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The Breeding Ecology of Horned
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Ann Marie Aglionby Harding

Presented in candidature for the degree of
Master of Science
Department of Biological Sciences
University of Durham
2001



26 APR 2002

CANDIDATE'S DECLARATION

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A.M.A. Harding
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The Breeding Ecology of Horned Puffins (*Fratercula corniculata*) in Alaska.

M.Sc. thesis submitted by Ann Marie Aglionby Harding, 2001.

ABSTRACT

The Horned Puffin (*Fratercula corniculata*) is one of three North Pacific puffin species. Horned Puffins almost always nest amongst boulders and in rock crevices. This makes access to nest-sites and chicks difficult and, as a result, sample sizes are small for many their breeding parameters. I studied the breeding ecology of Horned Puffins at Duck Island, Alaska, over a period of five years (1995-1999) in order to improve our baseline knowledge of this species and the variability in its breeding ecology.

Adults fed their chicks primarily on sandlance (*Ammodytes hexapterus*), which comprised over 90% of the diet. Chick survival to fledging was generally high (83-97%), and there was no apparent difference among years in breeding success, despite evidence of poor food availability in 1998. There was, however, a large range of chick growth rates and fledging ages. Chick mass growth rate was lowest in 1998, and chicks also fledged at youngest ages in that year. The impacts of reduced food supply on growth differed between different body components, suggesting differential allocation of energy and nutrients into the growth of different body structures. There was no difference among years in either chick diet or the mass of food loads brought to the colony by adults.

Daily counts of Horned Puffins attending the colony were made throughout the breeding season in three consecutive years in order to examine the diurnal, seasonal and annual variation in colony attendance, and the implications of this variation for population monitoring. Peak diurnal attendance occurred between 2030-2130. Despite high seasonal and annual variation in colony attendance, overall mean numbers of birds present at the colony during both incubation and chick-rearing did not differ among years. There was greater variability in attendance during chick-rearing than during incubation, indicating that counts conducted during incubation may provide the better index of breeding population size.

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CHAPTER ONE

GENERAL INTRODUCTION



Species exhibit a wide range of life histories, with large variation in traits such as number of breeding attempts (semelparous species reproduce only once, iteroparous species may breed repeatedly), age at sexual maturity, reproductive rate after commencement of breeding, development pattern of offspring and adult life span. Life-history strategies result from trade-offs in the allocation of limited resources to competing demands, with natural selection favouring those trade-offs that result in the greatest evolutionary fitness (Cody 1966, Stearns 1992).

In many species, life-history evolution is constrained by physical or ecological factors that require the commitment of resources to particular systems (Boggs 1992, Stearns 1992). For example, allocation of resources to reproduction may be constrained by limited opportunities for breeding (e.g. Pruett-Jones and Lewis 1990), by specialized food resources or ecological requirements (e.g. Ligon and Ligon 1990), or by a high risk of predation (e.g. Wisenden 1993). Body size may additionally constrain growth and foraging (e.g. Bonduriansky and Brooks 1999), and in long-lived species, there may also be a high requirement for allocation of resources to self-maintenance, at the cost of a reduction in reproductive rate (e.g. Ashman and Schoen 1997).

Among avian species, the life histories of seabirds are characterized by long life-spans, deferred maturity, and low annual reproductive output (Charlesworth 1980, Ricklefs 1990). These traits are generally thought to reflect a low ceiling on annual reproductive rate, restricted by the sparse, patchy and unpredictable distribution of marine food resources (Lack 1968). However, Hamer *et. al.* (*in press*) have argued that low reproductive rates in seabirds may result more from preferential allocation of resources to promoting long life-spans than from chronically low food availability. According to Life History Theory, breeding adults trade-off current and future reproduction (Stearns 1992), and in variable environments they should adjust their behaviour during each breeding attempt to maximize their lifetime reproductive success (Williams 1966). Since a small reduction in adult survival of long lived species has a large negative impact on lifetime reproductive output (Charlesworth 1980), where food availability is low,

adults should abandon a breeding attempt if risks to survival are too high (Drent and Daan 1980).

Many studies have demonstrated that food availability can have a profound effect on seabird reproduction (e.g. Ricklefs *et al.* 1984, Coulson and Thomas 1985, Oka *et al.* 1987, Martin 1989, Monaghan *et al.* 1989, Burger and Piatt, 1990, Hatch and Hatch 1990, Hamer *et al.* 1991a, Danchin 1992, Shea and Ricklefs 1996). Both within and between species, different breeding parameters respond to changes and variation in prey availability in distinct ways (Cairns 1987, Baird 1990). For example, small species that spend a high proportion of their time feeding and have a restricted foraging range, like the Common Tern (*Sterna hirundo*), are more vulnerable than other species to food shortage (Pearson 1968, Monaghan *et al.* 1989). Species with specialized feeding habits or food searching techniques that are energetically expensive are also more vulnerable in this respect (see Furness and Ainley 1984 for a review). Responses to variation in food availability can be examined in the context of life-history resource allocation, life history traits and physiological and ecological constraints, and there is a need for further data on responses to changes in food availability among species with contrasting life-histories (Monaghan 1996, Ricklefs 2000).

The family Alcidae

The Alcidae are a group of marine birds, within the order Charadriiformes, that pursue prey beneath the water using wing-propelled diving (Strauch 1985). Within seabirds, the Alcidae are an ideal family to examine the influence of food availability and physiological and ecological constraints on resource allocation and life history traits, with a wide range in adult body size, breeding habitat, social behavior, feeding ecology and developmental pattern exhibited among the 22 extant species.

Alcids exhibit high variation in adult body size, with Least Auklets (*Aethia pusilla*) the smallest species, weighing only ca. 80-90 g, and Guillemots (*Uria* spp.) about 10 times heavier, weighing ca 900-1000 g (Gaston and Jones 1998). There are also large geographic and intersexual

differences in body size within some species (e.g. the Atlantic Puffin, *Fratercula arctica*; Bédard 1985).

Within some genera, there can be high diversity among species in nesting habitat and degree of coloniality. For example, whereas the Kittlitz's Murrelet (*Brachyramphus brevirostris*) nests solitarily on talus slopes in the mountains, often on stony areas between snow patches (Day 1995), the Marbled Murrelet (*B. marmoratus*) typically nests in old-growth trees (Singer *et al.* 1991). In contrast, both the Common Guillemot (*Uria aalge*) and Brünnich's Guillemot (*U. lomvia*) are highly colonial, usually breeding at high density in exposed habitat such as cliff ledges or low-lying, flat islands. Other alcids, such as the puffins (tribe *Fraterculini*) nest colonially, usually in burrows or crevices, with enclosed nests protected from both avian predation and the weather. Species also differ in their diet, foraging range and diving ability, with some auklets (tribe *Aethiini*) planktivorous, whilst other alcids, such as puffins, are mainly piscivorous (Gaston and Jones 1998).

The Alcidae exhibit marked variation in chick development and fledging patterns, between species (Gaston 1985, Ydenberg 1989). This variation encompasses three broad categories; precocial, intermediate and semi-precocial development (Sealy 1973a). For example, Ancient Murrelet chicks (*Synthliboramphus antiquus*) are precocial, spending only 1-2 days in the burrow before leaving for sea. Chicks are not fed at the colony, but parents continue to feed their chicks at sea until they are fully-grown (Gaston and Jones 1998). In contrast, the Common Guillemot, Brünnich's Guillemot and Razorbill (*Alca torda*) demonstrate intermediate chick development, with the chick leaving the nest-site at only 22/25% adult body weight (Birkhead and Harris 1985), and continuing development at sea whilst being fed by the male parent (Prince and Harris 1988). These three species use exposed breeding sites where one parent must remain with the egg or chick to protect against weather and predation. Puffin chicks have semi-precocial development, being fed at the nest-site until they have reached near adult size and possess complete juvenile plumage (Sealy 1973a), and are independent

after fledging. The four puffin species breed underground, in burrows or crevices (Gaston and Jones 1998).

There has been considerable interest in the selective pressures determining the evolution of different fledging strategies in the Alcidae (e.g. Lack 1968, Sealy 1973, Gaston 1985, Ydenberg 1989, Ydenberg *et al.* 1995, Houston *et al.* 1996). It has been suggested that the relative mortality risks associated with the open ocean and the nest-site play key roles (Cody 1971, Murray *et al.* 1983, Ydenberg 1989). Predator pressure at the colony may be important (Cody 1971), with intermediate species, using open or exposed nest-sites, at more risk of predation than the semi-precocial species that all use enclosed breeding sites. The enclosed breeding sites of the semi-precocial species provide protection against weather and avian predators, which allows both parents to forage simultaneously, leaving the chick unguarded once it has attained endothermy (Barrett and Rikardsen 1992).

Taking an inclusive fitness approach, Ydenberg (1989) assessed the costs and benefits associated with the nest-site and ocean, from both the chick's and parents' perspective. Ydenberg suggested that while the nest-site is a safe place, with lower mortality than the ocean, growth at the nest-site is slower due to the adults having to fly further for food. He suggested that differences between species in the balance between chick growth and mortality at the colony and at sea may select for different fledging strategies in different species. A model incorporating this trade-off accurately predicted chick mass and age at fledging in Common Guillemots (Ydenberg 1989).

Several authors have suggested that the intermediate pattern of development is the result of constraints on life-history evolution imposed by body size (Sealy 1973a, Birkhead and Harris 1985, Gaston 1985). Egg mass is a smaller proportion of adult body mass in larger species, and this may preclude them from a fully precocial pattern of development (Birkhead and Harris 1985). Conversely, the maximum food load that adults can carry is a smaller proportion of body mass in the larger species of alcid, a consequence of the exceptionally low wing area to weight ratio in the genera *Uria* and *Alca* (Gaston 1985). This may preclude them from a semi-precocial mode of

development if it prevents adults delivering food sufficient food to allow chicks to reach 70-90% adult weight at the nest-site (Birkhead and Harris 1985, Gaston 1985).

These ideas are supported to some extent by the fact that the largest alcids (Common and Brünnich's Guillemots) have an intermediate pattern of development. However, the data are confounded by the fact that in addition to being smaller than guillemots, the semi-precocial alcids are also burrow or crevice-nesters. This means that both parents can forage simultaneously without leaving the chick at high risk of predation. Thus, it may be burrow-nesting rather than small body size that has favoured semi-precocial development in the Alcidae. Moreover, there is an overlap in body size between the intermediate species and the largest semi-precocial species, Horned Puffins (*Fratercula corniculata*) and Tufted Puffins (*Fratercula cirrhata*). Most of our knowledge of the semi-precocial alcids is based on the smallest of the four puffin species, the Atlantic Puffin, and there are many fewer data on the larger semi-precocial species.

The Horned Puffin

The family Alcidae consists of five main lineages or tribes (Strauch 1985). Within the tribe *Fraterculini* there are four species of puffin; the Atlantic Puffin, and three species of Pacific puffin; the Horned Puffin, the Tufted Puffin and the Rhinoceros Auklet (*Cerorhinca monocerata*). Although the Atlantic Puffin has been studied extensively (e.g. Ashcroft 1979, Harris 1984, Harris *et al.* 1997), relatively little information exists on the breeding ecology of the larger congeneric Horned Puffin. There is some overlap in body size between Atlantic and Horned Puffins (Piatt and Kitaysky 2001), but whilst some studies of Atlantic Puffins have been conducted in Norway and Canada (e.g. Nettleship 1972, Barrett and Rikardsen 1992), the majority of studies on this species have been in Britain, where birds belong to the smallest subspecies *F. arctica grabae* (Harris 1984).

The Horned Puffin has a summer distribution ranging from 50° to 70° North latitude (Amaral 1977), breeding along the coast and on offshore

islands in British Columbia, the Gulf of Alaska, Aleutian Islands, Sea of Okhotsk, Kuril Islands, and the Bering and Chukchi Seas (Piatt and Kitaysky 2001). The estimated world population is 1.2 million birds (Gaston and Jones 1998), with ca. 80% found in Alaska and the majority (ca. 62%) breeding off the Alaska Peninsula.

Puffins spend the winter at sea, returning to the colony in the spring to breed (in May in Alaska). Horned Puffins almost always nest either in cracks in cliff faces, amongst boulders or in rock crevices. A single egg is laid in June, and is incubated by both parents for an average of 41 days ($n=20$, $SD \pm 3.4$, Petersen 1983). After hatching, the chick is brooded constantly for the first 5-7 days (Wehle 1980). Once the chick has attained endothermy it is left alone, attended only briefly during food delivery. Chick development is slow, with a typical nestling period of 37 to 46 days ($n=12$) (Peterson 1983). Both parents feed the chick, with loads of several small fish transported crosswise in the bill. Chicks are fed almost entirely fish, with sandlance (*Ammodytes hexapterus*), capelin (*Mallotus villosus*) and gadids (*Gadidae*) the most important prey species across their whole range (Piatt and Kitaysky 2001). Young at a single colony fledge over a period of about a month (Petersen 1983), with adult birds departing from the colony over this period after their chick has fledged.

Study Site

This study was conducted on Duck Island, a small island located about 0.4 km off the east of Chisik Island, in western Cook Inlet, Alaska (60° 09'N, 152° 34'W) (Figure 1:1). Duck Island has an area of approximately 2.4 hectares and maximum elevation of 49 meters. Chisik and Duck Islands were made part of the Alaska Maritime National Wildlife Refuge in 1980, and are important locations for breeding seabirds. A total of ca. 22,000 individual Black-legged Kittiwakes (*Rissa tridactyla*) and 6000 Common Guillemots breed on the two islands. Smaller numbers of Glaucous-winged Gulls (*Larus glaucescens*), Parakeet Auklets (*Cyclorhynchus psittacula*), Double-Crested Cormorants (*Phalacrocorax auritus*), Tufted Puffins, Pigeon Guillemots (*Cephus*

columba) and Common Eiders (*Somateria mollissima*) also breed there. An estimated 4-5000 individual Horned Puffins nest annually on Duck Island, in caves and in crevices amongst boulders.

This study was conducted in the context of a larger project, ‘Cook Inlet Seabird and Forage Fish Studies’ (USGS and USFWS 2001). Waters that surround Duck Island are estuarine, receiving glacier-fed freshwater from Tuxedni Bay and from rivers at the head of Cook Inlet (Robards *et al.* 1999). The water is stratified and relatively warm, with low salinity and low levels of primary productivity. As a result the area is unable to support a high biomass of planktivorous forage fish, with the fish present having a highly dispersed distribution (USGS and USFWS 2001). The waters have low densities of foraging seabirds, and concurrent study on the breeding Common Guillemot and Black-legged Kittiwake, suggested that birds breeding on Chisik and Duck Island have longer foraging trips and higher work rates during incubation and chick-rearing than other colonies in Alaska (Kitaysky *et al.* 1999, Zador and Piatt 1999, USGS and USFWS 2001). Field workers were present on Duck Island between May/June to August/September in 1995-1999.

Study context and thesis outline

Some species of seabird in Alaska have shown decreased productivity, diet change and population decline during the last few decades (Piatt and Anderson 1996). This decline is thought to be associated with a shift in fish community composition (Anderson and Piatt 1999), as a direct result of the ocean climate ‘regime shift’ that occurred in the North Pacific during the late 1970s (Hare and Mantua 2000).

Seabirds in Alaska also face a number of threats from oil and gas exploitation. The economy of Alaska has become increasingly reliant on the oil and natural gas industry, and development of these resources continues in offshore areas. Alcids are among birds most vulnerable to oil pollution, spending much time swimming on the surface and often aggregating together in large rafts (King and Sanger 1979, Piatt *et al.* 1990a). The *Exxon Valdez* oil spill in 1989 killed more than 300,000 seabirds, with alcids (predominately

Common Guillemots) comprising at least 80% of the dead birds retrieved after the spill (Piatt *et al.* 1990). As oil and gas development increases, the risk to alcids will increase.

In addition to oil and mineral exploitation, alcids are also vulnerable to commercial fishing operations, and many drown in gill nets. Fisheries can also affect seabird food webs, changing the levels of prey stocks and influencing predator-prey interactions. For example, the extended breeding failure of Atlantic Puffins in Norway has been linked to the over-fishing of North Sea herring (*Clupea harengus*) (Barrett *et al.* 1987). Intensive fisheries may also indirectly increase seabird forage fish abundance. For example, there are documented increases in sandeel (*Ammodytes* sp.) stocks as a response to reduced competition with mackerel (*Scomberidae*) and herring (Furness and Ainley 1984). Pollock (*Theragra chalcogramma*) and capelin are important species both commercially and in the diet of Horned Puffin chicks in Alaska, but little is known about the impact of commercial fisheries for these species on food availability and breeding success of Horned Puffins.

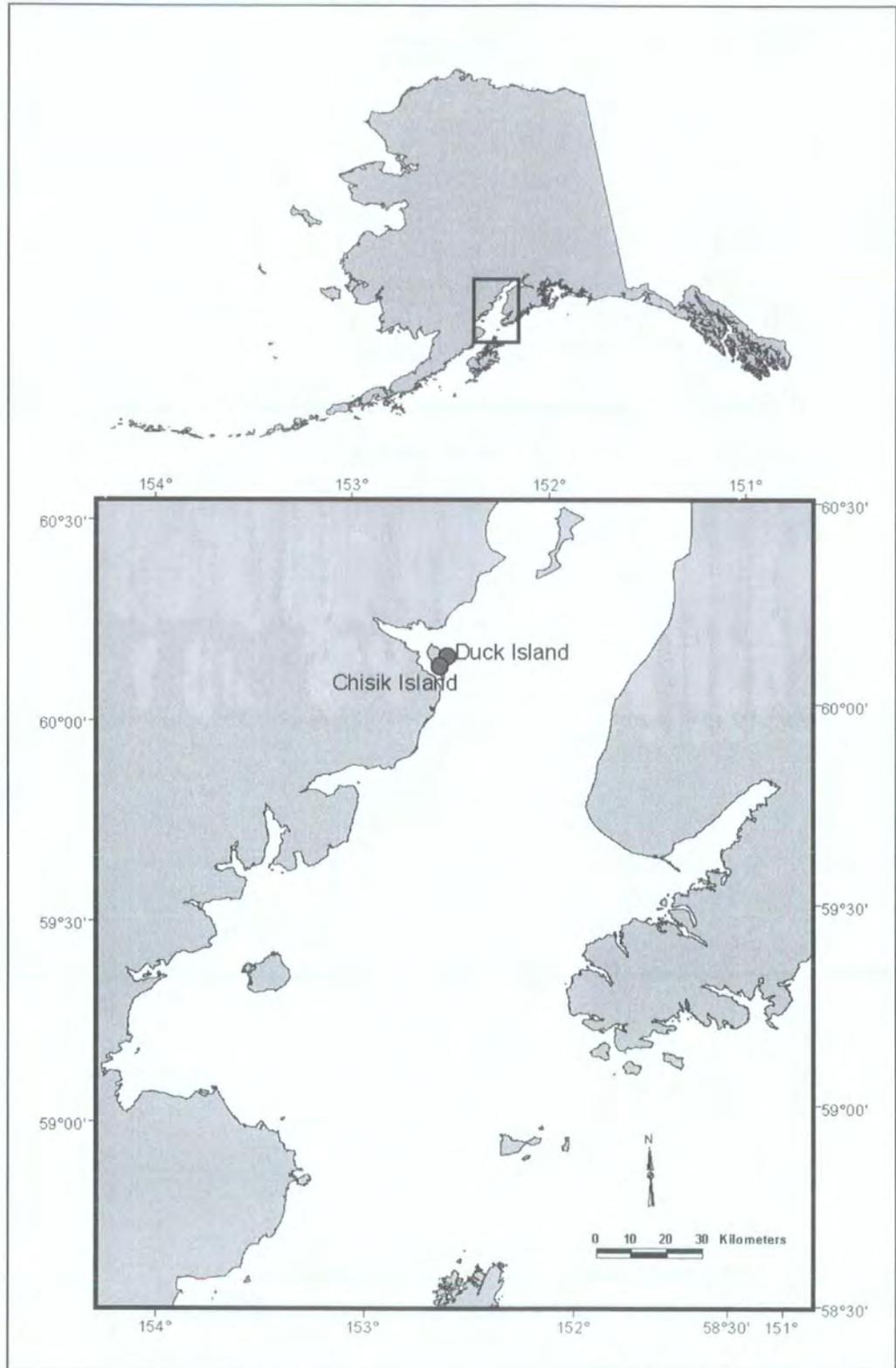
In addition to interest in the context of resource allocation and life history traits, many people have suggested that seabirds are potentially valuable indicators of oceanic conditions, and monitors of changes in the abundance and distribution of prey species (e.g. Ricklefs *et al.* 1984, Cairns 1987, Montevecchi *et al.* 1988, Baird 1990, Barrett and Furness 1990, Harris and Wanless 1990, Nettleship 1990, Springer *et al.* 1996).

Very few studies have focused on the Horned Puffin (e.g. Amaral 1977, Wehle 1980, Wehle 1983) and despite Alaska holding an estimated 80% of the world population of Horned Puffins, it remains one of the least studied seabirds in the state. There are data on the breeding ecology of Horned Puffins in Alaska, but sample sizes are small for many breeding parameters, especially chick growth and fledging age, and monitoring studies have focused on very few colonies. To be able to interpret changes in Horned Puffin breeding ecology much more information is needed on the 'normal' variability in breeding parameters, both between colonies and between years at the same colony. Although surveys suggest that populations of some

seabird species in Alaska have declined over the last few decades (e.g. Piatt and Anderson 1996), there is no standardized population census method for the Horned Puffin, and consequently very little is known about absolute numbers or trends in population size. Without firm knowledge of both the breeding ecology and population sizes of Horned Puffins, it is impossible to detect changes and distinguish between effects due to natural changes in the marine environment or those arising from human impact.

This thesis presents results from a five-year study (1995-1999) of Horned Puffin breeding and population ecology on Duck Island, Alaska. Chapter Two presents data on the breeding ecology of Horned Puffins, and examines annual variation in different breeding parameters. Chapter Three presents data on the pattern of colony attendance of Horned Puffins, examines the daily, seasonal and annual variation in colony attendance, and discusses the implications of this variation for population monitoring. In Chapter Four, the General Discussion, I discuss the wider implications of these results in the context of life-history theory, food availability and population monitoring.

Figure 1:1. Map showing the location of Chisik and Duck Islands in Cook Inlet, Alaska. (Courtesy G. Drew, ABSC.)



CHAPTER TWO

HORNED PUFFIN BREEDING ECOLOGY OVER A FIVE-YEAR PERIOD.

Introduction

The Horned Puffin (*Fratercula corniculata*) is one of three North Pacific puffin species with a summer distribution ranging from 50° to 72° North latitude (Amaral 1977). Alaska holds over 80% of the world population of Horned Puffins, with the majority (ca. 62%) breeding off the Alaska Peninsula (Gaston and Jones 1998). In contrast to the burrow-nesting habits of the Atlantic Puffin (*F. arctica*), Tufted Puffin (*F. cirrhata*), and the Rhinoceros Auklet (*Cerorhinca monocerata*), the Horned Puffin almost always nests among boulders and in rock crevices, making access to nest-sites and chicks difficult and complicating the study of their breeding biology. Consequently, very few studies have focused on the Horned Puffin (e.g. Amaral 1977, Wehle 1980, 1983), and it remains one of the least studied seabirds in Alaska.

Some data exist on the breeding ecology of Horned Puffins in Alaska, but sample sizes are small for many breeding parameters, especially chick growth and fledging age, and monitoring studies have focused on very few colonies. Many seabird species exhibit high inter-year variability in their breeding ecology, and numerous studies demonstrate that local food availability can influence breeding parameters (e.g. Coulson and Thomas 1985, Monaghan *et al.* 1989, Burger and Piatt 1990, Hamer *et al.* 1991a). For example, the Atlantic Puffin shows high variability within breeding parameters, both geographically and at the same colony among years (e.g. Harris 1985), with well documented evidence of reduced growth rates, extended fledging periods, shifts in chick diet, and even complete breeding failure in response to reduced food availability (e.g. Barrett and Rikardsen 1992). Such variability emphasises the need for knowledge of the breeding ecology of Horned Puffins to be based on different colonies and from a number of years.

Seabirds may act as valuable indicators of oceanic conditions and changes in the abundance and distribution of prey species (e.g. Cairns 1987, Baird 1990, Barrett and Furness 1990, Harris and Wanless 1990, Nettleship

1991). Some seabird species in Alaska have shown decreased productivity, changes in diet and population declines during the last few decades (e.g. Piatt and Anderson 1996). These changes are thought to be associated with a shift in fish community composition (Anderson and Piatt 1999), as a direct result of the ocean climate ‘regime shift’ that occurred in the North Pacific during the late 1970s (Hare and Mantua 2000). Seabirds in Alaska are also vulnerable to both oil and mineral exploitation and to commercial fishing operations.

To be able to detect and interpret changes in Horned Puffin breeding ecology, much more information is needed on the ‘normal’ variability in breeding parameters both among colonies and between years at the same colony. Without such knowledge, it is impossible to distinguish between effects due to natural changes in the marine environment and those arising from human impacts. In this study, Horned Puffins were studied on Duck Island, Lower Cook Inlet, Alaska, for five consecutive seasons (1995-1999). The aim of the study was to examine the breeding ecology of the Horned Puffin, in order to improve our baseline knowledge of this species and the variability in its breeding ecology.

Methods

Puffins are sensitive to disturbance during the incubation phase of their breeding cycle, and may abandon breeding in response to disturbance during incubation (Lockley 1934, Harris 1984, Rodway *et al.* 1996). Thus, nests were not disturbed until towards the end of the incubation period, when the island circumference was searched for active nest-sites with visible nest-chambers. Active sites were identified with a painted number on an adjacent rock. Nest-sites were visited every 3-5 days until hatching. During each visit the nest chambers were checked using a headlamp, and the presence of adult, egg or chick was recorded. Visits were kept as brief as possible to minimise disturbance. Where an adult blocked the sight of an egg or chick, the adult’s brooding posture and the presence of egg-shell fragments were used as evidence of hatching. In the few nest-chambers where chicks could move out

of sight, additional evidence of hatching was obtained from chick vocalisation and the presence of dropped fish in the nest chamber Median chick hatch date was used as a measure of annual timing of breeding.

Chick Measurements

Chicks were visited every 4-7 days during the chick-rearing period, and every 3-5 days during the fledging period. During each visit, the following body dimensions were measured (following Wernham and Byrant 1998): tarsus length using Vernier calipers, with precision ± 0.1 mm; culmen length, using Vernier calipers, from the tip of the upper mandible to the anterior edge of the growing cere; straightened wing length with precision of ± 0.1 mm using a stopped ruler and body mass using a Pesola balance, with precision of ± 1.0 g. Repeat measurements, taken in accordance with the procedure recommended by Barrett *et al.* (1989), were within 0.2 mm for tarsus and culmen, 1.0 mm for wing length and 1.0 g for body mass. Chicks were first handled when they were older than 5 days, and the parents had finished brooding. For the few nest sites with accessible chicks that were found later in the season, where hatch date was unknown, chicks were aged using the following linear regression of age on wing-length for chicks of known age; chick age (days) = 0.26 (SE ± 0.006) wing length (mm) - 0.54 (SE ± 0.6) ($R^2 = 0.86$; Figure 2:1). Known-age chicks ($n=40$) were aged to within 88.8% of their absolute age using the predictive value.

Productivity

Fledging success was calculated each year. Maximum hatching success and breeding success were also calculated; both these parameters are likely to be overestimates since nest-sites were not located until late in incubation, before which some eggs may have been laid and lost. The timing of the first nest-check during incubation varied among years (23 June to 16 July); to control for a possible bias in recorded egg-loss and therefore maximum hatching success in different years, I excluded from calculations of maximum hatching success each year all nest-sites where an egg was followed and lost before July 15.

Due to deteriorating weather conditions, and consequent departure of field crew, at the end of the field season I was only able to follow a total of 47% of chicks to fledging during the 5 years. Considering chicks from all 5 years ($n = 161$), twenty chicks (12%) were known to have died in the nest, with 80% of these deaths occurring at age 10 days or less, and with no mortality after 20 days old. To calculate fledging success, chicks ≥ 20 days old at the end of fieldwork were thus considered to have survived until fledging.

Dead chicks were not removed from the nest by parents or predators, and so, in order to calculate fledging age, I assumed that fully-feathered chicks (aged +25 days) that disappeared from the nest between visits had fledged. Due to the early departure of field crew in some years, fledging age was calculated only in 1996, 1998 and 1999.

Chick Diet

The diets of Horned Puffin chicks were assessed throughout the chick-rearing period each year (at different nest-sites from those used to estimate productivity and chick growth) using the following four methods:

1. **SCREEN:** Entrances to ca. 15 nest-sites were temporarily blocked using wire mesh screens (Hatch and Sanger 1992). After ca. 2 h, nest-sites were revisited, screens were removed, and food samples dropped by adults at the nest entrance were collected.
2. **GILL NET:** Gill nets (2-3 cm mesh) or mist nets were draped over boulder piles, blocking the entrances to several puffin nest-sites simultaneously, and observed from a distance. Adults caught in the nets were immediately removed and measured prior to release; any dropped food items were collected.
3. **DROPPED:** Food loads were sometimes dropped by flying or landing adult puffins, particularly when they were startled by a worker's presence. Freshly dropped fish were collected opportunistically throughout each season. Many complete bill-loads were collected whilst working in large caves with several Horned Puffin nests.

4. VISUAL: Puffins sometimes stand outside their nest-site for a short time before provisioning their chick. Bill loads held by adult puffins standing on boulders and cliffs in the colony were recorded. Prey species were identified using 10 x 42 binoculars and the number of fish in the bill was counted.

All prey collected were identified (using taxonomic keys; Hart 1973), weighed (using an electronic balance, ± 0.01 g) and measured (length to tail fork, using a steel ruler with precision of ± 0.1 mm). All prey items were weighed and measured within two hours of collection. Energy contents of prey were calculated using published wet mass energy density conversions (Van Pelt *et al.* 1997). All meal collections were identified as either a complete or incomplete bill-load. Items classified as complete bill-loads were either observed dropped loads, observed gill-net loads where no fish were lost, or visual identifications.

Feeding rates

Daily meal delivery rates to chicks were recorded for two days (0630-2200) at five nests in 1996 and for three days (0500-2300) at 5-7 nests in 1997. The low density of nest-sites on Duck Island and the high proportion of sites in crevices or caves with multiple or shared entrances made the simultaneous observation of many nests very difficult. During observations, the time of sunrise varied from 0430 on 26 July to 0540 on 24 August. All watches began within one hour of sunrise and continued until darkness. Speed of delivery made identification of meal size and composition difficult. Meal sizes were not measured, but the total numbers of daily meal deliveries were calculated per chick.

Adult Measurements

Breeding adult Horned Puffins were measured in 1998 and 1999. Adults were captured at their nest during the chick-rearing period by hand, or by using a gill net placed over the nest entrance during food delivery. The same body

measurements were taken as for chicks. In addition, total head plus bill length (headbill) was measured, to the nearest 0.1 mm using Vernier calipers, as the greatest distance from the back of the head to the tip of the upper mandible, with the upper surface of the calipers resting on the top of the head. Three additional bill measurements were also made; bill width, bill depth and length of cutting edge, all to the nearest 0.1 mm using Vernier calipers (Plate 2:1).

Figure 2:1. Linear regression of Horned Puffin chick age on wing length
(n = 67 chicks)

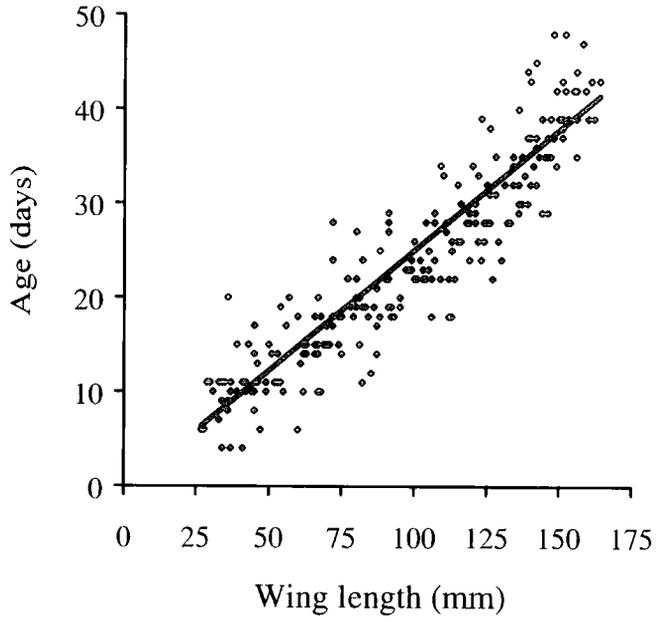
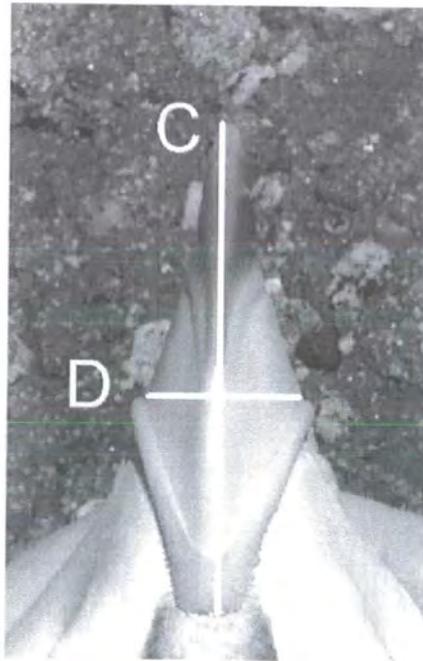
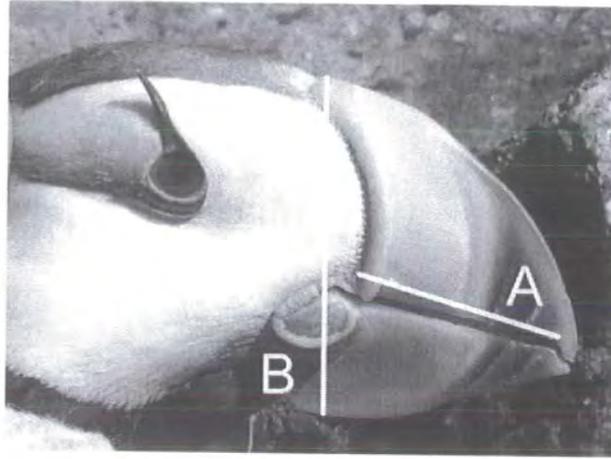


Plate 2:1. Horned Puffin adult bill measurements. Side view: A=cutting edge, B=bill depth. Aerial view: C=culmen and D=bill width



Results

Productivity and Timing of Breeding

Maximum hatching success varied from 67% to 84% of eggs, and fledging success varied from 83% to 97% of chicks. No eggs were depredated and eggs failing to hatch were cracked or addled, either as a consequence of embryo death or a lack of fertilisation. There was no difference among years in hatching success, fledging success or maximum breeding success ($P > 0.05$ in all cases; Table 2:1). Median chick hatching date ranged from 19 July in 1996 to 29 July in 1998. There was a significant difference in medium chick hatching date between years (Kruskal Wallis ANOVA $H_4 = 39.05$, $P < 0.001$); Table 2:1).

Chick growth and Fledging

Fledging success was highest (97%) in 1999, and so I took this year to indicate normal chick growth during favourable conditions. Figure 2:2 shows growth of body mass and external measurements in 1999. There was an initial rapid linear increase in mass (10.8 g/day on average) until about age 30 days. This linear phase of growth was followed by a period of very slow mass gain (1.39 g/day on average), up to a peak of 386 g (SD \pm 51.9) at about 38 days. A short period of mass recession (1.25 g/day on average) then occurred prior to fledging. Mean adult body mass was 531 g ($n = 21$, SD \pm 44.0; Table 2.2), and chicks in 1999 fledged on average at 75.5% of this mass (Table 2.3).

Wing, culmen and tarsus lengths had different growth trajectories (Fig 2.2). Wing length increased more or less linearly throughout the nesting period, and the mean wing length of chicks at the last check before fledging was 156mm ($n = 16$, SD \pm 5.2), which was 79.2% of adult wing length (mean = 197 mm, $n = 22$, SD \pm 5.5). In contrast, tarsus had a longer decelerating period of growth, and tarsus lengths of fledglings were very similar (within 2%) to those of adults (Tables 2:2 and 2:3). Although there are a number of equations for describing chick growth (eg. Ricklefs 1967), these rely on good data on the

asymptotes and fledging and I therefore restricted growth analysis to the linear phase. To compare growth among years, I calculated growth rate (using linear regression) for different body components during the linear phase of growth (10-30 days for body mass and wing length; 0-15 days for culmen and tarsus length; Fig 2.2). These data were used to calculate a single growth rate, for each body component, for each chick, which were then compared among years using analysis of variance (ANOVA) followed by post-hoc range tests.

There was a significant difference among years in mass growth rates of chicks (Table 2.4), with much slower growth in 1998 than in other years. This was due to a marked difference in growth at age 15-30 days (Figure 2.3: one-way ANOVA: $F_{4,71} = 7.3$, $P < 0.001$), whilst there was no difference in growth at age 0-15 days (Figure 2.3: one-way ANOVA: $F_{4,51} = 1.2$, $P = 0.337$). In addition to mass growth rate, chick body mass at age 30 ± 3 days also differed significantly among years (Table 2.5: one-way ANOVA: $F_{3,53} = 10.2$, $P < 0.001$), with chicks in 1999 heavier than chicks in 1996 and 1998.

There was a significant difference among years in wing growth rates of chicks (Table 2:4), with growth highest in 1997 and lowest in 1998. Wing lengths of chicks aged 30 ± 3 days differed among years (one-way ANOVA: $F_{3,53} = 4.2$, $P = 0.01$), with wing length in 1999 significantly longer than in 1998 (Table 2.5). Culmen and tarsus growth rates did not differ significantly among years (Kruskal Wallis ANOVA for non-normal data: Table 2:4). Chick tarsus length at 30 days old was, however, shorter in 1998 than in 1997 or 1999 (Table 2.5; one-way ANOVA $F_{3,53} = 9$, $P < 0.001$), but there was no significant difference in culmen length at age 30 days old between years (Table 2.5; $F_{3,51} = 2.35$, $P = 0.1$).

Chick fledging ages were recorded in 1996, 1998 and 1999 (Table 2:6). There was a significant difference among years (oneway ANOVA: $F_{2,69} = 15.66$, $P < 0.001$), with chicks fledging youngest in 1998, which was the year in which chick mass growth was poorest (Figure 2:4).

Chick Diet

A total of 1738 prey items was collected between 1995 and 1999. Sandlance (*Ammodytes hexapertus*) was the dominant prey species numerically, constituting $\geq 90\%$ of the chick's diet in each year (Table 2:7). Most other prey were capelin (*Mallotus villosus*) or salmon (*Onchorhynchus* sp.). Invertebrates comprised $< 0.5\%$ of chick diet.

Sandlance differed significantly among years in length (Table 2:8; one-way ANOVA: $F_{4,1029} = 9.2$, $P < 0.001$), mass ($F_{4,985} = 13.6$, $P < 0.001$), and predicted energy content ($F_{4,718} = 5$, $P < 0.001$). Differences in the size of sandlance among years may be explained by sandlance growth and annual differences in the time of Horned Puffin breeding (Table 2:1).

Meal Size and Feeding Frequency

Mean bill-load mass over all 5 years was 16.4g ($n = 63$, $SD \pm 6.4$), and the mean number of prey items per load was 6.2 ($n = 132$, $SD \pm 3.4$). There was no significant difference among years in either the mean mass of prey per load (Table 2:9; oneway ANOVA: $F_{3,57} = 0.8$, $P = 0.97$) or the mean number of prey items per load ($F_{3,124} = 1.54$, $P = 0.2$).

Chicks were delivered a mean of 6.1 meals/day ($n = 20$ chick-days on two days, $SD \pm 2.1$) during the late chick-rearing period in 1996; 3.2 meals/day ($n = 12$ chick-days on two days, $SD \pm 1.0$) during early chick-rearing in 1997 and 2.6 meals/day (1 day, $n = 7$, $SD \pm 1.0$) during mid-chick-rearing in 1997.

Table 2:1. Horned Puffin productivity and timing of breeding in different years at Duck Island, Alaska.

Year	1995	1996	1997	1998	1999	χ^2	df	p
Total no. nests	21	51	48	61	47			
Maximum hatching Success	0.71	0.84	0.67	0.69	0.77	5.19	4	>0.5
Fledging Success	0.92	0.83	0.96	0.89	0.97	4.71	4	>0.5
Maximum breeding Success	0.66	0.70	0.64	0.62	0.70	5.19	4	>0.5
Median chick hatch date	21-Jul	19-Jul	25-Jul	29-Jul	26-Jul			

Hatching, fledging and reproductive success are compared between years using chi-square contingency tables.

All tests were non-significant, with four degrees of freedom.

Table 2:2. Body measurements of breeding adult Horned Puffins in 1999

	mean	n	SD
mass (g)	530.6	21	44.0
wing (mm)	197.2	21	5.6
tarsus (mm)	31.9	21	2.1
headbill (mm)	82.7	21	2.2
culmen (mm)	49.2	21	1.7
depth (mm)	41.9	21	2.0
cutting edge (mm)	26.9	21	0.5
width (mm)	13.1	15	1.0

Table 2:3. Fledging measurements for Horned Puffin chicks in 1999

	mean	n	SD
Fledging age (days)	40.7	28	4.1
Fledging mass (g)	400.6	16	45.2
Fledging wing (mm)	155.8	16	5.2
Fledging tarsus (mm)	31.3	16	1.3
Fledging headbill (mm)	70.2	15	1.7
Fledging culmen (mm)	31.9	16	1.6

Table 2:4. overleaf**Table 2:5.** Body mass and external measurements of chicks at age 30 days in different years.

Year	mass (g)			wing (mm)			tarsus (mm)			culmen (mm)		
	mean	n	SD	mean	n	SD	mean	n	SD	mean	n	SD
1996	325.0 a	14	45.8	123.4	14	12.1	29.7	14	1.3	28.5	13	1.6
1997	337.9	10	51.6	128.3	10	10.8	30.4 a	10	1.3	28.5	10	2.0
1998	285.8 b	16	43.6	119.2 a	16	8.2	28.6 ab	16	1.3	28.4	16	1.9
1999	375.0 ab	17	48.2	131.0 a	17	10.4	30.7 b	17	1.3	29.8	16	1.6

Means followed by different letters are significantly different as determined from Tukey multiple comparison tests.

Table 2:4. Linear growth rates of Horned Puffin chicks at Duck Island in different years.

Year	Body Mass (g/day)			Wing (mm/day)			Culmen length (mm/day)			Tarsus (mm/day)		
	mean	n	SD	mean	n	SD	mean	n	SD	mean	n	SD
1995	12.8 b	14	3.1	3.9 ab	14	1.05	0.39 a	14	0.08	0.37 a	15	0.08
1996	9.4 b	18	2.6	3.5 ab	18	0.91	0.28 a	11	0.16	0.39 a	12	0.21
1997	10.5 b	16	3.3	4.3 a	16	0.57	0.39 a	11	0.11	0.46 a	13	0.10
1998	3.7 a	22	6.9	3.4 b	22	1.08	0.27 a	10	0.13	0.30 a	12	0.16
1999	9.6 b	21	3.0	4.0 ab	21	0.43	0.29 a	10	0.13	0.36 a	10	0.10
	<i>F</i>	df	<i>P</i>	<i>F</i>	df	<i>P</i>	<i>H</i>	df	<i>P</i>	<i>H</i>	df	<i>P</i>
treatment	11.7	4	<.001	3.33	4	0.014	8.3	4	0.081	6.51	4	0.164
error		86			86							

Means followed by different letters are significantly different as determined from Tukey multiple comparison tests.

Table 2:6. Horned Puffin chick fledging ages in different years.

Year	Fledging Age (days)			
	mean	n	SD	range
1996	42.06	25	4.925	31-48
1998	34.74	23	5.667	29-49
1999	40.71	28	4.099	33-45

Table 2:7. Horned Puffin chick diet composition at Duck Island.

Prey Items	1995		1996		1997		1998		1999	
	n	%	n	%	n	%	n	%	n	%
Pacific sandlance <i>Ammodytes hexapterus</i>	91	98	825	94	465	95	158	90	103	99
Capelin <i>Mallotus villosus</i>	2	2	27	3	9	2	3	1.7	0	0
Salmon sp. <i>Onchorhynchus sp.</i>	0	0	16	2	7	1	8	4.6	1	1
Pacific Lamprey <i>Lampetra tridentatus</i>	0	0	4	0.5	0	0	2	1.1	0	0
<i>Gadidae</i>	0	0	0	0	2	0	0	0	0	0
Euphasiid	0	0	0	0	6	1	1	0.6	0	0
Sculpin sp. <i>Cottidae sp.</i>	0	0	0	0	1	0	0	0	0	0
Sandfish <i>Trichodon trichodon</i>	0	0	1	0.1	0	0	0	0	0	0
Unidentified Smelt <i>Osmeridae</i>	0	0	0	0	0	0	1	0.6	0	0
Unidentified fish species	0	0	0	0	0	1	2	1.1	0	0
Total prey items	93		875		491		175		104	

Table 2:8. Mean size and energy content of sandlance in Horned Puffin chick diets in different years.

year	length (mm)				mass (g)				energy content (kJ)		
	mean	n	SD	range	mean	n	SD	range	mean	n	SD
1995	92.7 abc	93	24.7	45-180	2.9 bcd	93	2.6	0.5-21.0	16.1 ab	93	15.2
1996	85.2 a	542	31.5	47-223	2.1 a	560	1.8	0.3-14.3	13.8 b	293	10.1
1997	86.0 ac	143	19.1	57-164	2.5 ad	142	2.3	0.6-18.7	13.1 b	142	13.7
1998	93.0 bc	158	16.2	51-146	2.7 bcd	94	1.5	0.5-7.8	14.4 ab	94	8.0
1999	100.2 b	101	8.5	64-123	3.3 bc	104	1.0	0.8-7.0	18.7 a	101	6.2

Means followed by different letters are significantly different as determined from Tukey multiple comparison tests

Table 2:9. Horned Puffin bill-loads (complete chick meals).

YEAR	Mass/load (g)				No. prey items/load			
	mean	n	SD	range	mean	n	SD	range
1995	15.2	3	4.2	12.0-20.0	7.7	3	3.8	5-12.
1996	17.4	15	8.1	2.5-34.5	6.9	16	2.8	4-15.
1997	16.0	16	7.2	6.6-32.0	6.3	67	3.3	1-22.
1998	16.5	8	7.1	7.8-21.5	6.0	24	3.4	1-13.
1999	15.7	22	6.1	6.4-25.6	4.9	21	1.8	2-8.
1995-1999	16.4	64	6.4	2.5-34.5	6.2	131	3.4	1-22.

Figure 2:2. Horned Puffin chick growth in 1999, (mean \pm 1SE).
 Sample sizes are shown above each age class (total n=28 chicks).

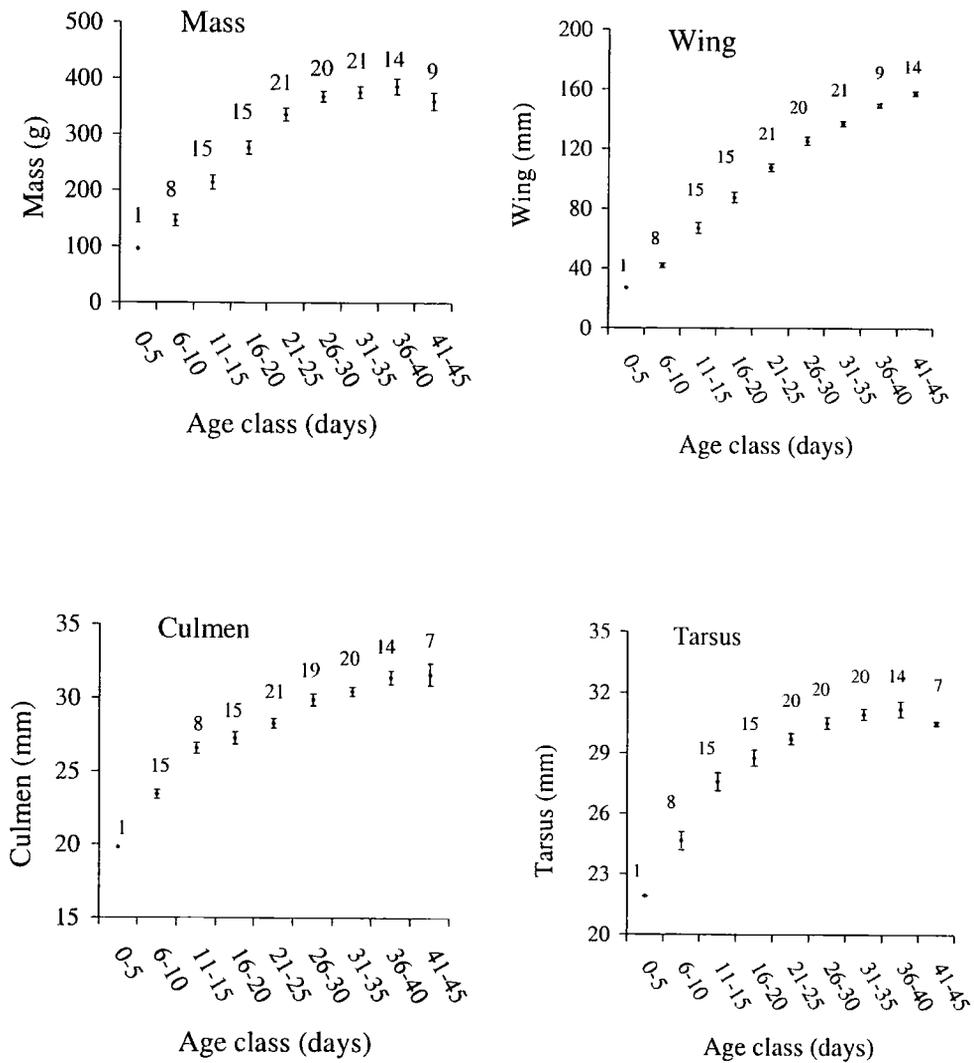


Figure 2:3. Mass growth of Horned Puffin chicks in different years.

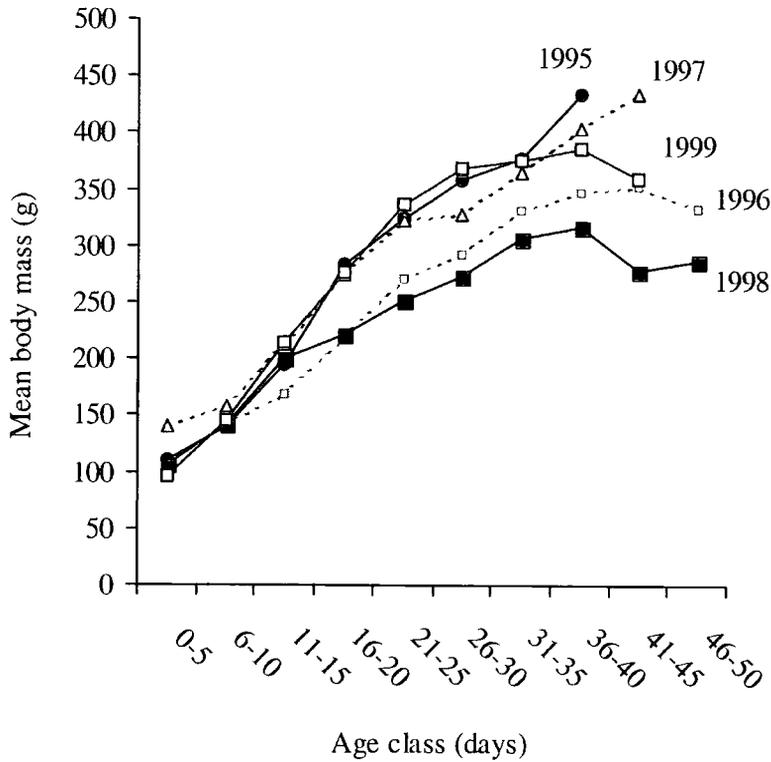
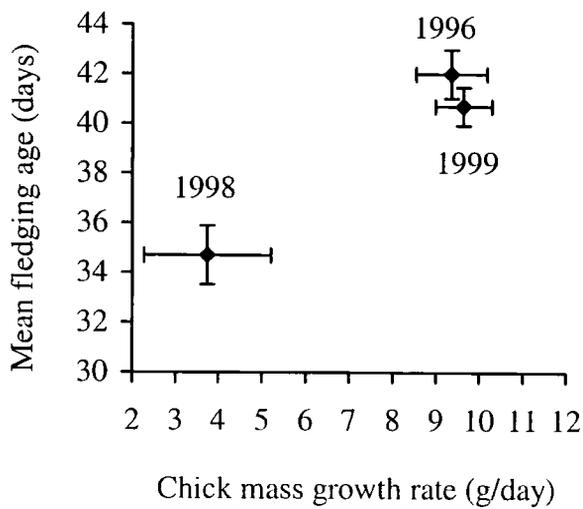


Figure 2:4. Chick fledging age and chick mass growth rate in different years (means \pm SE). Sample sizes given in Tables 2:4 and 2:6.



Discussion

Productivity

Since I only followed eggs from late incubation, it is difficult to compare the hatching and breeding success on Duck Island with other studies of Horned Puffins. The mean fledging success for the 5 years (91.4%), was, however, relatively high in comparison with other studies which have reported fledging success ranging from 25-100%, with a mean of 73% (n = 39 colony-years at 9 colonies; Piatt and Kitaysky 2001).

Chick Growth and Fledging

Previous knowledge of Horned Puffin chick growth has been based on small sample sizes. The large range of growth rates observed over the 5 years of this study (yearly mean range 3.7-12.7g/day; Fig 2:4) encompasses the range of values reported in other studies (from 3.4 g/day (n = 3) in the Semidi Islands, to 12.6g/day (n = 8) at the Shumagin Islands; Petersen 1983), and indicates the importance of collecting data in more than one year.

Under favourable conditions in 1999, chicks fledged at 75% of adult body mass on average, a similar pattern to that observed in Atlantic Puffins, which fledged at 78% adult mass (Ashcroft 1979). The total range of fledging ages in this study was 29-49 days (Table 2:6), a slightly wider range than those previously recorded in the field, although earlier data were based on very small sample sizes (38-42 days, n = 2 (Amaral 1977); 34-43 days, n = 4, (Wehle 1980); 37-46 days, n = 12 (Petersen 1983)).

1998 was an exceptional year with unusually early nest site departures. This could be ascribed to relatively high pre-fledging mortality, with starving chicks departing the nest-site prematurely. However, whereas studies on Atlantic Puffin colonies during seasons of breeding failure and nestling starvation have recorded hungry young chicks leaving their burrow, either dying or being depredated outside the nest-site (e.g. Lid 1981), no chicks were observed either predated or dead outside nest-sites or near their nest-entrance in this study. Furthermore, although chicks in 1998 left the nest-site at an early age on average,

the youngest fledglings had similar amounts of down to chicks fledging in other years. Although there can be no certainty of successful fledging, I therefore assume that data from 1998 indicates younger fledging ages and not higher pre-fledging mortality of chicks. However, it must be pointed out that the youngest fledglings in 1998 may have been unable to fly from the nest. Although most Atlantic Puffin fledglings fly from the colony (Harris 1984), Horned Puffins may fledge by flight or by walking from the nest-site directly to the water (Piatt and Kitaysky 2001). Nest sites on Duck Island are within 20m of the shore and puffin fledglings have been observed to walk to the water's edge before swimming away from the colony in other years (pers. obs.), thus flight is not necessarily a requirement for successful fledging.

The wide range in fledging ages observed on Duck Island indicates that Horned Puffins have a high degree of flexibility in age of fledging. Body mass and condition at fledging play an important role in determining the survival of chicks in some species (Gaston 1985, Phillips and Hamer 1999). However, evidence for a positive relationship between body mass at fledging and post-fledging survival has not been found in Atlantic Puffins (Harris 1984, Harris and Rothery 1985), and Ydenberg (1989) suggested that since puffins fledge at only approximately 70% of adult body mass, fledgling size may not be as closely linked to post-fledging survival in puffins as it is in species that complete their growth at the nest-site. Flexibility in age of fledging is usually interpreted as a trait associated with highly variable and unpredictable food supplies (Lack 1968). I return to this topic below, when variability among years is discussed.

Chick Diet

Horned Puffin chicks are fed almost entirely fish, with sandlance, capelin and gadids being the most important prey species across their North Pacific range (Piatt and Kitaysky 2001). Over the five years of this study, chick diet was dominated numerically by sandlance, comprising $\geq 90\%$ of the prey in each year (Table 2:7). Capelin and juvenile salmonids together comprised up to 5% of the diet and various other species, including euphausiid crustacea, were observed in very small numbers. These data are similar to those recorded on Duck Island in

1979, where 99% of prey fed to chicks were sandlance (Jones *et al.* 1980). Across their North Pacific range, sandlance comprise 60% of Horned Puffin chick diet (Piatt and Kitaysky 2001), indicating a relatively high reliance on sandlance at Duck Island.

The size of sandlance delivered to chicks at Duck Island differed among years (Table 2:8), but were similar to the range reported in other studies (56-164mm (Wehle 1983); 25-164mm, mean=70mm (Hatch and Sanger 1992)). Chicks in this study received meal loads weighing 16g and comprising six fish on average (Table 2:9). Other studies have recorded a similar number of prey items per bill-load (1-11 (n=15) (Wehle 1983); mean=7, (n=619) (Hatch and Sanger 1992)). Mean bill load mass in this study is high compared to other studies, which reported an average of 9.3 g per load across 12 colony-years (Piatt and Kitaysky 2001). This difference may be explained by the different methods of meal load collection. Whereas most studies have collected meal loads by blocking nest-sites using wire mesh screens (Hatch and Sanger 1992), this study only classified and weighed bill-loads either where a whole load was observed to be dropped or when loads were collected using a gill-net, and it was known that no fish had been lost. Loads collected using the screening method are probably underestimated since adults may eat food if prevented from delivering to the chick (Piatt *et al.* 1998) and meals may be taken by gulls (pers. obs.).

Due to the crevice-nesting and often scattered location of Horned Puffin nest sites, little is known about their feeding frequency. Data from this study are limited, ranging from an average of 2.6 meals/day during mid chick-rearing to 6.1 meals a day during late chick-rearing. These are similar frequencies to those reported elsewhere (2-6 meals/day; Manuwal and Boersma 1977), but more data are needed to accurately describe changes in feeding frequency during chick growth.

Variation between Years

Oceanographic data indicate that the marked El Niño Southern Oscillation in 1997-8 resulted in reduced salinity of surface water in the vicinity of Duck Island and an increase of 1-2 °C in winter water temperature (USGS and USFWS 2001).

In association with this anomaly, Common Guillemots (*Uria aalge*) at Duck Island experienced almost complete breeding failure in 1998, in contrast to high breeding success in the other four years of this study (USGS and USFWS 2001). The diet of guillemots on Duck Island overlaps with the Horned Puffins, with guillemot diet composition averaging 24% sandlance (USGS and USFWS 2001). Guillemots have the ability to switch prey, and normally have considerable leeway in their time and activity budgets to increase their foraging effort in response to a reduction in food supply (Burger and Piatt 1990, Monaghan *et al.* 1994, Uttley *et al.* 1994, Zador and Piatt 1999). I therefore assume that the breeding failure of guillemots indicates the likelihood that forage fish availability in general, including sandlance, was relatively poor in the waters around Duck Island in 1998. This presented the opportunity to examine the relationship between prey availability and Horned Puffin breeding parameters.

Productivity

Complete breeding failure resulting from poor food availability has been frequently reported in the Atlantic Puffin, usually related to over-fishing (e.g. Lid 1981, Anker-Nilssen 1987, Barrett *et al.* 1987, Martin 1989, Barrett and Rikardsen 1992). Breeding failure has also been recorded in other burrow-nesting alcids (Vermeer *et al.* 1979, Vermeer 1980, Byrd *et al.* 1993).

In contrast, breeding failure has been rarely recorded in the Horned Puffin, and evidence from other studies suggests that the variability in the reproductive success of Horned Puffins among years and at different colonies is normally very low (Piatt and Kitaysky 2001, but see Byrd *et al.* 1993). In keeping with this, there was no apparent difference among years in Horned Puffin reproductive success at Duck Island. These results should, however, be viewed with some caution in view of the small proportion of chicks (ca 50%) that were followed to fledging each year. Moreover, the data from this and most other studies are limited by lack of knowledge of the proportion of birds that attempt to breed, and do not measure incubation success, which may be a key factor for overall reproductive success in puffins (Hatch and Hatch 1990).

Chick Growth and Fledging

Food limitation is known to reduce the daily growth rates of Atlantic Puffin chicks (Harris 1984), with well documented evidence from both experimental (Harris 1978, Hudson 1979, Øyan and Nilssen 1996) and field studies (e.g. Tzchanz 1979, Harris 1985, Barrett *et al.* 1987, Barrett and Rikardsen 1992). Mass growth rates of Horned Puffin chicks at Duck Island were exceptionally low in 1998 (Table 2:4), presumably reflecting poor food availability in surrounding waters.

The impacts of reduced food supply on growth differed between different body components (Tables 2:4 and 2:5), suggesting differential allocation of energy and nutrients into the growth of different body structures. Differences in chick size at age 30 days were most pronounced for body mass and wing length, with a smaller difference in tarsus length and no difference in culmen length. These results are in accord with those of experimental studies of Atlantic Puffins (Øyan and Nilssen 1996), and of Horned and Tufted Puffins (Kitaysky 1996), which also recorded that under conditions of reduced food supply, highest priority was given to the growth of the skull and bill and low priority to the tarsus. Wing feathers can continue to grow after fledging, and slightly shorter wings at fledging will not necessarily reduce flight or diving performance, since body mass at fledging is also lower in conditions of poor food supply. Culmen growth may be coupled with the growth of the skull and neurological development, or may indicate the importance of culmen growth for prey capture after fledging (Øyan and Nilssen 1996). The development of the brain and wing length relative to body mass may be especially important for puffin fledgling survival, since chicks are independent at fledging and require the skill and ability to chase and catch fast moving prey (Kitaysky 1996, Øyan and Nilssen 1996).

Chick mass growth in 1998 was sharply reduced after chicks reached about 15 days of age (Fig 2:3). Atlantic Puffin chicks receive most food in the middle third of their six week development (Harris 1984), when the combined requirements of body maintenance and growth are highest. Due to low food availability, Horned Puffin parents on Duck Island in 1998 may have been unable to increase their provisioning rates as chick requirements increased with age. The

reduction in growth after chicks reached 15 days old may also have reflected a decrease in local food availability during the second half of chick-rearing.

The young fledging ages of Horned Puffins in 1998 contrast with older fledging ages in conditions of poor food supply in the Atlantic Puffin (e.g. Nettleship 1972, Anker-Nilssen 1987, Barrett *et al.* 1987, Barrett and Rikardsen 1992, Ydenberg *et al.* 1995). The wide range of puffin growth rates and fledging ages recorded in the wild (eg. Nettleship 1972, Harris 1984) probably reflect a range in feeding conditions. Assumed younger fledging ages in 1998 may have resulted from adults abandoning breeding in order to preserve their future reproductive potential. Alternatively, chicks may have fledged early as an adaptive response to low food availability, if they could achieve higher growth rates by foraging for themselves at sea than by depending on their parents to deliver food from distant foraging areas.

Chick Diet

Annual or seasonal change in chick diet associated with a reduction in local food availability have been well documented (e.g. Lid 1981, Hislop and Harris 1983, Martin 1989, Baird 1990, Barrett and Furness 1990, Hamer *et al.* 1991b, Barrett and Rikardsen 1992). Seabird species differ in their level of flexibility and ability to switch prey in response to changes in local prey abundance (Baird 1990), with specialist surface feeders more vulnerable (Furness and Ainley 1992). Increased diversity in the diet of Atlantic Puffin chicks has been recorded during seasons of poor food availability (Barrett *et al.* 1987, Barrett and Rikardsen 1992), with breeding failure observed in colonies with no alternative prey (Martin 1989, Barrett and Rickarden 1992). It has also been suggested that the inability of Tufted Puffins to switch diet when sandlance were in short supply resulted in breeding failure (Vermeer *et al.* 1979). In contrast to the Tufted Puffin, Rhinoceros Auklets at the same colony maintained high reproductive success, having the ability to switch from sandlance to sauries (*Cololabis saira*; Vermeer, 1980). The diurnal feeding habits of the Tufted Puffin prevented the exploitation of sauries as an alternative food source, since sauries undergo vertical migration and only rise to the water's surface at sunset (Vermeer *et al.* 1979).

Although sandlance are a dominant prey species for Horned Puffin chicks, changes in chick diet composition have been observed in response to large scale shifts in the forage fish species composition in the Gulf of Alaska (Piatt and Kitaysky 2001). These documented changes in chick diet and the higher diversity of prey items observed in the adult's winter diet, including myctophids and squid (Piatt and Kitaysky 2001), suggest that although chick diet is highly dependent on sandlance, Horned Puffins do have the ability to feed on a variety of species and switch prey if local food abundance shifts or is reduced.

However, I found no change in chick diet composition over the 5 years of this study, despite suspected food shortage in 1998. Sandlance remained the dominant prey species, comprising $\geq 90\%$ of chick diet in each year (Table 2:7). Relative prey abundance is important in determining chick diet composition under reduced food availability. Data from annual mid-water trawl surveys conducted in Lower Cook Inlet suggested that although the absolute abundance of sandlance was presumably lower in 1998, relative abundance was high in comparison to other species of forage fish (USGS and USFWS 2001). This may suggest that although food resources were generally low in 1998, sandlance dominated the local forage fish species composition, allowing Horned Puffins to continue to specialize on sandlance as food for chicks.

In the Atlantic Puffin the frequency of chick feeds (Martin 1989, Barrett and Rickardsen 1992) and the mass of bill-loads (Harris 1985, Barrett *et al.* 1987, Martin 1989, Nettleship 1990, Barrett and Rickardsen 1992) have been commonly observed to decrease in years of poor food availability. In this study I observed no difference between years in bill-load mass or derived/predicted energy content (Table 2:8 and 2:9). Horned Puffins at Duck Island forage at long distances from the colony: at-sea surveys in Lower Cook Inlet recorded Horned Puffins regularly foraging 50-110km from Duck Island (Piatt and Kitaysky 2001). In accordance with the economic foraging perspective of central place foraging theory (Schoener 1979, Kacelnik and Cuthill 1990), Horned Puffins foraging at long distances from Duck Island should always maximize their bill-load mass per journey, and so low food availability would be expected to affect feeding frequencies of chicks rather than meal size.

Further study is now needed to increase our knowledge of annual and geographic variability in Horned Puffin breeding parameters, and our understanding of the causes underlying this variability. Specific gaps of knowledge include data on feeding frequency and the relationships between fledging age, fledging mass and post-fledging survival of chicks.

CHAPTER THREE

HORNED PUFFIN COLONY ATTENDANCE AND POPULATION MONITORING

Introduction

Reliable census methods are needed for seabird population monitoring. Seabirds are vulnerable to a variety of anthropogenic factors, such as oil pollution (e.g. Piatt and Lensink 1989, Evans *et al.* 1993, Irons *et al.* 2000) and the fishing industry (e.g. Anker-Nilssen and Røstad 1993), and they may also be valuable monitors of changes in marine ecosystems (e.g. Montevecchii 1993). As a result, many studies have focused on examining variation in colony attendance and on developing standard methods for population monitoring for a wide range of seabird species (e.g. Birkhead 1978, Birkhead and Nettleship 1980, Seabird Group 1980, Slater 1980, Wanless *et al.* 1982, Harris 1987, Hatch and Hatch 1988, Jones 1992, Byrd *et al.* 1983, Hildén 1994, Walsh *et al.* 1995, Weidinger 1996).

Accurate censusing of many species of auks is particularly difficult because numbers of birds attending the colony can be highly variable (e.g. Jones 1992). It is not uncommon to observe thousands of birds at the colony on one day, and none or very few the next day. Due to such extreme variation in colony attendance, methods of monitoring populations of Atlantic Puffins (*Fratercula arctica*) have focused on counts of apparently occupied burrows (e.g. Seabird Group 1980, Harris and Murray 1981, Anker-Nilssen and Røstad 1993, Walsh *et al.* 1995). Whilst such counts can provide accurate estimates of the sizes of breeding populations of Atlantic Puffins, this method is not normally suitable for the Horned Puffin (*F. corniculata*). In contrast to the burrow nesting habits of the Atlantic Puffin, Horned Puffins almost always nest in cracks in cliff faces, amongst boulders, or in rock crevices. To complicate matters further, many crevice nest-sites have multiple or shared entrances and are often deep within unstable piles of boulders, making access hazardous and nest-sites difficult to count or even identify. As a result, there is no

standardized method for censusing Horned Puffins and very little is known about absolute numbers or trends in population sizes.

In species such as the Horned Puffin where counts of nest sites are not possible, counts of birds attending the colony can provide a useful index of population size (e.g. Piatt *et al.* 1990b). For these counts to be used for monitoring population changes, patterns of colony attendance and the variability in numbers attending must be examined to determine the optimum time of day and breeding season for censusing, and the number of counts required to detect change. This chapter describes the results of daily counts of Horned Puffins made throughout the breeding seasons of 1997, 1998 and 1999 on Duck Island, Alaska. The main aim of this study was to examine daily, seasonal and annual variation in colony attendance and the implications of this variation for population censusing.

Methods

Seasonal variation in attendance of Horned Puffins at the colony was recorded in 1997, 1998 and 1999. A total of six all-day observations, covering the incubation and chick-rearing period, were made in order to determine the time of peak diurnal attendance. Observations were made from a marked station overlooking North Cove, with 10 x 42 binoculars. Horned Puffins present in North Cove were counted from 0500 - 2300 at 30-minute intervals. Birds were counted separately on water and land at each half hour. Water counts included all birds on the water, inside the cove boundaries and within 200 m. from shore; a set buoy was used for reference. Land counts included birds on all north-facing land visible from the observation station.

In addition to all-day observations, daily counts were made from 27 June to 31 August in 1997, from 26 May to 4 September in 1998 and from 23 May to 14 September in 1999. Counts of birds on water and land were made at 15 minute intervals during the evening peak in colony attendance (2030-2145; see results). Up to five counts were made during this period each day, and these were used to calculate mean daily values for the number of birds counted on

water, land and the total (land and water combined). Due to shortening daylight hours, counts towards the end of the season were brought forward to 2015h.

Daily count data was split into two groups, using breeding chronology (incubation and chick rearing). Chick-rearing was defined as starting at the median chick hatch date each year, and continuing until the median fledging date. The mean incubation period for Horned Puffins is 41 days (Petersen 1983), and so the period of incubation was defined as the 41 days prior to the median chick hatch date.

Results

There was high variability in both the diurnal pattern of attendance and the absolute numbers of birds attending the colony on different days (Fig 3:1). Diurnal attendance was more variable during chick-rearing than during incubation (Fig 3:2). Nonetheless, numbers of birds at the colony were generally lowest during the afternoon (1400-1600), with higher numbers in the morning and evening, and a peak in numbers from 2030-2130 (Fig 3:2). There was a strong correlation between the counts of birds on land and water at different times of day (Spearman rank correlation: $r = 0.71$, $n = 37$, $P < 0.01$).

There was marked variation in peak attendance from one day to the next (Fig 3:3), with no indication of any cyclicality in the data (Serial autocorrelations for time intervals of 1-10 days). The data were significantly heterostochastic (Levene's test: $F = 5.02$, $n = 201$, $P < 0.001$), with greater variability during chick-rearing (mean coefficient of variation 0.67) than during incubation (mean CV = 0.44) in all years, and greater variability during incubation in 1998 than in other years (Table 3:1). There were consistently more birds observed on water (Fig 3:3). Counts on water were more representative of the total numbers of birds attending the colony than counts on land, especially during incubation (Fig 3:4).

Five-day running means of the daily total number of birds (water and land combined) were calculated to smooth out daily variability and to examine

the seasonal pattern in colony attendance (Fig 3:5). Data on pre-lay attendance are limited by the duration of seasonal counts, and are confined to 1998 and 1999. Mean attendance in 1998 during the pre-lay period (22 days) was 116 individuals $SD \pm 21$, and mean prelaying attendance in 1999 (23 days) was 127 individuals $SD \pm 14$. Mean attendance was lower during prelaying than incubation (two-way ANOVA on ranked data, Sokal and Rohlf 2000: $H = 58.6$, $df = 1$, $P < 0.001$), but did not differ between years ($H = 3.13$, $df = 1$, $P > 0.05$).

In each year, the highest numbers of birds were present at the colony during the incubation phase of breeding. After the onset of chick rearing, numbers of birds at the colony declined progressively, except for a sharp increase at the end of August 1999 (Fig 3:5). Mean attendance was higher during incubation than during chick-rearing (two-way ANOVA on ranked data: $H = 283.2$, $df = 1$, $P < 0.001$), but did not differ between years (Figure 3:6; $H = 1.3$, $df = 2$, $P > 0.05$).

Table 3:1. Numbers of puffins attending the colony during the incubation and the chick-rearing period in different years.

Incubation	1997	1998	1999	Chick rearing	1997	1998	1999
mean	173.6	183.8	168.6	mean	104.0	99.8	99.8
SD	55.8	110.2	66.1	SD	53.9	74.3	76.2
CV	0.32	0.6	0.39	CV	0.52	0.74	0.76
Min	52	0	38	min	2	0	0
Max	287	402	383	max	243	227	393
n (days)	27	37	35	n (days)	38	27	37

C.V. = Coefficient of variation.

Figure 3.1. Diurnal attendance patterns of Horned Puffins on Duck Island.

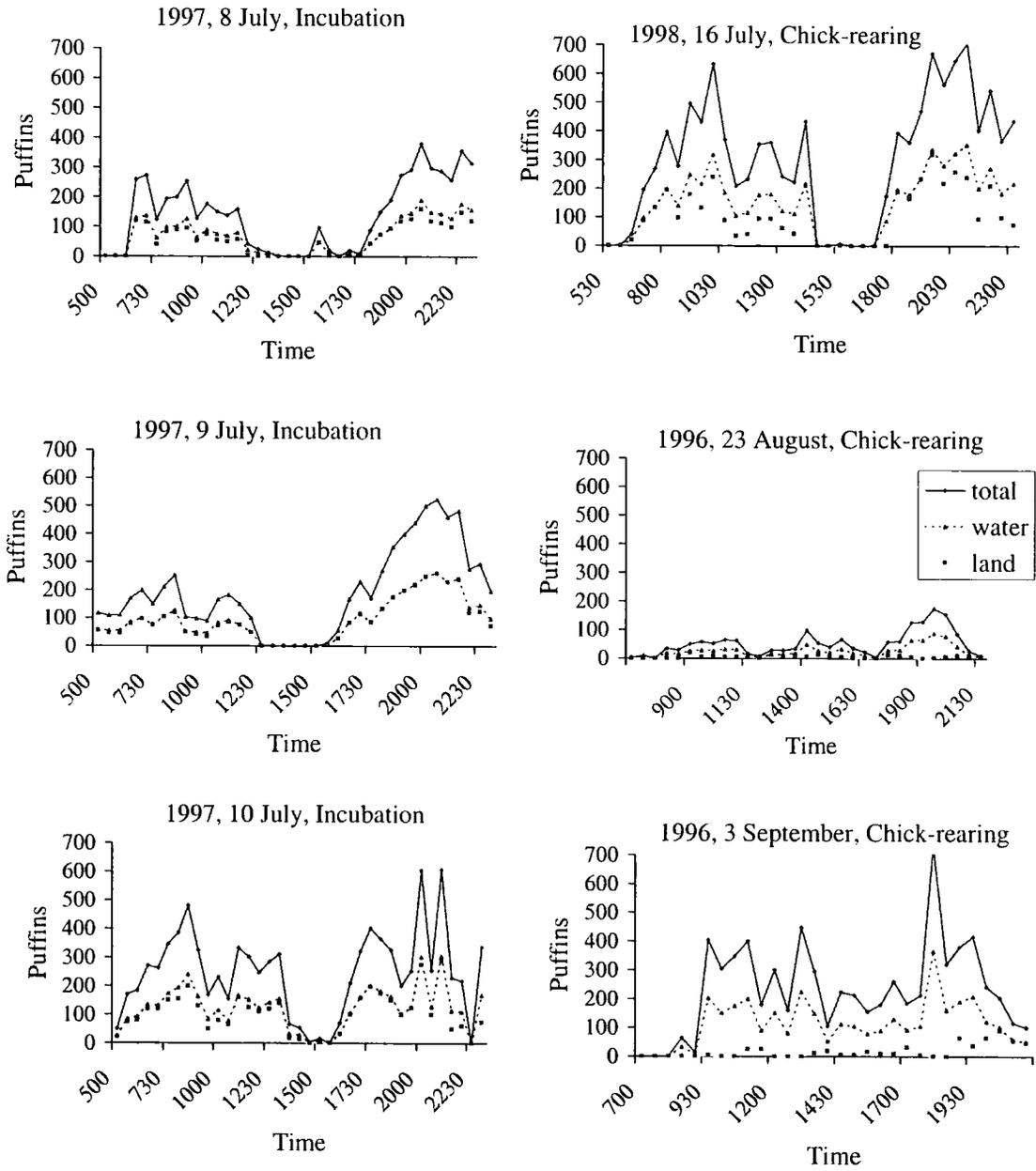


Figure 3:2. Diurnal Attendance of Horned Puffins. Total (water and land combined) numbers of birds attending the colony. Mean \pm 1 SE.

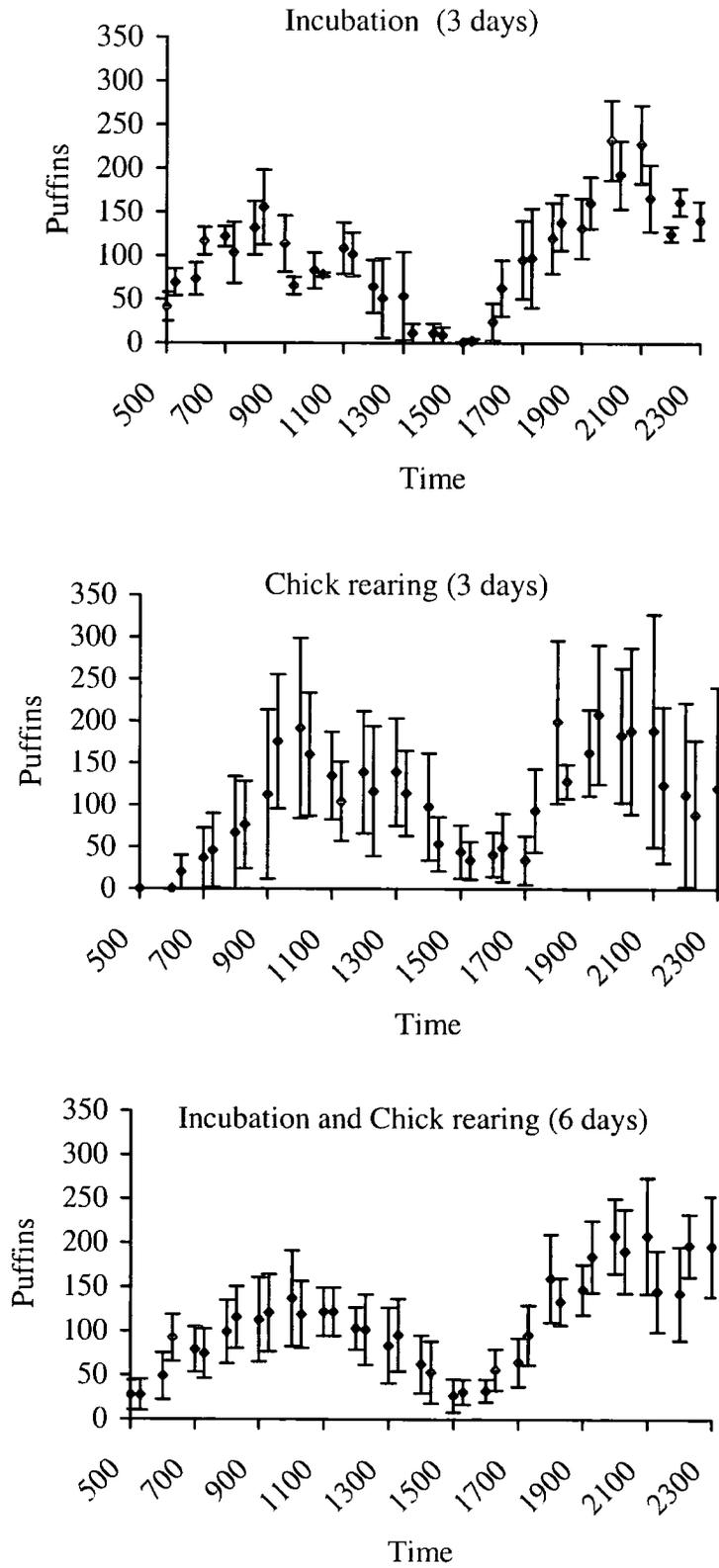


Figure 3.3. The seasonal colony attendance of Horned Puffins on Duck Island in different years. Daily mean water (W), land (L) and total (T) counts presented. Years aligned by date.

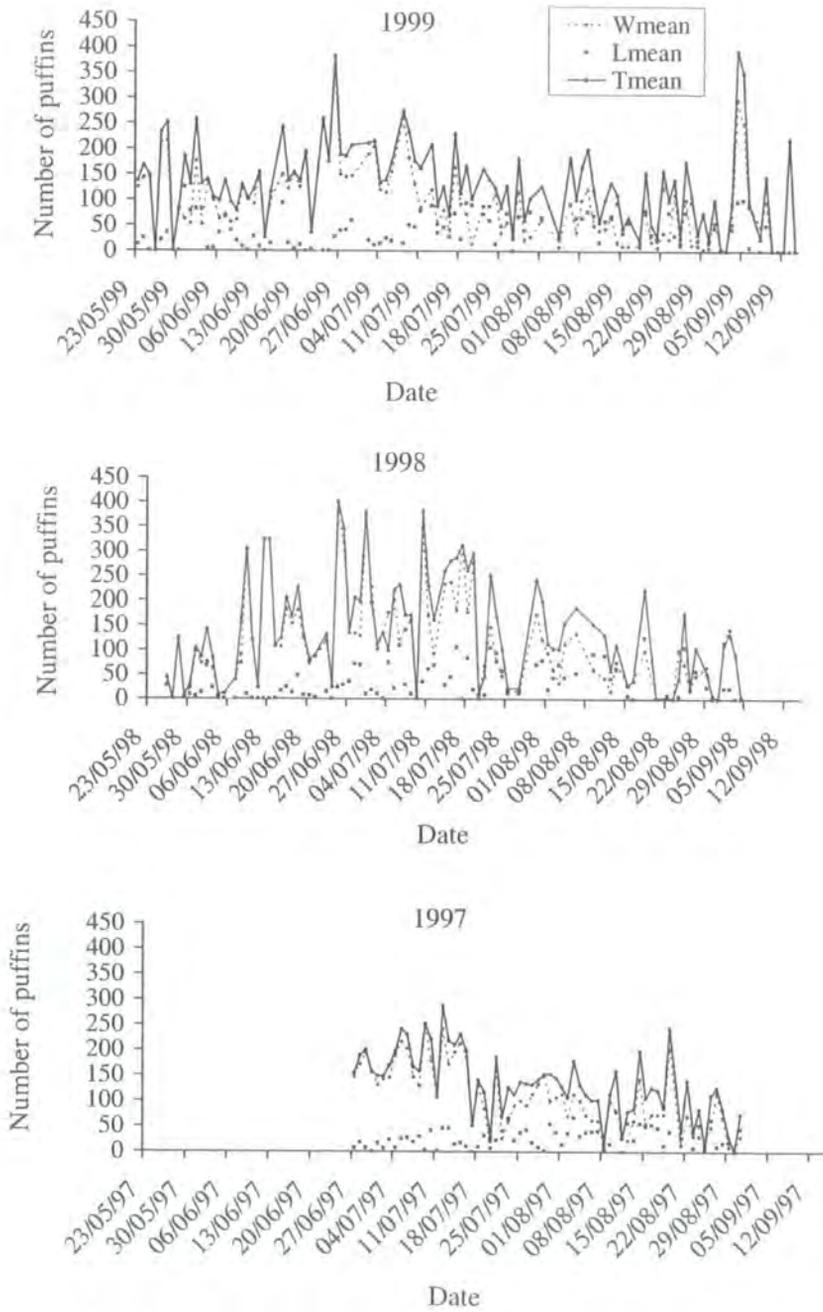


Figure 3:4. The proportion of birds on land and water in relation to the total number of birds (land and water combined) attending the colony during the incubation and chick rearing period. All years are combined.

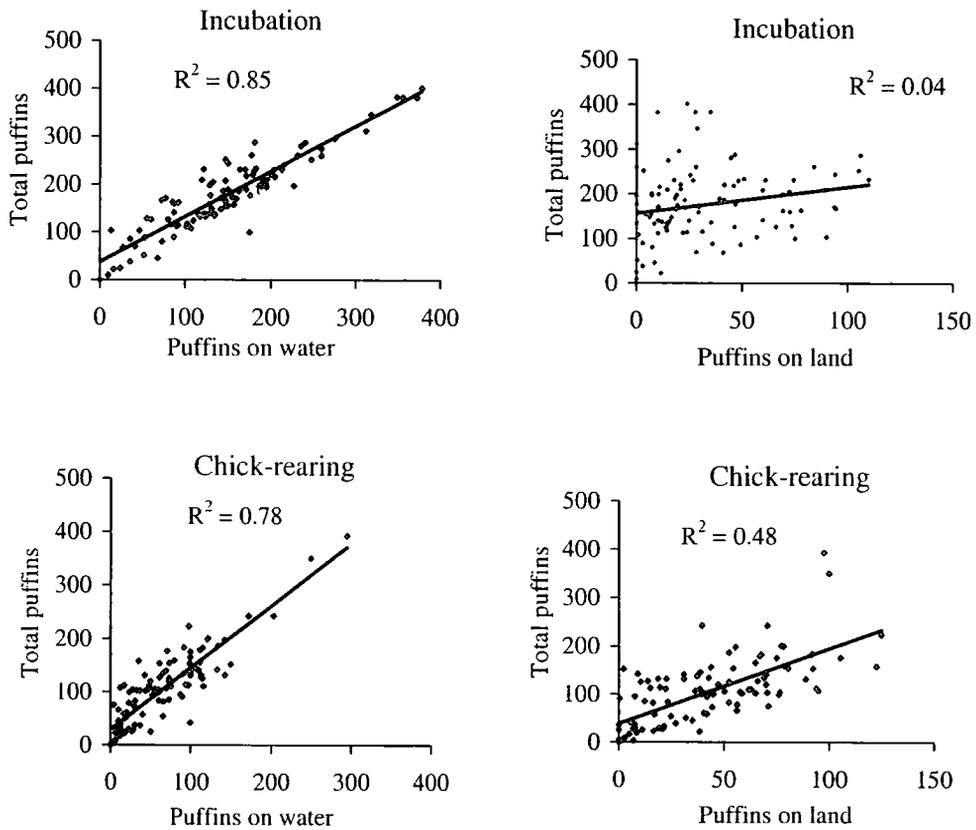


Figure 3:5. Pattern of Horned Puffin seasonal colony attendance in different years. 5-day running means.

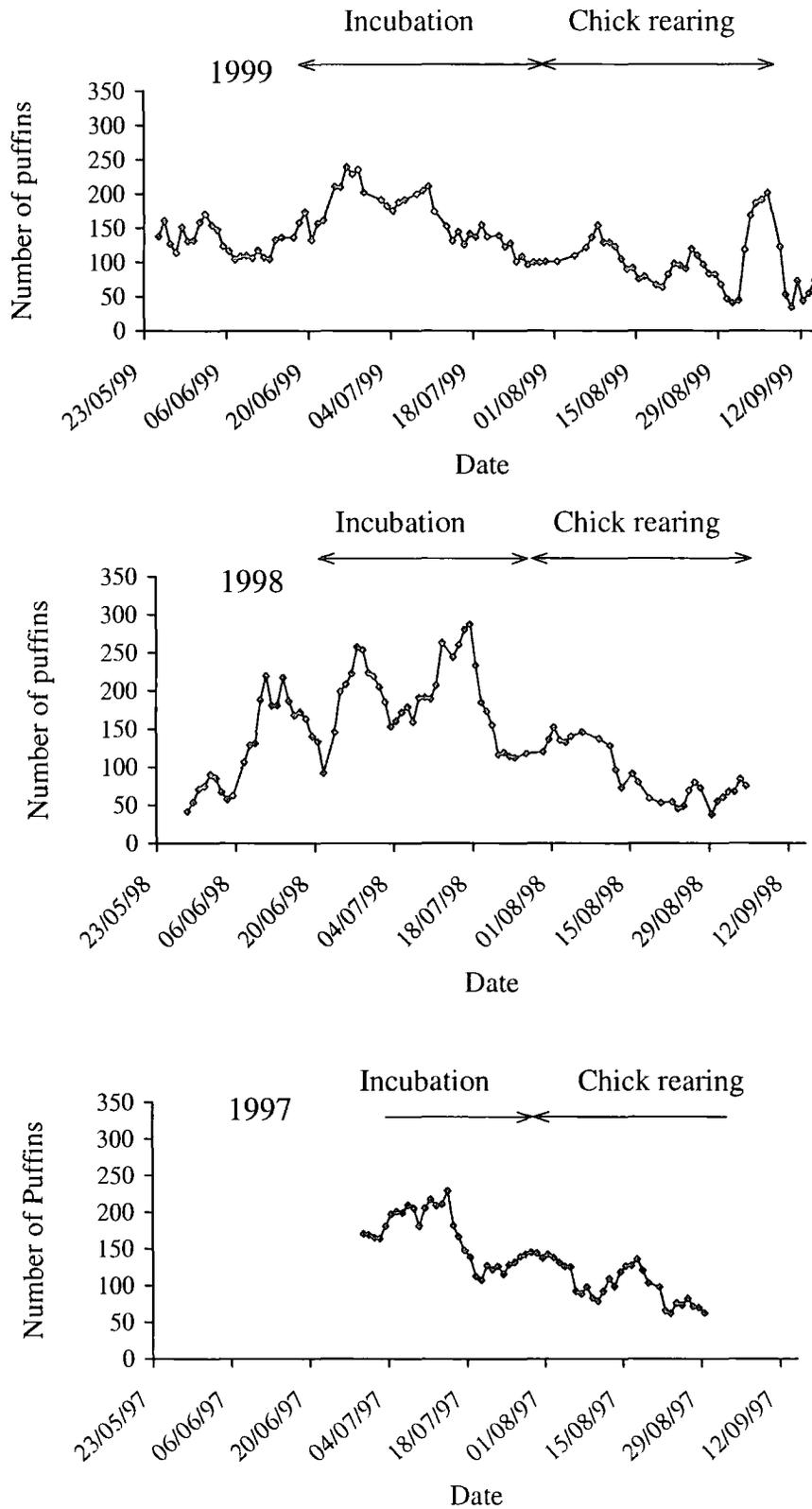
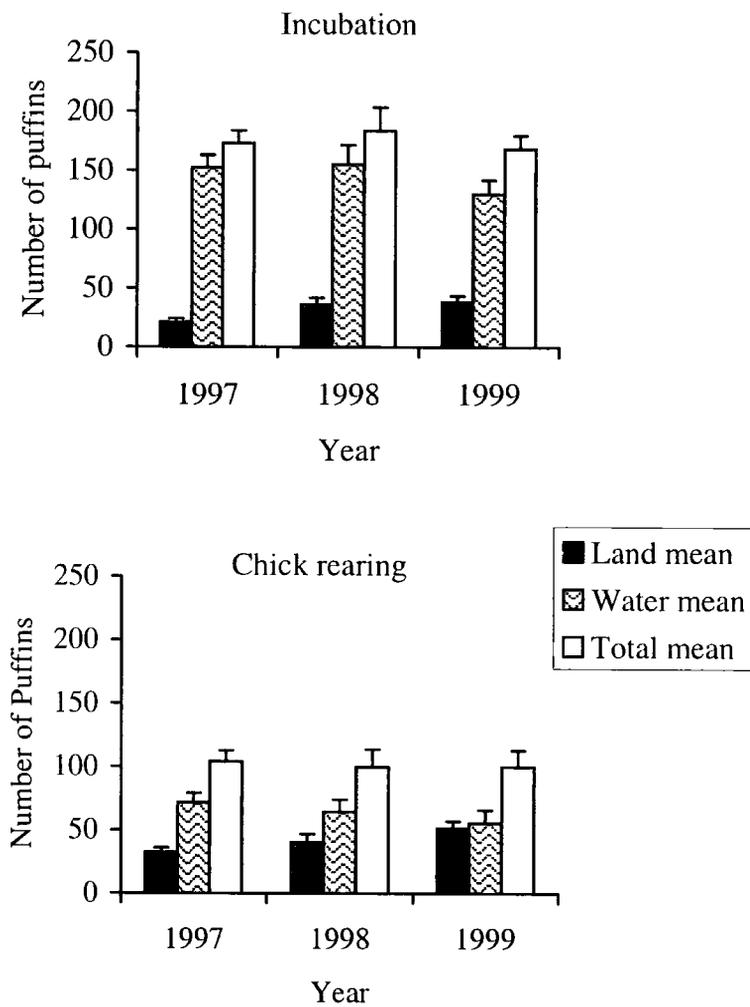


Figure 3:6. Overall mean colony attendance for the duration of incubation and chick rearing in different years. Mean \pm 1 SE.



Discussion

This study examined the seasonal colony attendance of Horned Puffins during 3 consecutive years in order to examine seasonal and annual variability in attendance patterns, and the implications of this variation for population censusing. A key assumption in this approach was that colony population size did not change between the 3 years of the study. Annual adult survival of Horned Puffins is assumed to be high and similar to the Atlantic Puffin, which averages 95% (Ashcroft 1979), and has relatively high colony fidelity (Harris 1984). We therefore assume that the actual population size on Duck Island was relatively stable between the 3 years of this study.

Patterns in colony attendance may be partly determined by food availability, with the distance and density of prey influencing foraging time at sea and therefore time spent at the colony (e.g. Birkhead 1978, Gaston and Nettleship 1982). Numbers attending the colony will be high when food is abundant and foraging time minimal. A few studies (e.g. Hatch and Hatch 1988, Jones 1992) have highlighted the complexity of population count interpretation, discussing the effect that annual variation in food availability and breeding effort and behaviour have on colony attendance. Population censuses should be aimed at the time a) of peak diurnal attendance, b) of least seasonal variability, c) with the maximum presence of breeders, d) with the minimum presence of immatures and failed breeders e) of least sensitivity to food supply.

In this study, numbers of birds attending the colony showed a general evening peak in attendance between 2030 and 2130. The timing of this peak presumably varies with latitude. Atlantic Puffins also show an evening peak in colony attendance, about 2 hours before sunset (Ashcroft 1979).

Despite the high seasonal and annual variation in colony attendance patterns, overall mean numbers of birds present at the colony during both the incubation and chick-rearing period were very similar between years. Several lines of evidence suggest that food availability for Horned Puffins at Duck Island was low in 1998 (see Chapter 2). Despite this, there was no difference

among years in the overall mean numbers of birds attending the colony during incubation or chick rearing (Fig 3:6), indicating the importance of using mean values to characterize attendance for the purpose of population monitoring.

Pre-laying numbers may provide a good measure of the size of breeding population, with few sub-adults present (Ashcroft 1979). However, numerous counts would be required since daily attendance is very erratic during this period (Fig 3:3), and the duration of pre-lay colony attendance differs considerably between colonies (Moe and Day 1977, Sealy 1973b). Moreover, Moe and Day (1977) reported a difference of two weeks in the mean arrival date at two colonies, despite similar laying dates. Thus data collected during incubation and chick-rearing could be more reliable. Although overall mean counts during both incubation and chick-rearing were similar between years, I suggest that counts conducted during the incubation period may provide the better index of breeding population size for the following reasons:

1. The number of birds attending the colony during incubation was consistently higher than during chick rearing in all 3 years, and the variation in daily counts was lower during the incubation period. (Table 3:1; mean CV = 0.44 during incubation, 0.67 during chick rearing).
2. Young, prospecting individuals have been documented to arrive later in the season than breeders in a number of seabird species (eg. Hatch 1989, Brooke, 1990, Warham 1990). Although there are no data on the return dates of Horned Puffin sub-adults, I assume that the pattern is similar to the Atlantic Puffin, with younger birds arriving later than breeders (Ashcroft 1979). Non-breeding Atlantic Puffin four-year olds return to the colony during the incubation stage, three-year olds arrive about a month later during chick-rearing, and two-year olds arrive even later towards the end of the breeding season (Davidson 1994). Counts during incubation should therefore be more focused on the breeding population, whereas counts during chick rearing may include a high and varying proportion of sub-adults and non-breeders.

3. Local feeding conditions are known to influence time spent at the colony (eg. Gaston and Nettleship 1982). Although there are costs associated with egg formation and incubation (Monaghan and Nager 1997), parental time budgets should be especially sensitive to local food availability during chick rearing, due to the added foraging effort required for chick provisioning. Foraging behaviour during incubation should be less constrained by local feeding conditions, and consequently less sensitive to annual variation in food availability.

In this study, counts on water were more representative of the total number of birds attending the colony, especially during incubation, and I therefore suggest that counts should include numbers on water. Evening counts during incubation may be used to give an indication of the whole population size for small and accessible colonies, where the coast can be easily circumnavigated and viewed. Where colonies are extensive, or have inaccessible stretches of breeding habitat or coastline, sample plots can be established to monitor trends in population size.

The extent of daily variation in numbers attending the colony differed considerably between years, making it hard to suggest the minimum number of days needed to accurately characterize attendance. For example, many more counts would have been needed in 1998 to give an accurate measure of the mean number of birds attending during incubation. Data from this study suggest that the overall mean numbers of birds attending the colony during incubation may provide a reasonably accurate index of population size, thus data would ideally need to be collected for the whole incubation period.

A detailed study on a banded population is needed to determine the age of first breeding and colony return and the presence of failed and non-breeding Horned Puffins at a colony. Daily and seasonal variation in the colony attendance of Common Guillemots (*Uria aalge*) is largely due to the high fluctuation of non-breeding individuals attending the colony (Gaston and Nettleship 1982, Harris *et al.* 1986). The proportion of non-breeding adults

may vary between colonies, and populations that are increasing in size may contain proportionately more non-breeders than stable populations.

Until more information is available, the interpretation of attendance patterns and the use of counts to assess population changes must be made with caution. For long-lived species with low annual productivity and high adult survival, such as the Horned Puffin, adult survival is one of the most important factors regulating populations (Croxall and Rothery 1991). Thus, effort should be aimed towards establishing banded populations of Horned Puffins for monitoring of adult survival.

CHAPTER FOUR

GENERAL DISCUSSION.

This study has provided a more detailed understanding of the breeding ecology of Horned Puffins (*Fratercula corniculata*) than was previously available, in particular extending our knowledge of chick development patterns, adult food loads, and annual variability in breeding parameters.

Horned Puffins were able to maintain high fledging success over the five years of this study, despite poor local feeding conditions and the almost complete breeding failure of Common Guillemots (*Uria aalge*) at the same colony in 1998. The ability of Horned Puffins to successfully rear a chick over a wide range of food availability reflects a number of adaptations for exploiting a variable and sometimes scarce food supply. These adaptations include flexible chick development and fledging age, and the differential allocation of limited food resources to the growth of different body structures (Chapter Two). Puffins are also able to adjust the number of fish carried per chick meal delivery, unlike the Common Guillemot that only carries one prey item at a time. In addition to these physiological and behavioural adaptations, burrows may provide puffins with an ecological buffer affording protection against adverse weather and avian predators during chick-rearing, allowing parents the added flexibility to forage simultaneously and/or increase foraging trip duration.

The breeding ecology of Horned Puffins showed many similarities with that of the congeneric Atlantic Puffin (*Fratercula arctica*). Both species exhibit a high degree of developmental plasticity, with flexibility in the rate of growth, the allocation of growth to different body structures, and the ages of chicks at fledging (This thesis Chapter Two, Harris 1985, Barrett *et al.* 1987, Øyan and Nilssen 1996). There is also close similarity in the general pattern of mass growth, with chicks of both species entering a short period of mass recession before fledging at ca. 70-80% adult body mass (Chapter Two, Ashcroft 1979, Harris 1985). However, unlike Atlantic Puffins where food shortage resulted in chicks fledging at an older age (e.g. Nettleship 1972, Anker-Nilssen 1987, Harris 1985, Barrett and Rikardsen 1992), Horned Puffin chicks experiencing presumed food shortages in 1998 fledged at younger ages than in other years with more normal food availability.

This difference between species may possibly be explained by the generally larger body size of Horned Puffins. Flight costs associated with transport of food to the nest are proportionately higher in larger alcid species, and so the maximum food load that adults can carry is a smaller proportion of body mass in the larger species (Gaston 1985). This may result in Horned Puffins having less capacity than smaller species such as the Atlantic Puffin to maintain adequate food supply to the chick in conditions of poor food availability at sea. Thus, from the chick's perspective, the tradeoff between growth rate and predation risk at the colony and at sea (Chapter One) may favour early fledging in Horned Puffins and delayed fledging in Atlantic Puffins when food supply is poor. Conversely, from the parents' perspective, the tradeoff between current and future reproduction may favour early termination of chick-rearing in Horned Puffins and prolonged chick-rearing in Atlantic Puffins under such conditions. As a result of their greater body size, Horned Puffins may thus be closer than Atlantic Puffins to the alcid species with an intermediate pattern of development (see Chapter One). However, these data are based on only one year of poor food supply and there are currently no data on the relationships among fledging age, size and post-fledging survival in Horned Puffins. Moreover, there is some overlap in body size between the largest bodied populations of Atlantic Puffin and the smallest bodied populations of Horned Puffins (Bédard 1985, Piatt and Kitaysky 2001), and there is little difference in the relative sizes of food loads carried by both puffin species (see below). Thus, more information is needed before any firm conclusions can be drawn.

Chapter Three presented data on the variation in colony attendance of Horned Puffins on Duck Island. In addition to providing essential information needed for effective population censusing, colony attendance patterns are of general ecological interest, often indicating important features of a species' social system and annual breeding cycle (Hatch 1989). There has been much interest in the highly variable colony attendance observed in many species of seabirds, with studies examining the influence of weather variables, tidal cycles, food availability, and social behaviour such as defense or acquisition of

breeding sites and partners (e.g. Ashcroft 1976, Slater 1976, Gaston and Nettleship 1982, Hatch and Hatch 1988, Hatch 1989, Jones *et al.* 1989, Piatt *et al.* 1990). Such studies have indicated that in some cases the patterns in colony attendance may be influenced by food availability, with the distance and density of prey influencing foraging time at sea and therefore time spent at the colony (e.g. Birkhead 1978, Gaston and Nettleship 1982).

The decrease in numbers of Horned Puffins attending Duck Island after the start of chick rearing (Chapter Three) may be explained to some extent by the increased foraging effort required by parents to provide food for chick provisioning. However, Horned Puffins on the Semidi Islands (Hatch 1978 in Petersen 1983) and Atlantic Puffins on Skomer Island, Wales, (Ashcroft 1976, 1979; Davidsen 1994) showed no such decrease. This difference may reflect a greater impact of increased nutritional requirements post-hatching on Horned Puffin adult time-activity budgets at Duck Island, where food availability is generally low (This thesis Chapter One, USGS and USFWS 2001).

There was a progressive decrease in the numbers of Horned Puffins attending Duck Island from the start to the end of chick-rearing, perhaps reflecting the increasing nutritional requirements of growing chicks. In contrast, the average number of Atlantic Puffins on Skomer Island increased throughout chick rearing, reaching a peak towards the end of the breeding season. This pattern was partly explained by the successive arrival of younger non-breeding birds as the season progressed (Ashcroft 1976, 1979, Davidsen 1994). The pattern at Duck Island could thus indicate a relatively small proportion of subadults at the colony. Foraging efficiency increases with age in seabirds (Burger 1980, Greig *et al.* 1983), and so low food availability would be expected to have a marked effect on young pre-breeders. For instance, a study of colony attendance by prospecting pre-breeding Brunnich's Guillemots (*Uria lomvia*) indicated that older birds with higher feeding efficiency were able to spend more time at the colony than younger birds (Gaston and Nettleship 1982). The seasonal decline in numbers of Horned Puffins attending Duck Island may therefore be partially explained by an inability of young prebreeding birds to spend much time at the colony. However, there are

currently no individually marked birds of known age with which to test this hypothesis.

There has been much interest in the selective pressures favouring the evolution of different chick development patterns in the Alcidae, and it has been suggested that the intermediate pattern of development is the result of constraints on life history evolution imposed by body size (Chapter One). However, despite a general association between pattern of chick development and adult size there is an overlap in body size between the smallest of the intermediate species, the Razorbill (*Alca torda*), and the larger semi-precocial puffins (Houston *et al.* 1996). For example, whereas the body mass of Razorbills on Skokholm, Wales, ranged from 530–720g (Houston *et al.* 1996), the Tufted Puffin (*Fratercula cirrhata*) weighs 763 ± 70 g ($n=263$) in the Alaska Peninsula (J. Piatt unpublished) and Horned Puffin body mass varies from 487g in the Western Aleutians to 633g in the Chuchi Sea (Chapter Two, Piatt and Kitaysky 2001).

Moreover, Birkhead and Harris (1985) suggested that the large size of Common Guillemots and Razorbills limits chick meal size, with both species able to carry only 1-2% of their body mass (Chapter One). Yet, Atlantic, Tufted and Horned Puffins deliver meal loads with small relative masses comparable to those of the intermediate species. For example, Atlantic Puffins on the Isle of May, Scotland, delivered loads averaging just over 2% of adult body mass (mean load mass = 9.4g, average breeding adult mass = 405g (Harris 1984, 1985)). Similarly, an average 16g chick-meal for Horned Puffins at Duck Island (Chapter Two) represents 3% adult body mass, and Tufted Puffins deliver food loads representing 1-2% of adult body mass (average load mass = 14.9g from the Barren Islands, adult body mass = 763g from the Alaska Peninsula (Amaral 1977, Gaston and Jones 1998)).

These data suggest that although the small semi-precocial species may carry relatively large chick meals (e.g. 7% of adult body mass in Crested Auklets (*Aethis cristatella*) (Birkhead and Harris 1985)), differences in relative meal size cannot fully explain the difference in chick developmental strategy exhibited between the intermediate species and the semi-precocial puffins.

Guillemots may have high energy demands at the colony associated with brooding and the often antagonistic interactions with close-neighbouring conspecifics, and neither guillemot or Razorbill leave their chicks unattended. Guillemot chicks may also face higher energetic costs than the chicks of burrow nesting species due to their higher mobility, social interaction and exposure to the elements. Chick development pattern may thus be influenced as much by nest-site characteristics as by body size.

Whilst this study has provided much needed information on the breeding ecology of Horned Puffins, further data are now required on adult survival and longevity, the relationships between chick fledging age, condition and post-fledging survival, chick feeding frequency and adult foraging trip duration, measures of parental effort and the behaviour of subadults and non-breeding birds. Collection of many of these data would be greatly facilitated by the establishment of a sample of individually marked birds. Study at colonies with breeding Tufted Puffins, Rhinoceros Auklets, and Horned Puffins would also allow inter-specific comparison of the way closely related species respond to the same environmental conditions. Integration of population dynamics and breeding ecology would allow greater understanding of the life history of Horned Puffins, and would advance inter-specific comparisons of life history strategies within the Alcidae.

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