughout summer. The study area is a 2 x 2.5 km block of low-lying, coastal wetland tundra on the southern shore of East Bay, with a complex of brackish and freshwater ponds, typical of the area. Within the plot, sub-habitats are few and distinct, and categorized into 6 main types – gravel ridge, dry heath, scrub willow, sedge meadow, moss carpet, and inter-tidal zone (Table 4.1). In general, wetland areas are characterized by mosses, sedges and grasses, and drier areas are dominated by dwarf shrubs (*Salix* spp.) and Mountain Avens (*Dryas integrifolia*). As a product of the low relief, brackish ponds extend several hundred metres from the shoreline. The inter-tidal area is colonized by few plants, with bare sandy or rocky substrate sparsely broken by small patches of sedges and mosses.

4.3.2 NEST SITES

Within the study area, Sabine's Gull nests were located by searching on foot. The location (latitude and longitude) of each nest was recorded with a hand-held GPS unit (Garmin GPS II Plus, Garmin Corp., KS), and nests were marked on aerial photographs. Co-ordinates were entered into MapInfo (MapInfo Pro, v. 5.0, MapInfo Corp., NY) as decimal degrees. Mean inter-nest distances were calculated in MapInfo using a MapBasic

Table 4.1: Characteristics of the main habitat types in the study area at East Bay, Southampton Island, Nunavut.

Habitat Type	**Characteristics**
Gravel ridge	Bare gravel with little vegetation present Colonised sparsely by mountain avens (*Dryas integrifolia*) at low edges Flora restricted to a handful of herbs and lichens in highest and driest areas Visibly raised from the surrounding areas
Dry heath	Ericaceous shrubs dominant, extensive mountain avens Some willows, lichens abundant, herbs moderate in richness and abundance Substrate a variable mixture of soil, rock and gravel Relief varies from relatively flat to hummocked Typical in drier areas further from shore
Scrub willow	*Salix spp.* among dominant plants Herbs, grasses, sedges and lichens also present in some abundance Substrate largely exposed soil, with rocks of various sizes (<30cm) Typical in drier areas near shore
Sedge meadow	Moss covers substrate and sedge/grasses tall and dense Herbs abundant and diverse, few rocks present Relief varies from flat to hummocked Typical in moist areas and pond edges far from shore
Moss carpet	Living moss covers substrate Sparse to moderate abundance of grasses and sedges Numerous herbs; patchy and sparse, but not uncommon Typical of pond edges in areas between inland and littoral habitats
Intertidal zone	Within splash range of fall storms Living moss and gramminoids sparse and patchy Dead moss (organic crust) of moderate abundance

programme, called 'CalcDist'. Nests were visited approximately every 3 days throughout incubation and hatching (except during extreme weather conditions) to identify losses to predation. At each nest, details of the location, vegetation, substrate, and distance to water were recorded. Within a 1m^2 quadrat centred on each nest, the percentage of ground cover was estimated for each general habitat type: sedge, heath (ericaceous shrubs), willow (*Salix* spp.), moss, exposed soil, rock/gravel, and standing water.

4.3.3 VEGETATION CHARACTERISTICS

To characterize vegetation types within the study area, a plot of 1.5 x 1.5 km, representative of the entire study area, was divided into 16 transects running perpendicular to the shore. Potential vegetation sampling points occurred at 50 m intervals along each transect. A random sample of 80 points was drawn from across the entire plot (from points that fell on transects 0, 4, 8 and 12). Twenty-two of these fell on open water and were discarded, leaving a sample of 58 locations from across the study area. A further 30 random points, from across the entire plot, which fell in moss carpet habitat were used to represent Sabine's Gull general nesting habitat. Within a 1m^2 quadrat at each location, the percentage of ground cover was estimated, using the same habitat categories noted above for nests, as was the distance to nearest water (i.e. pond edge).

4.3.4 PREY AVAILABILITY

The relative temporal and spatial availability of terrestrial invertebrates in each habitat type was quantified in 2000 and 2001 with the use of pitfall traps. These consisted of round plastic containers, 108 mm in diameter, with a circumference of 340 mm. These were placed flush with the substrate and filled with approx. 1 cm of propylene glycol. Trap contents were filtered through a reusable coffee filter, all invertebrates were collected and the filter was flushed clean between each sample collection. Rarely, a few traps were lost, due to the combination of rising groundwater and strong winds, and are thus missing from some sampling intervals.

Sampling was stratified by habitat, with 20 pitfall traps set at random points within non-randomly chosen patches of the 6 broad habitat categories (Table 4.1). Each trap was placed at least 3-4 m from the next, and all traps were placed well within a habitat patch (i.e. avoiding edges). In 2000, all traps were placed in habitat patches in the western half of the study area. They were set out on 30 June, and the contents were collected on 3 occasions over the breeding season (8, 16, 24 July). In 2001, traps were divided evenly between the 2000 sites (n = 10) and similar sites in the eastern half of the study area (n = 10). Traps were set out on 21 June, and emptied on 4 occasions (29 June, 7, 15, 23 July).

An index of the biomass of invertebrates in each habitat was estimated by measuring the mean volume per individual for each invertebrate species/group, then multiplying this by the number of individuals present in each sample. The mean volume of each invertebrate was calculated as follows: individual invertebrates from each species/group were placed into a known quantity of fluid in a graduated cylinder until a measurable amount (at least 0.2 ml) was displaced, this was repeated five times, and an overall mean was established.

Although the use of pitfall traps has a long history in ecological studies, they are known to be selective in trapping different invertebrate species and different life-stages (Topping & Sunderland 1992). That is, the mobility of a specific invertebrate species, or life stage, is related to the probability that it will fall into a trap. However, they are useful in measuring the abundance of active invertebrates (Van den Berghe 1992), which are likely to be caught by foraging birds.

4.3.5 STATISTICAL ANALYSES

A Principal Components Analysis (PCA) was used to reduce the number of variables in the habitat data, and two-tailed t-tests were used to compare principal component (PC) scores between groups, such as nests and random points. T-tests were also used to compare the proximity of nests and random points to the nearest water. Analyses were carried out using DataDesk statistical software v. 6.1 (Data Description Inc., Ithaca, NY). Throughout, statistical significance was recognized at $P \leq 0.05$, and values reported are means ± SD, unless otherwise stated.

4.4 RESULTS

4.4.1 VEGETATION CHARACTERISTICS OF STUDY AREA

On average, $1m^2$ quadrats at random points across the study area consisted of moss (38 %), heath (24 %), and rock/gravel (20 %), with small amounts of sedge (5 %) and willow (3 %), and very little standing water (0.03 %; Table 4.2).

In the principal components analysis, only the first principal component (PC1) explained a considerable proportion of the variance (31%), while the second component explained only 17% (Table 4.3). Moss, a damp habitat, loaded negatively and heath, rock/gravel and exposed soil, which are dry habitat types, loaded positively for PC1, suggesting that this component is a general measure of moisture content.

4.4.2 VEGETATION CHARACTERISTICS OF NESTING HABITAT

Vegetative cover within the nesting habitat was much less varied than the wider study area (Table 4.2). On average, $1m^2$ quadrats at random points within the nesting habitat were dominated by moss (71 %), with a considerable amount of exposed soil (14 %) and more standing water (0.17 %). There were no ericaceous shrubs (heath) recorded in this habitat (Table 4.2).

4.4.3 NESTING DISTRIBUTION

Sabine's Gull nests at East Bay were restricted to the moss carpet habitat, which occurs in a band between approximately 200 and 1100 m from shore (Fig. 4.1). The

Table 4.2: Mean percentage cover (±SD) of vegetation types (1m^2 quadrats) and distance to nearest water at random points across the study area (*n* = 58), random points within nesting habitat (*n* = 30), and at Sabine's Gull nests (*n* = 70) at East Bay, Southampton Island, Nunavut.

% cover	Study area	Nesting habitat	Nests
Sedge	5 ± 6	8 ± 7	4 ± 18
Heath	24 ± 30	0	0
Willow	3 ± 5	3 ± 6	3 ± 10
Moss	38 ± 40	71 ± 26	80 ± 25
Exposed soil	10 ± 21	14 ± 16	<1 ± 2
Rock/gravel	20 ± 27	7 ± 13	2 ± 4
Standing water	<1 ± 0.3	<1 ± 1	10 ± 14
Distance to water (m)	25.0 ± 25.9	10.9 ± 14.2	0.7 ± 0.6

Table 4.3: Habitat variables, component loadings and eigenvalues for the first three principal components of 1m^2 quadrats centred on Sabine's Gull nests, random points across the study area, and random points within nesting habitat at East Bay, Southampton Island, Nunavut.

Variable	PC1	PC2	PC3
Sedge	0.24	0.66	0.27
Heath	0.63	-0.50	0.19
Willow	0.19	-0.07	0.70
Moss	-0.95	0.03	0.11
Exposed soil	0.43	0.62	-0.38
Rock/gravel	0.71	-0.22	-0.29
Standing water	-0.32	-0.27	-0.49
Eigenvalue	2.19	1.20	1.09
% variation explained	31.2	17.1	15.3
Total variation explained	31.2	48.3	63.8

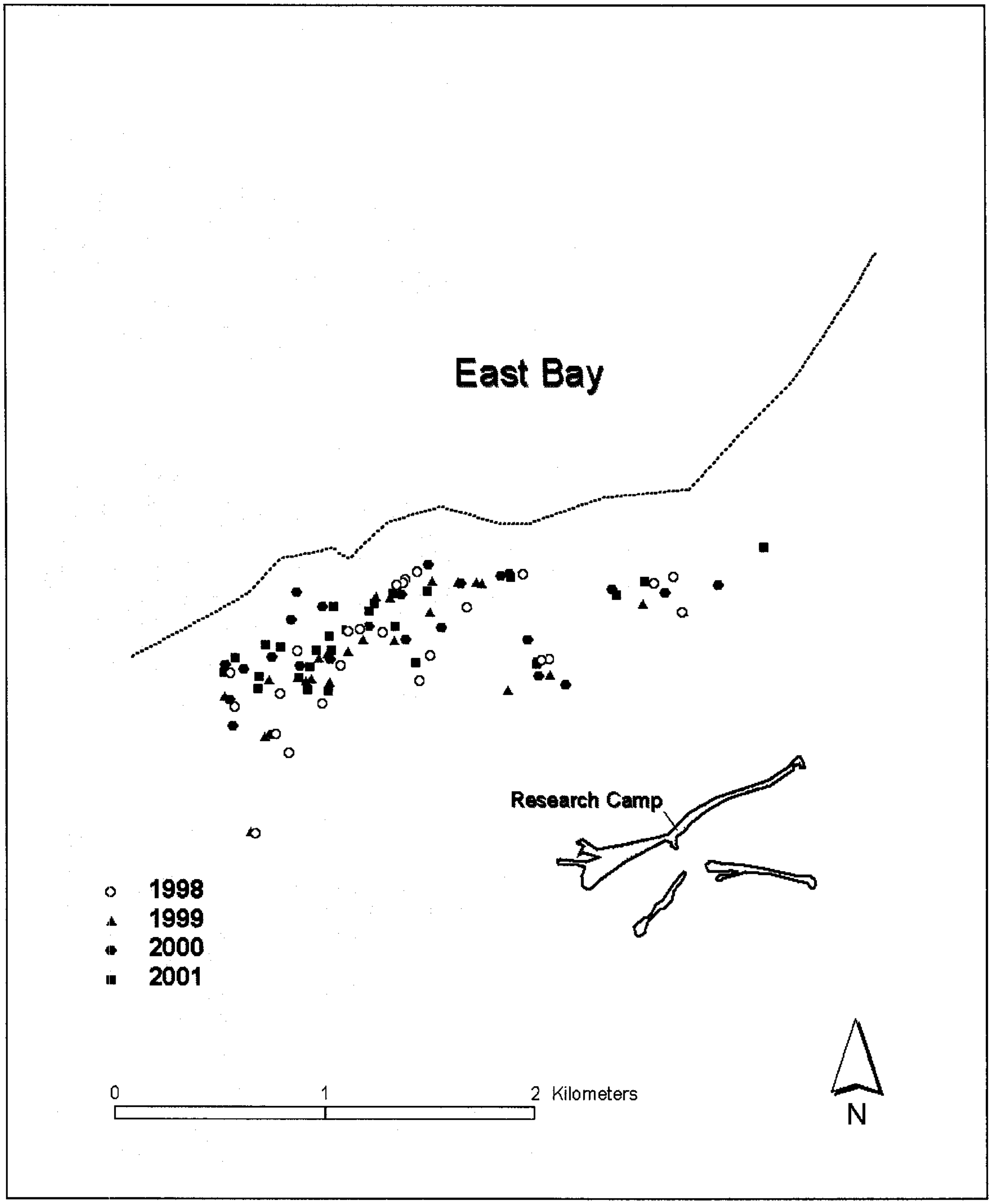

Fig. 4.1: The distribution of Sabine's Gull nests in the study area at East Bay, Southampton Island, Nunavut, in each year (solid line = gravel ridge, dotted line = shore).

number of Sabine's Gull nests located on small islands within ponds (versus pond edges) ranged from 22-40 %, and the proportion was not significantly different among years (χ^2_3 = 2.41, $P = 0.49$). Due to evaporation, the area of ponds often changed over the course of the breeding season at East Bay, so that nests originally on small islands occurred on pond edges by mid- to late July.

The vegetative cover around Sabine's Gull nest sites showed a similar amount of sedge and willow as random points across the study area, but nests were strikingly different in all other vegetation types, and in the proportion of standing water (Table 4.2). A t-test on the mean PC1 scores for nests (-0.61 ± 0.50, $n = 70$) and random points across the study area (0.78 ± 1.07, $n = 58$) showed a highly significant difference ($t_{77} = -9.1$, $P \leq 0.0001$) between these two groups, indicating that Sabine's Gulls selected damp, mossy areas. A t-test also showed a highly significant difference ($t_{56} = -7.10$, $P \leq 0.0001$) in the mean distance to nearest water between nests (0.67 ± 0.64, $n = 65$) and random points across the study area (25.0 ± 25.9, $n = 57$).

Within the general Sabine's Gull nesting habitat (i.e. moss carpet), the vegetative cover around Sabine's Gull nests showed a similar amount of willow as random points. However, nests were again strikingly different from random points within nest habitat in the proportion of all other vegetation types (Table 4.2). The proportion of moss cover and standing water were much higher at nests, due to the gulls nesting at the edges of ponds. A t-test on the mean PC1 scores for nests (-0.61 ± 0.50, $n = 70$) and random points within nesting habitat (-0.08 ± 0.65, $n = 30$) showed a highly significant difference ($t_{44} = -4.0$, $P \leq$

0.0001), indicating that, even at this finer scale, nests were non-randomly distributed and Sabine's Gulls selected particularly mossy sites. There was also a highly significant difference in the mean distance to nearest water between nests (0.67 ± 0.64 m, $n = 65$) and random points within nesting habitat (10.93 ± 14.16 m, n = 30; $t_{29} = -3.97$, $P = 0.0004$), with nests being much closer to water.

4.4.4 SUCCESSFUL AND UNSUCCESSFUL NESTS

T-tests showed no differences in the mean PC1 scores for successful (-0.67 ± 0.41, $n = 41$) and unsuccessful nests (0.54 ± 0.59, $n = 29$; $t_{68} = -1.07$, $P = 0.29$), or in the mean distance to nearest water between successful (0.56 ± 0.45, $n = 38$) and unsuccessful nests (0.83 ± 0.83, $n = 27$; $t_{36} = -1.50$, $P = 0.14$). However, the variance around the mean PC1 scores for unsuccessful nests (SE = 0.11) was twice that of successful nests (SE = 0.06).

4.4.5 PREY AVAILABILITY

The 'biomass' of terrestrial invertebrates across the study area differed between habitats ($F_{5,41} = 7.77$, $P = 0.003$) and across the season ($F_{3,41} = 15.0$, $P = 0.0005$), but not between years ($F_{1,41} = 2.46$, $P = 0.15$); and there were no significant interactions. Dry heath, scrub willow, and sedge meadow showed a greater volume of invertebrates throughout the breeding season, compared to bare gravel, and the inter-tidal zone. However, the volume of invertebrates in moss carpet habitat was consistently intermediate between these groups (Fig 4.2).

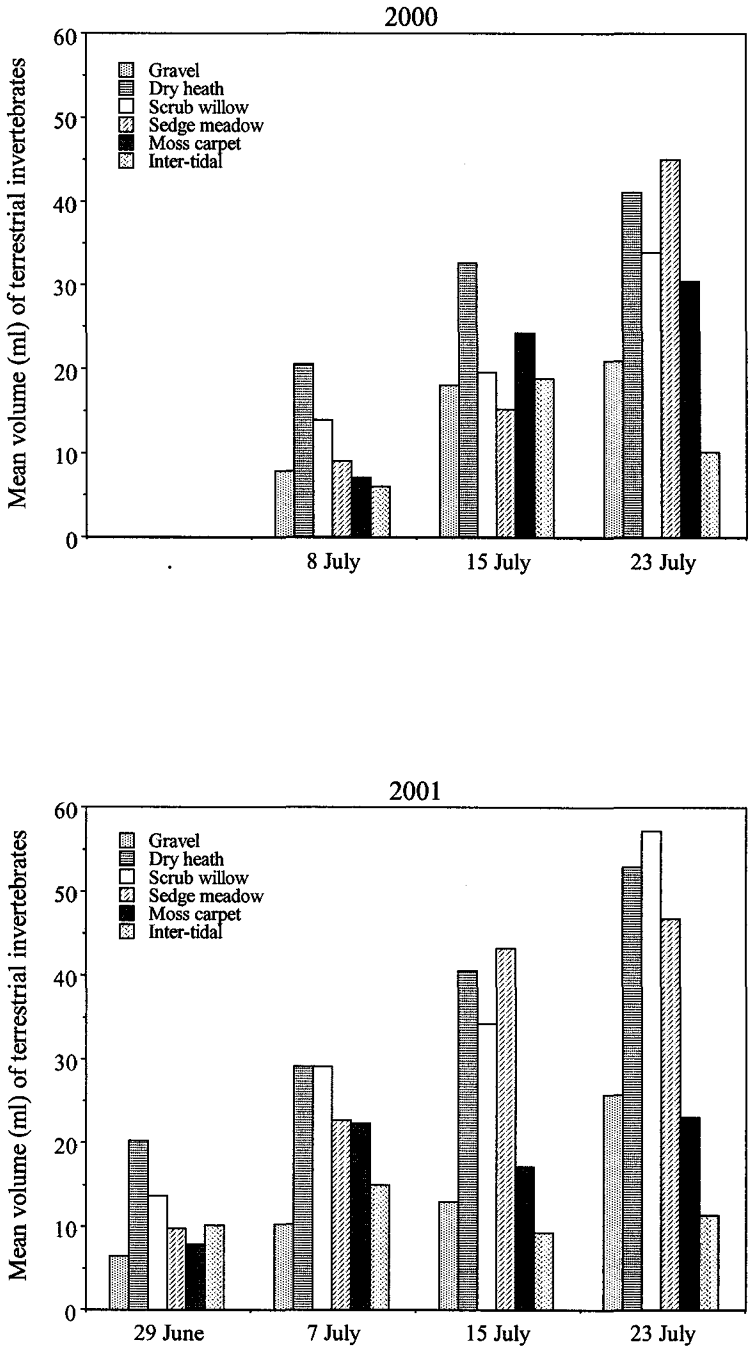

Fig 4.2: Total volume (ml) of terrestrial invertebrates in each habitat type in 2000 and 2001, at East Bay, Southampton Island, Nunavut.

4.5 DISCUSSION

Sabine's Gull nests were non-randomly distributed throughout the study area, where birds clearly selected damp, mossy areas. Nests were also non-randomly distributed within the general nesting habitat, and Sabine's Gulls selected particularly mossy sites close to standing water (i.e. pond edges). Interestingly, there were no significant differences detected between successful and unsuccessful nests. However, although natural selection is expected to occur when there are differences between successful and unsuccessful nests, differences of this type are likely to be subtle and difficult to detect (Martin 1998). The considerably greater variance around the mean PC1 scores for unsuccessful nests suggests that there may be higher nest failure at the extremes of their habitat gradient, thus, breeding habitat selection in Sabine's Gulls may be under the influence of stabilizing natural selection (Clark & Shutler 1999). That is, the choice of specific characteristics found at successful nests is constantly reinforced through the process of natural selection.

Although Sabine's Gulls feed around their nests, the moss carpet habitat in which they nest was not the most productive for terrestrial invertebrates. In fact, moss carpet was intermediate between the most productive habitats (dry heath, scrub willow, sedge meadow) and least productive habitats (gravel ridge, intertidal zone). However, moss carpet was the most productive habitat closest to the shore of the bay, where breeding Sabine's Gulls take their chicks immediately after hatch (Forchhammer & Maagaard 1991, Stenhouse *et al.* 2001). On the small island of Renskaeret, in northeast Greenland, where there are no freshwater ponds, Sabine's Gulls forage in saltwater, at openings in sea ice, throughout the breeding period (Forchhammer & Maagaard 1991). Ice cover is generally solid in East Bay until late June or early July, preventing Sabine's Gulls from foraging in saltwater during incubation. However, East Bay is usually free of pack ice in mid-July, when Sabine's Gull chicks hatch (Stenhouse *et al.* 2001), and families may make the move to the shore immediately after hatch so that adults can feed in saltwater during the provisioning period near their chicks. In addition, by selecting moss carpet habitat, Sabine's Gulls 1) nest in the most productive habitat nearest to shore, 2) limit the distance they have to move with small chicks, and 3) stay away from drier inland areas where their main predators breed, such as the Arctic fox (*Alopex lagopus*) and the Herring Gull (*Larus argentatus*).

Sabine's Gulls also feed in ponds within their nesting habitat during incubation, particularly freshwater ponds (Abraham 1984), and their breeding habitat selection may be strongly influenced by the production and availability of aquatic invertebrates among habitats. However, the relative abundance of aquatic invertebrates was not examined in this study.

Over the course of the breeding season, shallow ponds at East Bay can dry up completely, especially in inland areas and close to shore (pers. obs.). However, in the moss carpet habitat, ponds often shrink in area but rarely dry up completely, thus the moss carpet habitat may also be the least variable from year to year in the amount of water retained in ponds over the summer.

Arctic Terns (*Sterna pardisaea*), Ruddy Turnstones (*Arenaria interpres*), and Red Phalaropes (*Phalaropus fulicaria*) also breed in the moss carpet habitat. However, none of these species appeared to show the same restriction to this habitat observed in Sabine's Gulls, and breed over a much wider area (pers. obs.). Although some or all of these species are seen together at times, particularly when mobbing predators (see Chapter 5), their proximity may simply reflect an overlap in habitat selection, rather than any 'true' nesting association, inter-specific advantages of mutual cooperation in anti-predator behaviour, or the protection of one species by another.

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5.0 Anti-predator behaviour in Sabine's Gulls, the extent of predation and the influence of alternative prey

5.1 ABSTRACT

Among ground-nesting birds, nest defence may be critical in reproductive success. The defensive response of Arctic-breeding Sabine's Gulls (*Xema sabini*) toward natural predators was recorded in 2000 and 2001, and toward predator decoys and a human intruder in 2001. Herring Gulls (*Larus argentatus*) and Parasitic Jaegers (*Stercorarius parasiticus*) were the most commonly encountered potential predators. The distance at which nesting Sabine's Gulls first reacted to predators and the relative intensity of their response did not differ with incubation stage, but did differ among predator types and between pairs. In response to decoys, Sabine's Gulls distinguished between threatening and non-threatening species. The distance at which Sabine's Gulls first swooped at a human intruder was variable, with no consistent trend over the season. In their nest defence, Sabine's Gulls were often joined by conspecifics and by Arctic Terns (*Sterna pardisaea*) and occasionally by shorebirds nesting nearby. However, the proximity of the nearest neighbouring conspecific nest did not influence the number of Sabine's Gulls involved in attacks.

The alternative prey hypothesis (APH) links cycles in productivity observed in Arctic-breeding birds with those of small mammal populations, through common predators. In years with a low abundance of primary prey (small mammals), predators

switch to alternative prey (eggs and young of ground-nesting birds). The reproductive success of Sabine's Gulls breeding in the eastern Canadian Arctic, and the presence of lemmings and Arctic foxes in the study area, was followed over four years. As predicted by the APH, Sabine's Gulls suffered higher rates of reproductive failure in the absence of rodents. Overall, annual fluctuations in predation pressure appeared to be a major influence on the breeding productivity of Sabine' Gulls. Further examination of common behavioural features of highly successful pairs may provide insight into the evolutionary effects and/or consequences of episodic selective events.

5.2 INTRODUCTION

Predation is a powerful selective pressure on many species particularly during reproduction (Lack 1954, Krebs 1973). Among birds, predators are often the main cause of nest failure (Clark & Wilson 1981). The extent of predation suffered by a prey species is influenced by the abundance of predators, and, if their predators are generalists, by the availability of alternative prey (Bêty *et al.* 2002). Vulnerable species may forego breeding altogether in years of intense predation pressure (see Spaans *et al.* 1998), while others attempt to limit the extent of predation via life-history (Martin 1995) or behavioural adaptation (Kruuk 1964). In habitats where vegetation is sparse or too short to provide concealment, ground-nesting species may be particularly vulnerable to predation (Buckley & Buckley 1980).

Anti-predatory behaviour is widespread in a broad range of animal taxa, including birds (Curio 1976, Redondo 1989). Among ground-nesting birds, where the nest is easily accessible to predators, nest defence can be critically important in reproductive success (Gochfeld 1984). Defensive response and intensity may vary, however, in relation to the species of predator, stage of breeding, and risk to adults, eggs and/or small chicks (Kruuk 1964, Curio 1975, Andersson *et al.* 1980, Patterson *et al.* 1980).

The Sabine's Gull (*Xema sabini*) is an Arctic-breeding, ground-nesting species. Breeding Sabine's Gulls exhibit conspicuous aggressive and defensive behavioural displays towards a range of potential predators (Day *et al.* 2001). Sabine's Gulls are vulnerable to mammalian and avian nest predators: Arctic foxes (*Alopex lagopus*), Herring Gulls (*Larus argentatus*), Parasitic Jaegers (*Stercorarius parasiticus*) and Common Ravens (*Corvus* *corax*). Peregrine Falcons (*Falco peregrinus*) have been observed to attack isolated adults in the air during breeding (Day *et al.* 2001, Parmelee *et al.* 1967).

In northern ecosystems, populations of small mammals exhibit cyclic fluctuations, typically peaking every 3-5 years (Ylönen 1994, Hanski & Korpimäki 1995). Furthermore, the breeding success of ground-nesting birds has been shown to fluctuate in synchrony with small mammal populations (Summers 1986, Summers & Underhill 1987, Järvinen 1990). The Alternative Prey Hypothesis (APH) predicts that in years with a low abundance of primary prey (small mammals), predators switch to alternative prey (eggs and young of ground-nesting birds). The APH is believed to be the main mechanism linking the abundance and density of small mammals and the reproductive success of ground-nesting birds, via their shared predators (Angelstam *et al.* 1984, Summers 1986, Sutherland 1988, Underhill *et al.* 1989, Summers *et al.* 1998, Bêty et al. 2001, Wilson & Bromley 2001). The influence of fluctuations in primary prey species on avian reproductive success can also be affected, however, by changes in breeding strategies employed by birds. For example, during years of low primary prey, Arctic breeders may increase their reproductive success by nesting at high density (Raveling 1989), synchronizing their breeding effort (Findlay & Cooke 1982), nesting in association with aggressive species (Summers *et al.* 1994), or by actively defending their nests against predators (Stickney 1991, Syroechkovskiy *et al.* 1991).

Over four years, I tracked the annual reproductive success of Sabine's Gulls, the influence of predators, and the presence of alternative prey. Specifically, I examined, through observation and experimental manipulation, whether Sabine's Gulls (1) distinguished between ‘threatening’ and ‘non-threatening’ species in their defensive response, (2) responded differently to avian versus mammalian predators, (3) exhibited variation between pairs in their responses to predators, and (4) were under greater threat of egg loss in years of low alternative prey. Finally, I discuss the results of this study in relation to APH dynamics.

5.3 METHODS

Fieldwork was conducted from late May to mid-August 1998-2001 in the East Bay Migratory Bird Sanctuary (64°01'N, 81°47'W), Southampton Island, Nunavut, in the eastern Canadian Arctic. The East Bay sanctuary encompasses an area of approximately 1,200 km^2, and, despite being located within the Low Arctic region, is generally High Arctic in character, influenced in its ecological and physical characteristics by the deep, cold waters of the Foxe Channel. Land-fast sea ice generally remains in East Bay well into July and daily minimum temperatures are usually close to freezing throughout summer (Jun-Aug).

The study area is a 2 x 2.5 km area of low-lying, wet tundra, with a complex of brackish and freshwater ponds, typical of the region. Within the study area, sub-habitats are few and distinct, with wetland areas characterized by mosses and sedges, and drier areas dominated by dwarf shrubs (*Salix* spp.) and Mountain Avens (*Dryas integrifolia*). As a product of the low relief, brackish ponds extend ~1 km inland from the shoreline. This high salinity area is colonized by few plants, with bare sandy or rocky substrate sparsely broken by small patches of vegetation.

East Bay supports a diverse avian community (Abraham & Ankney 1986). Over the years of this study, the study area supported 23-28 breeding pairs of Sabine's Gulls, 20-25 breeding pairs of Herring Gulls, and 2 breeding pairs of Parasitic Jaegers. One Peregrine Falcon nest was located at the nearest cliff face, approximately 15 km east of the study area. Common Ravens were occasionally observed flying over the study area, but were never seen to land.

5.3.1 ANTI-PREDATOR BEHAVIOUR

5.3.1.1 Response to predators

The defensive response of breeding Sabine's Gulls to predators was recorded from blinds during 3 hr behavioural watches at 3 nests in 2000 (69 hr) and 8 nests in 2001 (162 hr). Observations concentrated on the behaviour of the nesting pair in response to the presence of predatory species, the time the nesting pair spent in the interaction and the distance of the predator from the nest at first reaction. The intensity of response was measured using the following index: 0 = no response, 1 = flies out, 2 = chases, 3 = chases and calls, 4 = swoops/dives, 5 = strikes predator. Occasionally, interactions were missed, as Sabine's Gulls appeared to react to predators that could not always be seen from the blind. Nest phenology was calculated from known laying dates of first eggs, or back-calculated from the hatch date of the first egg, based on a 21-day incubation period (Day *et al.* 2001). Nesting stage was categorized as early incubation (d 1-7), mid-incubation (d 8-14), late incubation (d 15-21) or hatch (d 22-24). During interactions involving other birds (group defence), the identification of the species involved and the response score of the extra-pair individual(s) was also recorded.

5.3.1.2 Response to predator decoys

In 2001, decoys of two predators, a Red Fox (*Vulpes vulpes*) and a Herring Gull, and a novel control species, a female Harlequin Duck (*Histrionicus histrionicus*), were used to examine the type and relative intensity of parental response. Observations were carried out at 8 nests. Each decoy was presented twice at each nest, on separate days, and decoys were presented in a randomized order. Decoys, covered by sack cloth attached to a line, were placed 25 m from nests in a random direction, and were clearly visible from nests. The observer then retreated to approx 50 m from the nest. Once the incubating bird had been back on the nest for 10 minutes, the decoy was exposed by tugging on the line and the behaviour of the nesting pair and neighbouring birds was recorded for 15 minutes. Nest phenology was controlled for in this experiment, as all trials were carried out in late-incubation.

An attack was defined as any swooping or diving behaviour directed at the decoy. For each trial, decoy type, nest phenology, distance to nearest neighbouring Sabine's Gull nest, time to first attack (latency), total time spent in attack (duration), number of birds involved in an attack, and the intensity of the attack were recorded. An intensity index based on the behaviour of the nesting pair ranged from 'none/little' to 'mild' or 'intense' response (Table 5.1). This experiment examined whether predator type affected the

Table 5.1: Intensity index, response type and behaviour of Sabine's Gulls in response to predator decoys close to the nest.

Index	Behaviour	Response type
0	No response from either parent	little
1	Incubating bird calls from nest, no response from mate	
2	One bird circles over decoy	mild
3	Both birds circle over decoy	
4	One bird attacks decoy	intense
5	Both birds attack decoy	

behavioural response of Sabine's Gulls, by comparing their reactions to threatening species (fox, gull) and a non-threatening species (duck), as well as detecting any variation in the intensity of response shown to mammalian versus avian predators.

The presentation of stationary decoys does not mimic the approach of a natural predator, particularly for avian species. The reactions of Sabine's Gulls, however, appeared to be unaffected by the sudden appearance and the static nature of the decoys, thus decoys appeared to be effective in eliciting a natural and realistic response.

5.3.1.3 Response to human intruders

Nest defence behaviour was also measured by recording the response to a human intruder. In calm, dry weather, nests were approached at a slow, steady walk, in a direct line of sight of the incubating bird. The distances at which the behaviours of the incubating bird changed were measured with a rangefinder. These included: flew up, called, swooped, made contact, defecated, and exhibited distraction display. The number of Sabine's Gulls involved in the attack, as well as the number and species of other birds involved, were also recorded. The intruder remained standing over the nest for approximately 2 minutes and continued to record any changes in behaviour. Nest phenology was calculated and categorized as above.

5.3.2 MONITORING REPRODUCTIVE SUCCESS AND ALTERNATIVE PREY

Hatching success of Sabine's Gulls was monitored in all nests located within the study area, from 1998-2001. Nests were located by searching on foot and were generally visited daily until the clutch was completed. Nests were visited on average every three days during incubation and daily during the hatching period. Eggs that disappeared from nests prior to their projected hatching date (21 days; Stenhouse *et al.* 2001) were assumed depredated. In addition, the presence or absence of Greenland Collared Lemmings (*Dicrostonyx groenlandicus*) and Arctic foxes in the study area was recorded each day. Some days were missed during each season, due to extreme weather conditions, so these observations are expressed as a proportion of days spent in the study area i.e. the percentage of field days in which lemmings and foxes were observed.

5.3.3 STATISTICAL ANALYSIS

Relationships between two variables were measured using the Pearson product-moment correlation. Differences among sample means were examined using Analyses of Variance (ANOVA). Associations among categories were explored with the Bonferroni post hoc test. Where multiple observations were recorded at each nest, predictor variables were nested within gull pairs for analysis in a nested ANOVA design. When the dependent variable was binary (i.e. in pairs at ultimately successful or depredated nests), logistic regression was used to examine differences. Statistical significance was recognized at $P \leq 0.05$, and error distributions were examined for homogeneity, normality, and independence of residuals. Values are reported as means ± 1 SD. All statistical tests were performed using DataDesk statistical software v. 6 (Data Description Inc., Ithaca, NY).

5.4 RESULTS

5.4.1 ANTI-PREDATOR BEHAVIOUR

5.4.1.1 Response to predators

A total of 124 interactions with natural predators were observed; in 2000, responses were recorded for only two potential predators; 93 % of these involved Herring Gulls, and the remaining 7 % involved Parasitic Jaegers (n = 29; Table 5.2). In 2001, responses were recorded for six different potential predators, 56 % of these involved Herring Gulls, 20 % involved humans, 19 % involved Parasitic Jaegers, 2 % involved Arctic foxes, 2 % involved Glaucous Gulls (*Larus hyperboreus*), and 1 % involved a Peregrine Falcon (n = 95; Table 5.2).

The distance at which nesting Sabine's Gulls first reacted to predators did not differ with incubation stage ($F_{12, 123} = 1.5$, $P = 0.14$), but did differ among predator types ($F_{17, 123} = 2.5$, $P = 0.003$; Table 5.3) and among individual pairs ($F_{10, 123} = 2.2$, $P = 0.03$). The relative intensity of their response did not differ with incubation stage ($F_{12, 123} = 1.7$, $P = 0.08$), but, again, did differ among predator types ($F_{17, 123} = 2.6$, $P = 0.002$) and among pairs ($F_{10, 123} = 1.9$, $P = 0.05$). There were no differences, however, in the length of time that pairs spent in behavioural interactions with predators.

Predation pressure was not high in either 2000 or 2001. Of the 3 pairs under observation in 2000, none lost eggs, and of the 8 pairs under observation in 2001, only one lost eggs due to predation. This depredated pair showed the lowest response score toward predators (1.75 ± 1.35; range for other 10 pairs = 2.14 - 3.7).

Table 5.2: The number of observations, mean (± SD) distance of predator from nest at response, mean (±SD) response intensity score, and the percentage of interactions involving group defence for natural predators observed in 2000 and 2001.

Year Predator	*n*	Distance from nest (m)	Response score	Group defence (%)
2000				
Herring Gull	27	126 ± 64	2.3 ± 1.1	55
Parasitic Jaeger	2	163 ± 18	5.4 ± 0.7	100
2001				
Herring Gull	53	166 ± 74	3.1 ± 0.9	55
Parasitic Jaeger	18	189 ± 102	3.2 ± 1.3	33
Glaucous Gull	2	275 ± 106	4.0 ± 0.0	100
Peregrine Falcon	1	350	3.0	100
Arctic fox	2	250 ± 71	4.5 ± 0.7	100
Human	19	146 ± 93	1.9 ± 1.4	38

The likelihood that other Sabine's Gulls (extra-pair birds) joined in defensive attacks was weakly negatively related to the proximity of the nearest neighbouring conspecific nest ($F_{1, 123} = 3.9$, $P = 0.052$). During communal defence, the following species participated: Sabine's Gulls in 30 % of observed interactions, Arctic Terns (*Sterna pardisaea*) 13 %, Ruddy Turnstones (*Arenaria interpres*) 2 % and White-rumped Sandpipers (*Calidris fuscicollis*) 1 % ($n = 124$).

5.4.1.2 Response to model predators

There were no significant differences between the two trials of each decoy type, so trials were lumped for further analysis. The mean time to initial response ($F_{2, 47} = 43.0$, $P < 0.001$), duration of attack ($F_{2, 47} = 17.8$, $P < 0.001$), intensity of the attack response ($F_{2, 47} = 88.6$, $P < 0.001$), and number of birds involved in attacks ($F_{2, 47} = 13.6$, $P < 0.001$) were all significantly different among decoy types. In all cases, the difference lay between the non-threatening species (duck) and the threatening species (gull and fox; Table 5.3). There were no significant differences, however, between the two threatening species in terms of the time it took Sabine's Gulls to respond, or in the duration or the intensity of attacks that they elicited. The number of Sabine's Gulls involved in attacks did not increase the total number of swoops at a predator ($r^2 = 0.20$), nor did it appear to have any association with the proximity of the nearest neighbouring Sabine's Gull nest ($r^2 = 0.03$). During communal attacks on decoys, Sabine's Gulls and Arctic Terns were involved in 8 and 10 % respectively ($n = 48$). None of these were aimed at the non-threatening decoy.

Table 5.3: The mean (±SD) latency time, attack duration, and response score, and the percentage of interactions involving group defence, for each predator decoy type.

Decoy type	Latency (s)	Duration (s)	Response score	Group defence (%)
Duck	778 ± 277	15 ± 35	0.9 ± 1.2	0
Gull	164 ± 234	308 ± 162	4.2 ± 0.4	6
Fox	125 ± 136	371 ± 264	4.6 ± 0.5	19

5.4.1.3 Response to human intruders

There were no significant differences in the mean distances at which Sabine's Gulls first flew, called, or struck a human intruder in relation to nest phenology. There were, however, significant differences in the distance at which they first swooped at a human intruder at different stages ($F_{14, 30} = 3.6$, $P = 0.03$) and among pairs ($F_{14, 30} = 6.3$, $P = 0.007$). The mean distance at first swoop was lower in mid-incubation than in early or late incubation, and highly variable among pairs throughout. There were no significant differences in the response distances or intensity of Sabine's Gulls to human intruders in relation to nest outcome, although sample sizes are admittedly small for such a comparison.

Although there was no significant difference in the mean number of birds involved in attacks in relation to incubation stage ($F_{15, 39} = 2.3$, $P = 0.06$) there was a difference among nest sites ($F_{8, 39} = 7.1$, $P < 0.001$), with some pairs gaining extra-pair birds in their attacks more often than others. The number of Sabine's Gulls involved in attacks, however, did not have a strong association with the proximity of the nearest neighbouring Sabine's Gull nest ($r = -0.48$). One pair displayed both the greatest mean distance to first swooping at a human intruder (81.5 ± 14.9 m), and on average more birds were involved in attacks at that nest (4.5 ± 2.4 birds). Overall, extra-pair Sabine's Gulls participated in 47 % of interactions, Arctic Terns in 15%, and Herring Gulls in 5 % ($n = 40$).

5.4.2 REPRODUCTIVE SUCCESS AND ALTERNATIVE PREY

Over the years of this study, there was a strong negative association between the percentage of days Arctic foxes were observed and the percentage of days that lemmings were observed ($r^2 = 0.63$; Fig 5.1). Also, there was a strong negative relationship between the hatching success of Sabine's Gulls and the percentage of days foxes were observed in the study area ($r^2 = 0.64$: Fig. 5.2). In three out of the four years of this study, egg loss in Sabine's Gull eggs ranged from 27-28 %, however, it reached 75% in 1999 (Table 5.4). In 1999, there were no lemming sightings and a considerable increase in the percentage of days in which Arctic foxes were present in the study area, in stark contrast to the other years of this study (Fig. 5.3). During 2000, lemmings were extremely abundant and Arctic foxes were rarely seen on the study area (Fig. 5.3), apparently preferring drier, hummocky tundra inland, where they denned. These findings suggest rodents are the primary prey of Arctic foxes on Southampton Island, as they are across much of the Arctic (Larson 1960, Summers & Underhill 1987, Stickney 1991, van Impe 1996), even in years of low lemming abundance (Dalerum & Angerbjörn 2000). In 2001, the hatching success of Sabine's Gulls was lower than in 1998 and 2000, despite lemmings being observed on more days than in either of these years, and foxes on fewer days than in 1998 (Table 5.2). However, this reduction in hatching success in 2001 was not associated with an increase in egg loss but rather was the result of a period of intense rain and flooding early in the incubation stage.

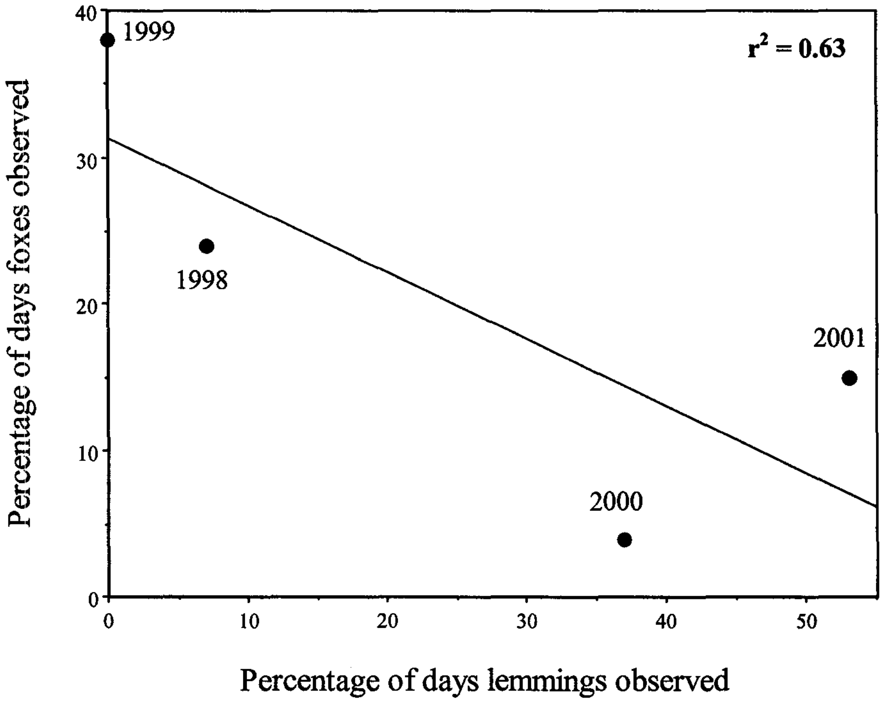

Fig. 5.1: The percentage of days that Arctic foxes and lemmings were observed in the study area at East Bay, Southampton Island, Nunavut, in each year.

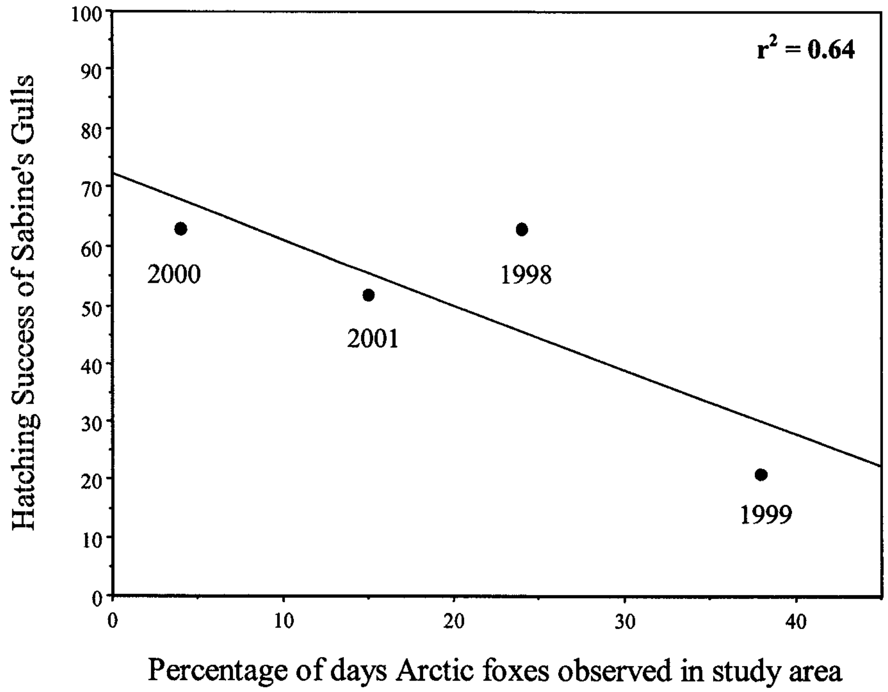

Fig. 5.2: The hatching success of Sabine's Gull and the percentage of days Arctic foxes were observed in the study area at East Bay, Southampton Island, Nunavut, in each year.

Table 5.4: The number of Sabine's Gull nests followed, the total number of eggs laid, hatching success, and the number and percentage of eggs depredated in each year, 1998-2001, at East Bay, Southampton Island, Nunavut.

	1998	1999	2000	2001
No. nests	23	25	25	28
No. eggs laid	60	57	59	75
Hatching success	0.63	0.21	0.63	0.52
No. eggs depredated	16	43	16	21
% Depredated	27	75	27	28

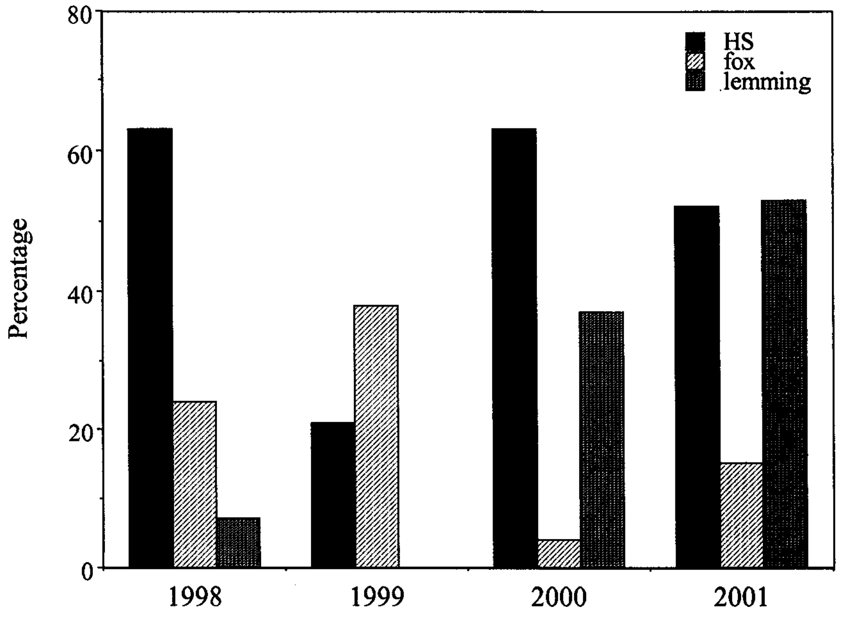

Fig. 5.3: The hatching success of Sabine's Gulls (HS), and the percentage of days Arctic foxes and lemmings were observed in the study area at East Bay, Southampton Island, Nunavut, in each year.

5.5 DISCUSSION

5.5.1 FACTORS AFFECTING ANTI-PREDATOR BEHAVIOUR

5.5.1.1 Predator type

Sabine's Gulls reacted intensely to Arctic foxes, Glaucous Gulls and Peregrine Falcons at considerable distances (250-350 m), but these predators were rarely encountered in 2000 and 2001 (Table 5.3). During interactions with Herring Gulls and Parasitic Jaegers, Sabine's Gulls reacted at a shorter distance (~130-190 m), and with a lesser degree of intensity, than with the rarer predators. Herring Gulls were attacked most often by Sabine's Gulls, likely because they were the most commonly encountered predator. Behavioural interactions with Parasitic Jaegers, however, likely occurred more often than their nesting density in the study area would predict, suggesting that they represent a greater threat than Herring Gulls. Of these two species, Sabine's Gulls reacted at greater distance and intensity to Parasitic Jaegers than to Herring Gulls. Sabine's Gulls also responded to humans approaching the nest at a relatively short distance (150 m) and with a comparatively weaker intensity.

The response of Sabine's Gulls towards the different decoys showed that they could clearly distinguish between threatening and non-threatening species. However, they did not differ in their reactions towards an avian (gull) versus a mammalian (fox) predator. It is assumed that the level of nest defence would reflect the potential threat posed by a predator to the eggs and/or young, but that this may be offset by the potential threat posed by the predator to the parents themselves. Thus, it might be expected that a mammalian predator would represent a greater threat to eggs and young of a ground-nesting bird than an avian predator, and would, therefore, elicit a greater response. However, a mammalian predator might also pose a greater threat to adults than an avian predator would, which could dampen the intensity of response (Kruuk 1964). Alternatively, due to the more consistent presence of avian predators and the greater likelihood of dissuading an avian predator than a mammalian predator, it might be expected that Sabine's Gulls would react more intensely to the gull decoy than to the fox. The results, however, suggest that these predators either posed a similar threat to eggs/young, or that the fox was a greater threat towards adults themselves, or some combination of both.

The fresh remains of a few adults found within the study area suggests that breeding adults are at risk to predation during breeding, although these cases all appeared to be the result of attacks by Peregrine Falcons. Peregrines are occasionally seen over the study area, and, although they are unlikely nest predators, they are known to take both young and adult Sabine's Gulls in flight (Day *et al.* 2001). Thus, Sabine's Gulls involved in chases and attacks focussed on other predators may put themselves at greater risk of attack by Peregrines.

5.5.1.2 Communal defence

In response to predators and 'threatening' decoys, most cases of communal defence involved other Sabine's Gulls, either failed or non-breeders in the area or neighbouring breeding birds. Arctic Terns were also involved when these species nested close together. On a few occasions, shorebirds nesting close to Sabine's Gulls also contributed to communal defence, particularly Ruddy Turnstones (*Arenaria interpres*).

Interestingly, Red Phalaropes (*Phalaropus fulicaria*) were never observed to be involved (pers. obs.), despite nesting at a relatively high density in the same area as Sabine's Gulls (P. Smith, pers. comm.).

Unlike attacks on predators and decoys, Herring Gulls became involved in attacks on human intruders on occasion, but only at the few sites where they nested in close proximity to Sabine's Gulls. This was likely due to the fact that human intruders can be seen at considerable distance in the flat landscape of East Bay and, therefore, Herring Gulls considered the intruder a threat toward their own nests, rather than any deliberate contribution on their part to communal defence.

5.5.1.3 Nest phenology

In their responses to predators and human intruders, there was no trend to suggest that the level of anti-predatory behaviour displayed by Sabine's Gulls changed over the course of the incubation period. There were no changes in the distance at which birds first reacted to predators, or in the intensity of their responses, nor were there any changes in the distance at which they first called or flew out at intruders. This suggests that neither habituation (a waning of response), nor positive reinforcement (an intensifying of response) were involved (see Knight *et al.* 1987). The observed difference in the distance at which birds first swooped at human intruders at different stages of incubation may not be biologically significant as it did not consistently increase or decrease.

5.5.1.4 Individual variation

Generally, Sabine's Gull pairs showed considerable variation in their response to predators and human intruders, with some pairs consistently attacking sooner and with greater intensity than others. This may be related to their age and/or breeding experience. In addition, some nesting pairs gained the help of conspecifics more often than others, although this did not appear to be due to the proximity of neighbouring nests and may be the result of more obviously aggressive attacks, particularly in the extent to which the pair vocalized during their attack. Vocally active pairs may be more likely to attract the attention of conspecifics, even at considerable distance, than less vocal pairs.

5.5.2 ALTERNATIVE PREY

The consistent level of egg loss observed in 1998, 2000 and 2001, is likely due to avian predators, such as Herring Gulls and Parasitic Jaegers, that are present in the study area each year in relatively constant nesting densities (K. Truman, K. Allard, pers. comm.), and incidental predation by Arctic foxes. If avian predation was similar in 1999, a low lemming year, Arctic foxes would be responsible for approximately 45 % of additional egg loss in that year. However, the extremely high level of egg loss experienced by Sabine's Gulls in 1999 was more likely the result of increases in both avian and mammalian predation. In addition, the high level of egg loss observed in only 1999, suggests that a threshold effect may occur at East Bay (Table 5.4). Arctic foxes appeared to target small ground-nesting birds only in the absence of lemmings in the area, and not in intermediate lemming years. This contrasts with other studies, where the proportion of successful nests of large ground-nesting birds, such as geese and swans, have also been affected by predation in intermediate years (Syroechkovskiy *et al.* 1991, Bêty *et al.* 2001). In peak lemming years, Arctic foxes apparently concentrate on rodents, while, in intermediate years, they prey on lemmings wherever possible, and enhance their diet with the eggs and young of large ground-nesting species. Perhaps only in crash years on Southampton Island, when lemmings are at their lowest densities, are Arctic foxes driven to search coastal wetland areas, where they find and prey upon the eggs and young of small ground-nesting birds, such as Sabine's Gulls, Arctic Terns, and shorebirds.

Years of increasing and peak lemming abundances have been observed to increase the reproductive success of Arctic foxes (Garrot & Eberhardt 1987, Wilson & Bromley 2001), resulting, at least in some areas, in an increased abundance of these predators in the following year (Elton 1942, Spaans et al. 1998). Despite lemmings being observed on more days in 2001 than in any other year, the hatching success of Sabine's Gulls was lower than in 1998 and 2000 (Fig. 5.3). Furthermore, compared with the other years of this study, 2001 was the only year in which more than one Arctic fox was observed in the study area at any one time. The reduced hatching success in 2001, however, was not associated with an increase in egg loss and is attributed to a period of severe weather conditions, which caused flooding early in incubation.

Collectively, these findings support the APH. Egg loss at Sabine's Gull nests was greatest in the year of lowest lemming presence, when Arctic foxes apparently switched to prey upon ground-nesting birds, including Sabine's Gulls. Similar results have been found in a wide range of avian species across the circumpolar Arctic, particularly waterfowl and shorebirds (Pehrsson 1986, Summers 1986, Summers & Underhill 1987, Järvinen 1990, Stickney 1991, Underhill *et al.* 1993, Spaans *et al.* 1998, Summers *et al.* 1998, Sittler *et al.* 2000, Bêty *et al.* 2001). Unlike large species, such as waterfowl, that lay clutches of many large eggs, smaller birds, such as Sabine's Gulls, may suffer an extreme increase in predation only in years of lemming population crashes. Although the reproductive success of Sabine's Gulls appeared to be influenced by the functional response of predators to fluctuations in their primary prey populations, it did not appear to be influenced by a numerical response in the year following a high lemming presence.

5.5.3 CONCLUSION

Birds cannot nest until the tundra is fully exposed and drained, hence the phenology of Arctic breeding, ground-nesters is undoubtedly influenced by the timing of spring melt. In coastal wetland tundra areas, nests also remain vulnerable to flooding throughout incubation. Models of climate change suggest that precipitation in the Arctic could increase considerably within a few decades (Räisänen 2001), and flooding may become an increasing problem for both ground-nesting birds and small mammals. Annual fluctuations in predation pressure, however, appear to be the current dominant influence on the breeding productivity of Sabine's Gulls.

Occasional events, such as years of high predation on ground-nesting birds, associated with fluctuations in the microtine rodent cycle, provide an example of episodic selection. Given the short duration of rodent cycles (Ylönen 1994), individuals of relatively long-lived species may be subject to more than one of these events during their reproductive lifetime. Under these circumstances, pairs that breed successfully in these particular years may contribute greatly to subsequent generations. Based on the extent of variation in anti-predatory behaviour observed among pairs in this study, some are clearly more aggressive than others and may be better at defending their nests in years of high predation pressure. Further examination of common behavioural features of highly successful pairs may provide insight into the evolutionary effects and/or consequences of episodic selective events.

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6.0 Philopatry, site tenacity, mate fidelity and adult survival of Sabine's Gulls

6.1 ABSTRACT

Quantifying the dynamics of populations is fundamental to understanding life history strategies, and essential for population modelling and conservation biology. Few details of the demography and life history of Sabine's Gull (*Xema sabini*) are known. Uniquely colour banded Sabine's Gulls breeding in East Bay, Southampton Island, Nunavut, in the eastern Canadian Arctic, were examined from 1998-2002 to quantify vital rates. Generally, birds banded as chicks first returned to the breeding area in their third year, and the earliest case of first breeding was confirmed at three years of age. Sabine's Gull pairs showed strong tenacity to their breeding site from year to year, with most pairs nesting within approximately 100 m of the previous year's site, whether previously successful or unsuccessful. Individuals also showed strong fidelity to their mates from year to year. However, birds whose previous partner failed to return, or returned late, were quick to re-mate. On rare occasions, birds were not seen in the study area in a particular year, but seen again in later years, either because they were missed, had dispersed outside the study area temporarily, or did not return to the breeding area in some years. Standard Capture-Mark-Recapture analyses were used to calculate local re-sighting and survival rates. Local annual survival rate of Sabine's Gulls was 0.89 ± 0.04, similar to adult annual survival estimates reported for other gull and tern species.

6.2 INTRODUCTION

Quantifying the dynamics of avian populations, such as survivorship and fecundity, is fundamental to understanding their life history strategies (Spear *et al.* 1987). Demography, the key to life history theory, allows assessment of the strength of selection on life history traits for many conditions (Stearns 1992). Clearly, it is important to establish baseline demographic information that will provide the basis for modelling population dynamics under different environmental stresses (Greenwood *et al.* 1993). Yet, to date, there has been little investigation of the demographic trends of many avian populations breeding in the Arctic. This is particularly troubling, given the extent of potential climate changes predicted for the Arctic region due to the influence of anthropogenic activities (Bengtsson 2001).

Arctic breeding birds tend to be characterized as having high adult survival rates, delayed age of first breeding, and generally low and variable annual reproductive output (Tuck 1961, Birkhead & Harris 1985). These traits have likely evolved as a response to the harsh and variable breeding conditions encountered each year by these birds (Freuchen & Salomonsen 1958). At high latitudes, where the breeding season is short, site tenacity could be high, as it may reduce time spent searching for a previous mate (Bried & Jouventin 2002). Mate fidelity between years could also be comparatively high, due to limited time available for the assessment of new partners (Flynn *et al.* 1999).

Sabine's Gull (*Xema sabini*) is a trans-equatorial migrant that breeds at high latitudes. It winters at coastal upwelling zones off western South America and southern Africa, and breeds in coastal areas of Arctic and Subarctic regions in North America, Greenland and Russia (Day *et al.* 2001). It generally breeds in dense colonies on small coastal islands (Forchhammer & Maagaard 1991) or solitarily at the edges of shallow ponds in coastal wetland areas (Abraham 1986, Stenhouse *et al.* 2001). Sabine's Gull is considered unusual within the gull family (Laridae) and is recognized as phylogenetically distinct (Chu 1998), as well as atypical in several aspects of its behaviour (Brown *et al.* 1967) and reproductive biology (Stenhouse *et al.* 2001). Yet, few details are known regarding its demography and life history. For example, Sabine's Gulls are assumed to first breed at two years of age (Day *et al.* 2001), based on the fact that they acquire mature adult plumage in their second spring moult (Grant 1986). However, this has never been confirmed.

Stenhouse *et al.* (2001) provided information on the breeding biology of Sabine's Gull, including fecundity, and compared it with other gulls. This study attempts to fill some of the remaining gaps in our knowledge of Sabine's Gulls, and presents results on natal philopatry, age at first breeding, nest site tenacity, and mate fidelity. Adult survival is estimated and compared to other gull and tern species.

6.3 METHODS

6.3.1 STUDY AREA

Field work was conducted from late May to mid-August 1998-2002 in the East Bay Migratory Bird Sanctuary (64°01'N, 81°47'W), Southampton Island, Nunavut, in the eastern Canadian Arctic. The East Bay sanctuary encompasses an area of approximately 1,200 km^2, and, despite being located within the Low Arctic region, is generally High

Arctic in character, influenced in its ecological and physical characteristics by the deep, cold waters of the Foxe Channel. Land-fast sea ice can remain in East Bay well into July and daily minimum temperatures are usually close to freezing throughout the summer. The study plot is a 2 x 2.5 km block of low-lying, coastal wetland tundra typical of the area, with a complex of brackish and freshwater ponds. Within the plot, sub-habitats are few and distinct, with wetland areas characterized by mosses, sedges and grasses, and drier areas dominated by dwarf shrubs (*Salix* spp.) and Mountain Avens (*Dryas integrifolia*). As a product of the low relief, brackish ponds extend a considerable distance from the shoreline. High salinity areas are colonized by few plants, with bare sandy or rocky substrate sparsely broken by patches of sedges and mosses. In summer, the area supports a diverse avian community typical of Arctic coastal wetlands (Abraham & Ankney 1986).

6.3.2 BANDING AND OBSERVATIONS

Breeding adult Sabine's Gulls were caught at the nest during incubation using a simple wire mesh 'fall trap' (Bub 1991). Chicks were caught by hand at the nest, although this had to be carefully timed as there is only a very short window of opportunity before the entire family leaves the nest area (~24 hr after last chick hatched), after which it is extremely difficult to find or get close to chicks. Throughout this study, adults were given a numbered metal band and marked with unique colour band combinations (3 colours), while chicks were given a numbered metal band and marked with a single colour band indicating year of hatch. However, some chicks were so small at day 1 or 2 after hatch that they lost their metal bands, which were found at the nest-site, but all appeared to retain their colour band.

All adult Sabine's Gulls observed within the study area, and further afield in East Bay, were checked for leg bands. Colour band combinations, or partial combinations, were recorded whenever conditions allowed. It was rare, however, to even glimpse bands of airborne birds, and confirmation required birds to land within 80-100 m of observers. However, observations were frequent, as Sabine’s Gulls at East Bay spent much of their time on the ground, searching for terrestrial invertebrates that they feed on during the breeding season (Day *et al.* 2001).

6.3.3 NEST LOCATION AND BREEDING SUCCESS

Nests were located by searching on foot, and adults at each nest were examined for leg bands at every visit. Due to their habit of communal mobbing (see Chapter 5), it often took several visits to confirm which adults were associated with a particular nest. Nests were generally visited daily until the clutch was completed, on average every three days during incubation, and daily during the hatching period, allowing assessment of reproductive success for each nest. Eggs that disappeared from nests prior to their projected hatching dates (21-23 days; Stenhouse *et al.* 2001) were assumed depredated.

6.3.4 SURVIVAL RATE

To calculate local survival rates (ϕ) and re-sighting rates (p), standard Capture-Mark-Recapture analyses (Pollock *et al.* 1990, Lebreton *et al.* 1992) were carried out in the program MARK (White & Burnham 1999). Encounter histories were created based on initial captures and subsequent re-sighting of adult birds. The candidate model set was restricted to models with time variation in survival and re-sighting rates (ϕ_t, p_t), and a model with a constant annual survival rate (ϕ, p_t). It was expected *a priori* that re-sight rates would vary among years, as efforts to re-sight birds varied among breeding seasons and was considerably lower in the last year of the study, so models with constant re-sight rates were not considered. Akaike Information Criterion, corrected for small sample size (AICc), was used to choose the best fitting model among the candidate models and AIC weights and model likelihoods were used to assess the relative fit of each model (Burnham & Anderson 1998). Goodness-of-fit was assessed with the program RELEASE (Burnham *et al.* 1987). In addition, the variance inflation factor ($\hat{c}$) was calculated, based on the parametric bootstrap, using 100 simulations and taking the ratio of the observed deviance to the expected deviance (Cooch & White 2001). A model with time variation in survival rate and re-sight rate (ϕ_t, p_t) was considered the global model, and used in the parametric bootstrap. Mean adult life expectancy was calculated using the equation $1/-\ln(\phi)$.

6.4 RESULTS

6.4.1 RETURN OF BANDED BIRDS

A total of 43 adults and 108 chicks were banded at East Bay (Table 6.1). Of the 26 adults banded in 1998, 81 % returned to the study area in the following year, but this was reduced to 46 % by the fourth year (2002). Of the 13 adults banded in 1999, 92 % returned in the following year, but this was reduced to 38 % by the third year (2002; Table 6.1).

In 1999, five breeding birds were banded at a secondary site approximately 8 km east of the study area, but none of these individuals was ever observed in the main study area in subsequent years.

6.4.2 NATAL PHILOPATRY

One bird (3 %) banded as a chick in 1998 returned to the study area in 2000, although it did not appear to pair successfully and did not breed in that year. Three (9 %) birds banded as chicks in 1998 returned to the study area in 2001 and in 2002. One of these was confirmed breeding in the study area in 2001, its third year.

The chance of seeing birds banded as chicks in 1999 return to the study site was considerably slimmer, due to the low number of chicks hatched and banded in that year. Of these, up to three were seen for the first time in 2002 (their third year), although none were confirmed breeding in that year. One of the chicks banded in 2000 was seen in the study area in 2002, but did not breed in that year (Table 6.1).

Table 6.1: Summary of banded Sabine's Gulls re-sighted at East Bay, Southampton Island, Nunavut, in subsequent years in relation to age.

	Year banded	No. banded	Total banded	Year re-sighted 1999	2000	2001	2002
Adults	1998	26	26	21	20	17	12
	1999	13	39	-	12	9	5
	2000	0	39	-	-	-	-
	2001	4	43	-	-	-	2
Chicks	1998	35	35	0	1	3	3
	1999	13	48	-	0	0	3
	2000	37	85	-	-	0	1
	2001	23	108	-	-	-	0

6.4.3 SITE TENACITY

Throughout this study, Sabine's Gulls showed strong tenacity to their breeding site from year to year. Of 13 pairs banded in 1998, two pairs re-used the same nest cup in 1999 as they had in the previous year, 9 pairs nested nearby (approx. 100 m), and only two pairs nested >200 m from their previous nest sites. The pair that moved furthest (410 m) had failed at their previous site due to predation of their entire clutch early in the 1998 breeding season. Movements of nesting pairs from 1999-2000, 2000-2001, and 2001-2002 were similar to those observed between 1998 and 1999.

Combining all years, and only examining movements of pairs where both birds were banded (n = 21), mean distance moved between years for those pairs which successfully hatched a clutch was 195 m (n = 7; range = 40-880 m), while mean distance moved after predation or abandonment of a clutch was 365 m (n = 14; range = 30-1330 m). Both of these means, however, are driven by one or two pairs in each group that moved considerable distances (>500 m). Most pairs (n = 16) nested close to the previous year's nest site, whether successful or otherwise (Mann-Whitney U-test, z = 0.59, P = 0.55).

6.4.4 MATE FIDELITY

Sabine's Gulls showed strong fidelity to their mates between years, with an overall annual mate fidelity rate of 66% (1st year = 84%, 2nd year = 68%, 3rd year = 26%). Throughout this study, there were only two confirmed cases of separation (i.e. where both members of a pair returned to the study area but did not breed together): in one pair, both were confirmed breeding with new mates, in the other, only one was confirmed breeding with a new mate (Table 6.2). Thus, Sabine's Gulls showed a minimum separation rate of 6%. However, in most cases of remating (12 % of all pair-years), the original partners were not seen in the study area again.

Of nine pairs banded in 1998, eight reunited in 1999, five in 2000, and one in 2001 and in 2002 (Table 6.2-A). In the pair that did not reunite in 1999, one member was not seen again, and the other nested with a new mate in that year, which it reunited with again in 2000, 2001 and 2002.

Three pairs did not reunite in 2000. In one, neither was seen again in the study area; one member of the second pair was not seen again, and the returning bird found a new mate in 2000. The third pair separated, with both finding new mates in 2000. Interestingly, this pair abandoned their clutch in the two previous seasons together but both were successful with their new mates in 2000. One of these birds was seen but did not breed in the study area in 2001, and neither was seen in 2002.

In two of the four pairs that did not reunite in 2001, one member was not seen again. In one of these, the remaining bird nested with a new mate in 2001, neither of which was seen in 2002. In the other, one bird was seen in 2001, but did not renest in the study area. The third pair separated, with one bird nesting with a new mate in 2001 and reuniting with it again in 2002. Interestingly, the other member of the original pair was also seen in the area in 2001, but apparently did not breed, and it was not seen in the area in 2002.

Table 6.2: The number of pairs reunited, and the fate of those that did not reunite, in each year for nine Sabine's Gull pairs banded in 1998 (A) and five pairs banded in 1999 (B) at East Bay, Southampton Island, Nunavut.

Year	Both present, and reunited	Both present, both remated	Both present, one remated	Both present, fate unknown	One absent, one remated	One absent, one unmated	Both absent
A							
1999	8	.	.	.	1	.	.
2000	5	1	.	.	1	.	1
2001	1	.	1	1	1	1	.
2002	1	.	.	.	.	.	.
B							
2000	4	.	.	.	1	.	.
2001	3	.	.	.	.	.	1
2002	1	.	.	.	.	1	1

Finally, both members of the fourth pair were seen separately in 2001, but did not breed in the study area. Whether they reunited and nested outside the study area or not is unknown, and neither of them was seen in 2002.

A further five pairs were banded in 1999. Of these, four reunited in 2000, three in 2001, and one in 2002 (Table 6.2-B). In the pair that did not reunite in 2000, one was not seen again, and the other nested with a new unbanded partner, was not seen in 2001, but nested with an unbanded bird again in 2002. In the pair that did not reunite in 2001, neither was seen in the area in 2001 or 2002, but they may have reunited and nested outside the study area. Two pairs did not reunite in 2002. In one, neither was seen in 2002. In the other, one bird was seen in 2002, but did not breed in the study area.

6.4.5 ADULT SURVIVAL

Based on the ratio of observed to expected deviances, $\hat{c} = 0.49 \pm 0.01$, considerably less than 1.0, suggesting that the data set may show under-dispersion (i.e. less variation than expected by chance). Similarly, the program RELEASE did not detect any sources of dispersion, (TEST 2 and TEST 3 combined $\chi^2 = 0.00$, df = 5, $P = 1.00$), also indicating evidence of under-dispersion. It is not clear whether to adjust $\hat{c}$ when it is less than 1.0 (Cooch & White 2001), thus no adjustment was made and the data were assumed to be distributed with a binomial error structure.

Based on AICc weights and model likelihoods, a model with a constant survival rate was 5.9 times better supported than a model with time variation in survival rates

(Table 6.3). Local annual survival rate for this model was 0.89 ± 0.04 (95% profile likelihood intervals: 0.79 - 0.94), which compares well with adult annual survival estimates for other gull and tern species (Table 6.4). Based on this survival estimate, mean (± SE) adult life expectancy for Sabine's Gulls at East Bay is 8.3 ± 2.8 years. Re-sight rates were consistently high for 1999-2001 (1999 = 0.90 ± 0.06, 2000 = 0.97 ± 0.03, 2001 = 0.92 ± 0.07) and dropped to 0.66 ± 0.11 in 2002.

6.5 DISCUSSION

The return of birds banded as chicks to the study area shows that Sabine's Gulls exhibit some natal philopatry. However, the rate of natal philopatry observed may be due to 1) high juvenile mortality during the first few years, 2) reproductive maturation beyond the second year, 3) the short temporal scale of this study, and/or 4) low detectability due to band loss. Although a few birds banded as chicks returned to the breeding area in their second year, these individuals did not establish territories. Instead, they often joined feeding flocks of failed breeders that built up over the course of the season each year, and did not appear to associate with a particular area. Despite the small sample size, it appears that breeding at two years of age is unlikely or uncommon in Sabine's Gulls. The earliest (and only) confirmed first breeding was a bird at three years of age.

Most birds in this study nested close to the site of their nest in the previous year. This site tenacity probably facilitates a reuniting of the pair, and could enhance reproductive success through familiarity with the breeding site (Greenwood & Harvey1982).

Table 6.3: Model selection results for Sabine's Gulls breeding at East Bay, Southampton Island, Nunavut, 1998-2002.

Model	Deviance	AICc	ΔAICc	AIC Weight	Model Likelihood	No. par
ϕ_t, p_t	7.40	152.70	0.00	0.855	1.000	5
ϕ, p_t	6.48	156.25	3.55	0.145	0.170	7

Table 6.4: Adult annual survival rate of Sabine's Gulls breeding at East Bay, Southampton Island, Nunavut, 1998-2002, compared with those of other gulls and terns.

Species	Survival rate	Source
Sabine's Gull (*Xema sabini*)	0.89	this study
Black-headed Gull (*Larus ridibundus*)	0.90	Prévot-Julliard *et al.* (1998)
Mew Gull (*L. canus*)	0.89	Rattiste & Lilleleht (1995)
California Gull (*L. californicus*)	0.91	Pugesek *et al.* (1995)
Herring Gull (*L. argentatus*)	0.88	Pons & Migot (1995), Wanless *et al.* (1996)
Glaucous-winged Gull (*L. glaucescens*)	0.83-0.87	Reid (1988)
Lesser Black-backed Gull (*L. fuscus*)	0.91	Wanless *et al.* (1996)
Black-legged Kittiwake (*Rissa tridactyla*)	0.90	Golet *et al.* (1998)
Roseate Tern (*Sterna dougallii*)	0.78-0.89	Spendelow *et al.* (1998)
Common Tern (*S. hirundo*)	0.85	Nisbet & Cam (2002)
Arctic Tern (*S. paradisaea*)	0.86-0.88	Coulson & Horobin (1976)

Interestingly, Sabine's Gull pairs usually returned to a breeding area despite their nest fate in a previous year (*cf.* Haas 1998). This might suggest that 1) there are no suitable alternative sites, which seems unlikely, or 2) that breeding failure is usually associated with some aspect of environmental stochasticity (e.g. predation, weather), rather than the specific characteristics of a particular nest site. Broad scale environmental features, such as a late snow melt, affect all nests in a given year, despite their location. In marginal years, however, familiarity with a breeding area may be of considerable importance in reproductive success.

Sabine's Gulls are socially monogamous and relatively long-lived. As such, members of a pair are likely to benefit by reuniting in successive breeding seasons. Mate fidelity may 1) promote early breeding, by saving time required to find a new mate each year, and 2) enhance reproductive success, by increasing cooperation and coordination in parental activities (Hamer *et al.* 2002).

As is common among seabird species (Wood 1971, Mills 1973, Ollason & Dunnett 1978, Bradley *et al.* 1990), Sabine's Gulls do not appear to maintain pair bonds throughout the year and members of a pair are believed to disperse separately and reunite at the beginning of each breeding season (Day *et al.* 2001). In this study, returning birds whose previous partner failed to return, or perhaps returned late, were quick to re-mate. Once re-mated, birds were found to reunite with their new mates in successive years, even if their original partner returned to the study area in later years. Given strong mate fidelity and site tenacity, the fact that some birds were not seen in the study area in a specific year, but seen again in later years, suggests that individuals were present, but not seen, or dispersed temporarily outside the study area. However, these explanations seem unlikely, given the extensive coverage of the study area and beyond in each year, and the relatively short distance moved between nesting attempts. A third possibility is that individuals of this species will forego breeding and not return to the area in some years, perhaps if they do not achieve a suitable body condition prior to migration in any given year (Forchhammer & Maagaard 1991).

It is unusual for re-sighting data to show evidence of under-dispersion, while over-dispersion is commonly indicated in many data sets (Prévot-Juilliard *et al.* 1998, Franklin *et al.* 2002). The under-dispersion detected in the data presented here could reflect both high survival and re-sight rates obtained in this study. When rates are high, most of the birds survive and are seen from one occasion to the next, leaving little opportunity for many birds to show radically different encounter histories. The relatively short duration of the study likely exacerbates this problem. Additionally, some of the birds in this study were paired, and, although it is unlikely that pairs remain together throughout the entire non-breeding season and suffer the same mortality source (Coulson & Wooller 1976, Spear *et al.* 1987), they may disperse from the study areas with equal frequency (either as a pair, or, if one fails to return, the surviving member may disperse). This statistical dependence among pairs could contribute to the observed under-dispersion. Further, all birds captured in this study were breeding adults. With a longer study period and eventual inclusion of younger breeding birds, the evidence of under-dispersion would likely diminish. Fortunately, under-dispersion is not likely to bias the estimate of survival rate, and the estimates of error presented assume a binomial distribution of random errors, so should not be biased low.

It should be borne in mind that, due to the difficulties of identifying emigration and band loss and in distinguishing them from mortality, the survival rate presented here is a minimum estimate. Although the best model indicated a constant survival rate, true survival rate was not necessarily constant in this study. In studies with a relatively small number of individuals, and only five occasions, reduced parameter models are generally better supported (Anderson *et al.* 1994). Random effect models show promise to incorporate process (or annual) variation and residual sampling variation in one estimate with appropriate error that can be decomposed into both sources (Burnham & White 2002). However, for this study, with only three estimates of survival, calculating a random effects model is not recommended (Burnham & White 2002). Even so, a random effects model did produce a similar estimate (0.89 ± 0.03) to the one obtained from the constant survival rate model.

Prior to this study, few details of the demography of Sabine's Gulls were known (Day *et al.* 2001). This circumstance has largely prevented meaningful comparisons with other gull and tern species (see Stenhouse *et al.* 2001). Such comparisons could help determine if species considered closely related share important demographic characteristics, such as age of first breeding. The survival rate presented here compares well with recent estimates of adult survival in other gulls and terns, among which percent survival estimates are typically in the mid- to high 80s (Table 6.4). Thus, the adult survival rate reported here for Sabine's Gulls is typical of gulls in general. Furthermore, in spite of displaying some aberrant behaviour (Brown *et al.* 1967, Abraham 1986, Stenhouse *et al.* 2001), Sabine's Gulls show typical larid life history patterns, including natal philopatry, nest site tenacity, and mate fidelity. Age at first breeding remains an open question, due to a small sample size, although this study found no evidence to support the assumption that Sabine's Gulls breed at two years of age.

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7.0 Summary

Sabine's Gulls have traditionally been considered an unusual species within the Laridae (Day *et al.* 2001), due to both morphological and behavioural peculiarities (Brown *et al.* 1967, Abraham 1986). Some aspects of their reproductive ecology do appear to be unusual, such as their relatively short incubation and fledging periods, and their departure from nests immediately after hatch (Day *et al.* 2001, Stenhouse *et al.* 2001). These aspects of their reproductive ecology, which differ from other small gulls, are likely adaptive traits that have evolved in response to characteristics of their Arctic breeding areas, such as the short breeding season and high rates of avian and mammalian predation (see Meltofte 1985). However, Sabine's Gulls also exhibit some behavioural and demographic patterns that are highly typical of gulls in general, such as their breeding behaviour and parental contributions to incubation and chick-rearing (Chapter 3). As such, the evolution of Sabine's Gull life history traits appears to have been influenced by both their phylogeny and the particular ecological conditions of their breeding environment, and/or interactions between these.

In this thesis, I have presented new information on the reproductive behaviour, ecology and demography of Sabine's Gulls, and how these parameters vary with climate, predation and individual variation in behaviour. I have shown that, in the eastern Canadian Arctic, Sabine's Gulls exhibit natal philopatry and return to the area where they were born in their second or third year (Chapter 6). They may not establish a territory or find a mate on their initial return, but, once mated, they exhibit strong mate fidelity and site tenacity from year to year (Chapter 6). Their arrival and breeding phenology depends largely on the onset and rate of snow melt (Chapter 2). At East Bay, they initiate egg-laying when approximately 90 % of the tundra is exposed and their nest sites have dried out sufficiently to allow egg laying (Chapter 2). At East Bay, they nest on the edges of ponds or on the edges of small islands within ponds, within approximately 1 km of the shoreline, and restrict nesting to particularly mossy sites (Chapter 4). Nests are generally well spaced, with most having conspecific neighbours within approximately 100 m (Chapter 4). They generally lay three eggs, begin incubating with the first egg, and each egg is approximately 10-13 % of the female's body mass (Chapter 2). Hatching success and predation pressure is highly variable between years, and throughout incubation eggs are at considerable risk of predation, particularly in years with low rodent populations (Chapter 5). Both members of a pair are aggressive towards predators and intruders close to their nest, and pairs from nearby nests often collectively attack predators (Chapter 5). Experimental studies showed that Sabine's Gulls can distinguish between threatening and non-threatening species, and do not waste time or energy attacking non-threatening species, even when they are close to the nest (Chapter 5).

Males and females share parental duties, such as incubation and chick-provisioning, but individuals vary considerably in their relative contributions (Chapter 3). When all chicks have hatched, they are lead from the nest by their parents to saltwater ponds along the shoreline. At these ponds, they appear to establish post-hatching territories, and parents in the area join together to communally mob predators (Chapter 2). Chicks grow rapidly and fledge within approximately 25-30 days. Adults have a relatively high survival rate (0.89 ± 0.04) and are estimated to return to their nesting area to breed over at least 8 breeding seasons (Chapter 6). Most of this information is entirely new for this species.

7.1 Systematics

Some authors, mainly in Europe, have inexplicably placed Sabine's Gull in the genus *Larus* (Vaurie 1965, Furness & Furness 1982, Cramp & Simmons 1983, Higgins & Davies 1996). However, in North America, Sabine's Gull has remained in the genera *Xema* (American Ornithologists' Union 1998, Day *et al.* 2001).

Based on structural characteristics, Chu (1998) suggested three nomenclatural arrangements for gulls which might better reflect their phylogeny: 1) divide gulls into six genera, one of which groups Sabine's Gull with the Swallow-tailed Gull (*Creagrus fircatus*) in the genus *Xema*, 2) divide gulls into two large clades, one of which groups Sabine's Gull with other 'tern-like' gulls, including Swallow-tailed Gull, Ivory Gull (*Pagophila eburnea*), Ross's Gull (*Rhodostethia rosea*), the kittiwakes (*Rissa* spp.), and Little Gull (*Larus minutus*) in the genus *Xema*, and 3) simply group all gulls together in the genus *Larus*.

However, recent phylogenetic analysis, based on mitochondrial DNA, provided strong evidence that Sabine's Gull is in fact a sister taxa to the Ivory Gull (Crochet *et al.* 2000). These species are estimated to have diverged very early, some 2 million years ago, compared with most other gull groupings, which are estimated to have diverged in the last million years (Crochet *et al.* 2000). Interestingly, differentiation between the Sabine's

Gull and the Ivory Gull is thought to have occurred within the Arctic, rather than these species separately colonizing the far north (Crochet *et al.* 2000).

Although Crochet *et al.* (2000) have considerably advanced our understanding of the phylogeny of the gulls, and included 32 gull species, their analysis was not exhaustive. Of the species missing from their sample, the Ross's Gull is particularly notable. I believe that, given the remaining uncertainties in our knowledge of gull phylogeny, Sabine's Gull should not be reclassified to *Larus* and should, at least for the time being, remain firmly in the genus *Xema*.

7.2 Conservation implications

Like all avian species breeding in the Arctic, Sabine's Gulls are influenced by broad scale environmental conditions, such as climate change. Possible changes in global climate have been modeled, but, to date, it remains unclear just how severely Arctic regions will be affected (Räisänen 2001). Clearly, any increase in precipitation early in the breeding season, and/or more rapid spring melting in the Arctic, will increase the risk of Sabine's Gull nests, and those of other species, to flooding. This could reduce their reproductive success considerably. As evidence for the influence of climatic conditions, population monitoring in Alaska indicated a serious decline (65%) in Sabine's Gulls in the summer of 1998 (Day *et al.* 2001). This followed the strongest El Niño-Southern Oscillation (ENSO) event of the 20th century and suggests that, like many other species (Schreiber 2002), the Pacific wintering population of Sabine's Gulls is subject to considerably increased mortality in ENSO years.

The results presented in this thesis form an important foundation of information that will allow future comparisons at East Bay, and elsewhere in the circumpolar Arctic. Through continued research, the response of Sabine's Gulls can be quantified if changes in climate occur. To interpret changes in their reproductive ecology, if they are detected, it is also important to track other anthropogenic sources of mortality that could affect Sabine's Gulls throughout the year. These include pollution and interaction with fisheries. Like most seabirds, Sabine's Gulls are also subject to contamination by pollutants, including heavy metals, petroleum products, and long range atmospheric transportation and deposition of toxins in the Arctic. Some heavy metals occur naturally in the marine environment, but are elevated due to anthropogenic activities to levels where they have become a chronic problem for marine birds (Burger & Gochfeld 2002). Oil pollution and oiling is also a major problem for any animal which spends considerable time at sea. However, due to foraging at the ocean surface (i.e. not diving for food) gulls are generally at less risk of oiling than diving birds. Compared with other gull and tern species in the northeastern Pacific Ocean, the Sabine's Gull has a slightly lower than average Oil Vulnerability Index score (44, on a scale of 1-100, versus 46; King & Sanger 1979). The ingestion of plastics by many seabird species, especially surface-feeders, is an increasing problem around the world's oceans (Burger & Gochfeld 2002). Although Sabine's Gulls have been observed to ingest plastic particles (Moser & Lee 1992), nothing is known about the extent of this problem in this species (Day *et al.* 2001).

Like most animals that spend much of their lives at sea, Sabine's Gulls will inevitably face interactions with commercial fisheries. Fisheries activities can have both positive and negative effects on seabirds. Direct effects include mortality through by-catch, disturbance (negative), and food provisioning via discarded offal (positive), while indirect effects include prey depletion, increases in predatory species (negative), and decreases in competitors (positive; Montevecchi 2002). Of these, the most likely to affect Sabine's Gulls is the provisioning of food via discards, a direct positive interaction. However, although Sabine's Gulls have been observed to concentrate and forage near fishing vessels in the Pacific Ocean, it is not clear if they scavenge on discards or actively catch prey there (Wahl & Heinemann 1979).

Although none of these factors individually may be a major influence on Sabine's Gull populations, the interactions between them and their cumulative effects may be considerable. However, the specific combination of environmental factors influencing Sabine's Gulls, and their effect on the population, is yet to be determined.

7.3 Future research directions

Despite new information presented in this thesis, much remains to be explored in the ecology of Sabine's Gulls and many other Arctic breeding species. The Sabine's Gull has not been given any special conservation status in North America or Greenland, largely due to a lack of information on population sizes and trends, rather than any secure knowledge that it does not warrant special status (Day *et al.* 2001). Thus, it is critical to gain information on colony size and population trends, and the adult survival estimate I derive here (Chapter 6) is an important contribution for modeling population demographics of this species.

Sabine's Gulls winter at Tropical and Sub-tropical coastal upwelling regions off of South America, in the eastern Pacific Ocean (Chapman 1969), and southern Africa, in the eastern Atlantic Ocean (Zoutendyk 1965, Lambert 1969). Although these two main wintering areas have been known for some time, it is not clear which breeding populations these birds come from. As it stands, birds from the western Canadian Arctic, Alaska and Russia are thought to winter in the Pacific Ocean, and birds from the eastern Canadian Arctic and Greenland are thought to winter in the Atlantic Ocean. Sightings of birds at sea and along coasts during migration provide some support for this (Day *et al.* 2001). However, the east-west divide in populations in North America is still completely unknown. Do birds breeding on Victoria Island, in the central Canadian Arctic, for example, go east in the fall to winter in the Pacific, or west to the Atlantic? This information may be important to assess factors which may affect their survival differently between the two oceans.

Like most seabirds around the world, little is known about the at-sea distribution and behaviour of Sabine's Gulls. Increasingly, seabird biologists are realizing that this major gap in our knowledge of seabird life histories is problematic and must be addressed if we are to improve conservation and management efforts (Boersma *et al.* 2002). However, identifying migration routes and establishing at-sea distributions are extremely challenging tasks, particularly for trans-equatorial migrants like Sabine's Gulls. This requires long-term studies and considerable funding commitment. The advent of satellite telemetry and the increasing advances in this technology will no doubt one day provide the opportunity to track more than just the largest seabirds, such as albatrosses and gannets, around the world.

Gaining information on both the summer and winter diets of Sabine's Gulls would be useful in improving our ability to assess the implications of potential Arctic climate changes, especially the influence of large-scale climate patterns, such as the NAO and ENSO. This may also help in identifying direct and indirect effects of commercial fisheries on these birds when migrating and wintering at sea.

Clearly, very little is known about the reproductive ecology and demography of many avian species that breed in the Arctic, particularly the other small Arctic gulls. Given that the phylogenetic relationships of these gull species remains unresolved, it would be particularly useful to compare the life-history traits, breeding biology, and behaviour of Sabine's Gulls with those of Ivory Gulls and Ross's Gulls. However, even less is known about these two species than was known about the Sabine's Gull when this study was initiated.

To address this, we must begin to collect critical baseline information for species like these that live their lives 'on the edge'. These species are predicted to be the first to face consequences of large scale climatic changes, if they occur, and, as such, may provide a window into a world to come.

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