

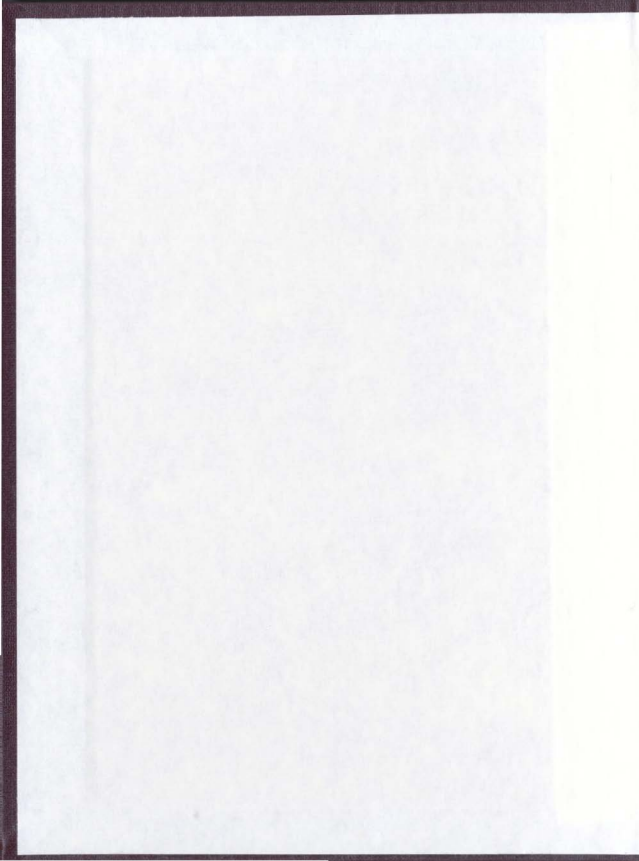
ECTOPARASITES OF AUKS (ALCIDAE) AT THE
GANNET ISLANDS, LABRADOR: DIVERSITY,
ECOLOGY AND HOST-PARASITE INTERACTIONS

CENTRE FOR NEWFOUNDLAND STUDIES

**TOTAL OF 10 PAGES ONLY
MAY BE XEROXED**

(Without Author's Permission)

SABIR BIN MUZAFFAR





National Library
of Canada

Acquisitions and
Bibliographic Services

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque nationale
du Canada

Acquisitions et
services bibliographiques

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence

Our file Notre référence

The author has granted a non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of this thesis in microform, paper or electronic formats.

The author retains ownership of the copyright in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

L'auteur a accordé une licence non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de cette thèse sous la forme de microfiche/film, de reproduction sur papier ou sur format électronique.

L'auteur conserve la propriété du droit d'auteur qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

0-612-55531-3

Canada

**ECTOPARASITES OF AUKS (ALCIDAE) AT THE GANNET
ISLANDS, LABRADOR: DIVERSITY, ECOLOGY AND HOST-
PARASITE INTERACTIONS**

by

©Sabir Bin Muzaffar

A thesis submitted to the School of Graduate Studies in partial
fulfillment of the requirements for the degree of
Master of Science

Department of Biology,
Faculty of Science,
Memorial University of Newfoundland
Atlantic Cooperative Wildlife Ecology Research Network

August, 2000

St. John's

Newfoundland

Table of Contents

List of Tables	iv
List of Figures.....	vi
List of Plates.....	vii
Acknowledgments	viii
 Chapter 1 General Introduction.....	 1
1.1 Rationale.....	1
1.2 Quantification of Patterns.....	2
1.3 Hosts.....	3
1.4 Thesis Layout.....	4
 Chapter 2 The diversity of ectoparasites of four auk species (Alcidae) at the Gannet Islands, Labrador.....	 5
Abstract.....	5
2.1 Introduction	7
2.2 Materials and Methods	12
2.3 Results	14
2.4 Discussion.....	15
2.4.1 Sampling technique.....	15
2.4.2 Acari.....	16
2.4.3 Mallophaga.....	20
2.4.4 Diptera.....	21
2.4.5 Siphonaptera.....	21
2.4.6 Coleoptera.....	22
2.4.7 Collembola.....	22
2.4.8 Thysanoptera	23

2.5 Summary	23
-------------------	----

Chapter 3 Does host coloniality influence the population structure of ectoparasites of four auk species (Alcidae)?.....	33
Abstract.....	33
3.1 Introduction	35
3.2 Quantification and Statistical Analyses.....	39
3.3 Results	41
3.3.1 Aggregation.....	41
3.3.2 Prevalence And Relative Abundance.....	42
3.4 Discussion.....	43
3.4.1 Aggregation.....	43
3.4.2 Prevalence and relative abundance	45
3.5 Conclusion	49

Chapter 4 Species-richness and nestedness in ectoparasite communities of four auks (Alcidae) -- evidence of structuring forces?	61
Abstract.....	61
4.1 Introduction	62
4.2 Quantification and Statistical Analyses.....	67
4.3 Results	69
4.3.1 Richness.....	69
4.3.2 Nestedness.....	69
4.5 Discussion.....	69
4.6 Conclusion	74

Chapter 5 General Discussion	81
5.1 Diversity and ectoparasite community structure.....	81
5.2 Future Research.....	82
Appendix I Classification.....	84
References.....	86

List of Tables

Table 2.1.1 Breeding pairs of the four auk species at the Gannet Islands, Labrador (Data from Lock et al., 1994).....	24
Table 2.2.1 Sampling technique and the number of auk species sampled at the Gannet Islands, Labrador, 1998.....	25
Table 2.3.1 Ectoparasites collected from the four species of auks.....	26
Table 2.3.2 Ectoparasites collected from the three species of auk chicks	27
Table 3.3.1 Variance-to-mean (s^2/\bar{x}) ratios for selected infrapopulations for the four host species.....	50
Table 3.3.2 Summary of the values of the k parameter calculated for all ectoparasite species collected from the four auks. χ^2 and P values indicate relative discrepancies between observed frequency distributions and expected negative binomial distributions based on the estimated k values	51
Table 3.3.3 k values of eight ectoparasite taxa. Values between zero and eight represent aggregated distributions. Since many values differed significantly from the expected k value of a binomial distribution, the k parameter was rendered unsuitable for analyses.....	52
Table 3.3.4 s^2/\bar{x} ratios for selected infrapopulations for the chicks of three host species. Values significantly greater than zero indicate aggregated distribution	53
Table 3.3.5 Variation in the values of Green's Index of aggregation selected ectoparasitic taxa on the four host species. Negative values indicate a uniform distribution; values close to zero indicate a poisson distribution and values greater than zero but below one indicate an aggregated distribution.....	54
Table 3.3.6 Prevalence (P; percentage of birds that are infested) and relative abundance (R.A.; mean number of ectoparasites /bird) of selected infrapopulations on the four host species.....	55
Table 3.3.7 Prevalence (%) of two louse genera and a feather mite genus. Values in parentheses indicate standard errors of the mean, estimated by bootstrap methods	56

Table 3.3.8 Relative abundance (Numbers/bird) of two louse genera and a feather mite genus. Values in parentheses indicate standard errors of the mean, estimated by bootstrap methods	57
Table 4.3.1 Mean species richness of the ectoparasite infracommunities from the four host species. Standard errors of the mean were estimated using bootstrap methods	76
Table 4.3.2 Relative nestedness indices (C) of the four Alcid species, and associated Cochran's Q and probability values	77
Table 4.3.3 Comparison between the relative nestedness (C) across the four auk species. ** indicates $P < 0.005$. z_{ab} refers to differences between the z-scores based on the relative nestedness (C) of hosts 'a' and 'b'	78

List of Figures

Figure 2.2.1. Map of the Gannet Islands, Labrador	28
Figure 2.2.2 The delouser used for the removal of ectoparasites of auks	29
Figure 3.1.1 Densities of individuals (numbers/m ²) at nesting sites recorded for the four auk species. Each bar shows the maximum, mean and minimum density of an auk species. ATPU=Atlantic Puffin; RAZO=Razorbill; TBMU=Thick-billed Murre and COMU= Common Murre (Data derived from Cramp et al., 1985).....	58
Figure 3.3.1 Frequency distribution of ectoparasites on adult Common Murres (circles) in relation to the frequency distribution predicted by the negative binomial model (line). (line).....	59
Figure 3.3.2 The hypothetical link between transmission of lice and feather mites and seabird host aggregation	60
Figure 4.1.1 Two hypothetical sets of infracommunities illustrating nestedness. Each row represents an infracommunity whereas the columns show the species (A-B) found in the various infracommunities (denoted by asterisks) a) shows species depauperate communities as perfectly nested subsets of species rich communities. b) shows a random pattern and species depauperate communities are not nested subsets of richer infracommunities. The average infracommunity richness and the average prevalence of each species are the same in both the examples. (Adapted from Poulin, 1998).....	79
Figure 4.3.1 Relationship between infracommunity richness and mass in Thick-billed Murres ($r^2= 0.05$; $P= 0.32$).	80

List of Plates

Plate 2.1 Louse genera collected from the four auks - a) <i>Quadriceps</i> (nymph); b) <i>Quadriceps</i> (male); c) <i>Quadriceps</i> (female); d) <i>Austromenopon</i> (male); e) <i>Austromenopon</i> (female); and f) <i>Saemundssonina</i> (male)	30
Plate 2.2 Feather mites of the genus <i>Alloptes</i> collected from the four auks - a) nymph, b) female and c) male.	31
Plate 2.3 Unclassified oribatid mite nymphs collected from the four auks.....	32

Acknowledgments

I would like to express my sincere gratitude to my supervisor, Dr. Ian Jones, for taking me on as a graduate student, providing relevant leads on parasite research and facilitating the means of carrying out this study. I also thank Dr. Murray Colbo for providing laboratory space and microscopes over the entire duration of the project and for providing helpful advice and comments on the thesis; Dr. Ted Miller for providing valuable comments on the thesis; Dr. David Larson for providing assistance in identifying some of the specimens and providing important references on identification.

I thank Memorial University of Newfoundland and the Atlantic Cooperative Wildlife Ecology Research Network for giving me the opportunity and the funding to undertake this study.

I am grateful to several people in the Department of Biology: Bill Brown for providing all the chemicals that I requested on short notice; Roy Ficken for assistance with the photography of specimens and the preparation of slides; Lisa Lee for helping with specimen photography at the electron-microscopy laboratory; and Martin Renner for comments on Randomization techniques and for translating German documents.

I am indebted to the field crew at the Gannet Islands for years 1998 and 1999. Brian Veitch, for capturing almost all the birds in the study; Mark Button and Johanne Dussureault for maneuvering turbulent and treacherous waters in the Zodiac and for assisting with the delightful task of "grubbing"; Peter Adams, for being the Gannet Islands comedian; Shawna Baillie, Rachel Bryant, Gail Fraser and SherryLynn Rowe for field-assistance; Drs. Richard Elliot and Greg Robertson for field assistance and valuable comments on the project. I also thank Randy Cahill for logistical support and Tricia Kinsey for her endurance.

Finally, I thank my family for constant encouragement and support on all aspects of my life.

Chapter 1

General Introduction

1.1 Rationale

Host-parasite interactions are diverse and widespread (Rothschild and Clay, 1957) but relatively little is known on how these interactions operate (Loye and Zuk, 1991; Clayton and Moore, 1997). Selected avian models have been investigated to illustrate host-parasite interactions and parasites have been shown to affect everything from behaviour and ecology to physiology and reproduction of their avian hosts (Clayton and Moore, 1997). Seabirds form a relatively small avian group (less than 2% of extant bird species; Gaston and Jones, 1998) with a wide range of parasites living in association with them. Although an enormous body of literature has been amassed on seabird life-cycles, behaviour, ecology and physiology (e.g., see review of the family Alcidae; Gaston and Jones, 1998), very few studies document the intricacies of host-parasite interactions in this avian group. A clear understanding of the community-level interactions of parasites is necessary in order to elucidate an individual host-parasite relationship (Holmes and Price, 1986). The elucidation of parasite communities also provides a better understanding of the ecology and distribution of their seabird hosts (Hoberg, 1986).

Ectoparasites of birds are very diverse but they generally represent two major groups: the insects (Insecta) and the ticks and mites (Acari) (Dogiel, 1964). In seabirds, ectoparasites have been shown to cause everything from minor irritation and disease transmission to nest-desertion and death of both adults and chicks (Eveleigh, 1974; Eveleigh and Threlfall, 1975; Eveleigh and Threlfall, 1976; Fitzpatrick and Threlfall, 1977; Choe and Kim, 1987; Morbey, 1996; Wanless et al., 1997; Duffy, 1983; Duffy, 1991; Gautheir-Clerc et al., 1998; Bergstrom et al., 1999). Nevertheless, large numbers of

ectoparasites continue to live with their hosts in many cases, without apparent harm to their seabird hosts (Choe and Kim, 1987). I undertook my study to provide a better understanding of ectoparasite community structure using four auks and their ectoparasites as a model, and to attempt to derive some general principles that might be responsible for the persistence of ectoparasites on their seabird hosts.

1.2 Quantification of Patterns

Host-parasite systems can be studied by measuring and analyzing aggregation patterns, which are characteristic of the vast majority of host-parasite systems (Taylor, 1961; Crofton, 1971; Anderson et al., 1982; Poulin, 1998). Aggregation refers to the non-random distribution of parasites within a host population, in which small numbers of hosts harbour many parasites while the majority of hosts harbour few or no parasites. The ubiquity of aggregation patterns implies that similar processes in different biological systems may be responsible for generating these patterns (Poulin, 1998). One such process in nature is group living which has been shown to decrease parasitic aggregation patterns by increasing contact transmission of ectoparasites (Rozsa et al., 1996).

Other quantitative measures, such as prevalence (the percentage of hosts in a given population that are infested by a parasite species), mean intensity (the mean number of parasites per infested host within a host population) and relative abundance (the mean number of parasites per host in a given population), can also provide information on the nature of the parasite communities (Margolis et al., 1982; Bush et al., 1997). Clear generalizations on how these variables change in parasitic communities are not available. Group-living seems to increase contact transmission, which in turn changes measures of parasite abundance (Poulin, 1991; Rozsa et al., 1996; Rekasi et al., 1997). However, some studies indicate that group-living might not necessarily affect parasitic abundance and factors such as host migration may influence distribution patterns (Poiani, 1992).

The analysis of species richness (the total number of species in an assemblage of species) has been shown to serve as an important means of assessing the structure of parasitic communities (Simberloff and Moore, 1997; Poulin, 1996, 1997, 1998). Species-richness alone, however, is insufficient in providing a complete picture of the community and analyses of patterns in richness and abundance is often useful. More recently, a pattern referred to as nestedness or nested subset structure has been utilized extensively in order to investigate community structure (Patterson and Atmar, 1986; Cook, 1995; Worthen, 1996; Poulin, 1998). A community or assemblage forming structured, non-random subsets of more species-rich communities is said to be nested (Patterson and Atmar, 1986). The nested subset pattern predicts that species-poor or depauperate communities would form distinct subsets of progressively richer communities of ectoparasites. Nestedness in ectoparasites of birds has never been investigated before although the potential importance of nestedness is recognized (Worthen, 1996).

1.3 Hosts

Many seabird species (e.g. the auks, family Alcidae) breed in large colonies during summer, making them ideal candidates for ecological studies (Gaston and Jones, 1998). Such seabird colonies are also ideal habitat for ectoparasites searching for a new host and many ectoparasitic species have become highly specialized in synchronizing their life-cycles with their hosts' (Eveleigh and Threlfall, 1975). Most of the 23 species of auks breed on off-shore islands, some being extremely remote (Gaston and Jones, 1998). Island colonies keep individual auks relatively safe from terrestrial predators as well as close to their marine food sources. Ground-dwelling ectoparasites, such as ticks, take advantage of this seasonal abundance of hosts by climbing on hosts to get blood meals (Eveleigh and Threlfall, 1975). The ectoparasites that live on the feathers (e.g. feather lice) also take this opportunity to search for and colonize suitable hosts to breed on (Eveleigh and Threlfall,

1976). How do such communities form and what factors shape them? The study of ectoparasitic communities in relation to the aggregation of auks could reveal patterns of ecological importance that help in the maintenance of these complex associations.

1.4 Thesis Layout

My thesis is presented in five chapters. The present chapter has summarized the rationale and background encompassing the objectives of the study and introduces the major group to which the host species in my study belong. Chapters 2, 3 and 4 are presented in the format of papers to be sent for publication in international, peer-reviewed, scientific journals. The quantifications and statistical analyses are different in each chapter and references are made to other chapters wherever appropriate. Chapter 5 summarizes the findings of Chapters 2, 3 and 4 in a more generalized form with suggestions for possible future research.

Chapter 2

The diversity of ectoparasites of four auks (Alcidae) at the Gannet Islands, Labrador

Abstract

Ectoparasites were collected using an improved dust-ruffling technique from 108 adult auks representing four species: Atlantic Puffin, *Fratercula arctica*; Razorbill, *Alca torda*; Thick-billed Murre, *Uria lomvia*; and Common Murre, *Uria aalge*. The technique involved applying a pyrethrin-based pesticide on captive hosts inside a specially designed bucket. The technique was harmless to the hosts and provided quantitative estimates of ectoparasites. A total of 28 different taxa were recorded belonging to the class Insecta (insects) and the subclass Acari (ticks and mites). Most taxa previously recorded from these hosts were represented. The three louse (Mallophaga) genera recorded were *Austromenopon*, *Quadraceps* and *Saemundssonina*. *Ixodes uriae* ticks (Parasitiformes) and feather mites of the genus *Alloptes* (Acariformes) were also recorded from all the auk host species. Phoretic organisms - oribatid mites (Acariformes), springtails (Collembola) and thrips (Thysanoptera) were collected. Feather mites of the genus *Alloptes* were numerically the most abundant ectoparasitic group, with numbers reaching as high as 538 individuals on one Atlantic Puffin. Razorbills and Puffins generally harboured the most feather mites, with means of 35.7 and 39.3 individuals/bird respectively. All other ectoparasite groups occurred in much lower numbers, no single group approaching means higher than 10/bird.

Chicks of Atlantic Puffins, Razorbills and Common Murres (N=68) were also sampled for ectoparasites. Most groups represented in the adults were also found on the

chicks. Feather mites were extremely rare and were collected from a few chicks only. The three louse genera and the Oribatida occurred in large numbers on the chicks. The most dominant ectoparasitic group on Common Murre chicks was the lice. Oribatid mites represented the most dominant group on Atlantic Puffin and Razorbill chicks. The presence of the different taxa on the auks and their chicks are compared to existing literature and potential relationships of uncertain and phoretic taxa are discussed.

2.1 Introduction

Diversity and the lack of data

Parasites form a very important part of the lives of their hosts (Rothschild and Clay, 1957). Nevertheless, relative to their enormous diversity, very little information is available on the intricate life cycles of the multitude of parasites that live in or on wild animals (Loye and Zuk, 1991; Clayton and Moore, 1997). What little is known tends to concern conspicuous organisms that are readily captured and isolated from their hosts. Less evident parasitic organisms, whether internal or external, are usually overlooked, and their complex interactions and potential influence on host life cycles are largely ignored.

Seabirds belonging to the family Alcidae are no exception to this general rule. Whereas an enormous body of literature has been amassed on their life cycles, behaviour, ecology and physiology (Gaston and Jones, 1998), few studies have documented the incidence of parasites (Eveleigh, 1974; Eveleigh and Threlfall, 1976; Fitzpatrick and Threlfall, 1977; Choe and Kim, 1987) and the extent to which some of these parasites influence the lives of their seabird hosts (Morbey, 1996; Wanless et al., 1997). Ectoparasites have been shown to cause nest desertion (Duffy, 1983; Duffy, 1991) and chick mortality in a range of seabirds (Gautheir-Clerc et al., 1998; Bergstrom et al., 1999) but, aside from these few studies, data on the response of seabirds to parasitic infestations is virtually non-existent.

Hosts

In this study, I investigated the range of ectoparasites living in association with four colonial seabird species: Atlantic Puffin, *Fratercula arctica*; Razorbill, *Alca torda*; Thick-billed Murre, *Uria lomvia*; and Common Murre, *Uria aalge*. I selected these four related host species (belonging to the family of Auks: Alcidae) because they are locally abundant in

Atlantic Canada and vary considerably in breeding habitat selection and in levels of aggregation at their breeding colonies (Gaston and Jones, 1998). This presented me with the possibility of exploring a wide range of questions relating to host-parasite interactions (See Chapters 3 and 4). These alcid species breed on small islands of the Atlantic coast (Lock et al., 1994; Gaston and Jones, 1998).

Atlantic Puffins nest in burrows (varying in length from 70 to 110 cm) on grassy slopes (Harris, 1984; Gaston and Jones, 1998). Densities of 3 burrows/m² are typical although the average number of occupied burrows range from 0.4-0.6 burrows/ m² (Harris, 1984) Each burrow is occupied by only one pair of Puffins and hence direct contact between individuals (other than mates) in a colony normally occurs outside of the nest. The population estimate for Atlantic Canada is about 350 000 pairs (Nettleship and Evans, 1985; Gaston and Jones, 1998).

Razorbills nest on crevices among boulders and on cliff-edges (Cramp et al., 1985; Gaston and Jones, 1998) and breeding sites are separated by at least 10 cm, but typically by more than 30 cm, with densities reaching 4 pairs/m² (Cramp et al., 1985). In some populations, many nest sites are located 10m or more from the nearest neighbour (Lloyd et al., 1991). Estimates on the world population range from 500 000 - 700 000 pairs (Lloyd et al., 1991) out of which only about 4% breed in Eastern Canada (Gardarsson, 1985). The largest Razorbill colony on the east coast of North America is located in the Gannet Islands, Labrador (Birkhead and Nettleship, 1982).

Thick-billed and particularly Common Murres nest in the densest aggregations of any auk species (Gaston and Nettleship, 1981; Nettleship and Birkhead, 1985; Gaston and Jones, 1998). Thick-billed Murres nest in dense clumps and their nesting sites are typically located on narrow ledges (as little as 10 cm wide) along steep cliffs directly adjacent to the sea (Gaston and Nettleship, 1981; Gaston et al., 1985) with individuals usually remaining

in contact with up to two neighbours from the sides on their nesting sites (Birkhead et al., 1985). Densities vary between 1 and 37 pairs/m² (Cramp et al., 1985).

Common Murres typically nest on broad, flat, rocky outcrops on headlands and offshore islands (Nettleship and Birkhead, 1985; Gaston and Jones, 1998). Birds clump next to one another with about a third of the birds being in physical contact with neighbors (Birkhead et al., 1985), with mean densities of 20 breeding pairs/m², although densities as high as 70 pairs/m² have been recorded (Cramp et al., 1985; Nettleship and Birkhead, 1985). This may perhaps be the densest nesting aggregations of any bird in the world (Nettleship and Birkhead, 1985) with breeding colonies being the largest among all the Atlantic auk species (e.g. 500 000 breeding pairs in Funk Island, Newfoundland; Nettleship and Evans, 1985).

Parasites

Parasitism has been variously defined in the literature (Baer, 1952; Dogiel, 1964; Cheng, 1986; Schmidt and Roberts, 1989) but the original concept defines a relationship in which one organism, the host, is used both as a habitat and for nourishment by a second organism (Dogiel, 1964). This leads to a lot of confusion when dealing with organisms that fall into categories of symbiosis other than parasitism, like *phoresis* (association in which an organism is transported or carried physically by another organism), *commensalism* and *mutualism*. Cheng (1986) suggested that phoresis leads to commensalism through to parasitism and mutualism and that organisms showing transitional phases between two categories reflect evolutionary history. Others regard parasitism as a biological and not a systematic entity (e.g. Dogiel, 1964) and suggest that parasites be treated with the same significance as terrestrial or aquatic animals in their ecosystems. Parasitologists largely agree that morphological, physiological, ecological or

evolutionary characteristics that might distinguish parasites, in general, from non-parasites do not exist (Brooks and McLennan, 1993). The controversy associated with the general definition of a parasite continues and a consensus is yet to be reached (Zelmer, 1998)

In this study, most arthropods living on seabird hosts, whether as temporary or permanent residents, are referred to as parasites or ectoparasites, although some of the taxa recorded may actually represent groups that are commensal or mutualistic. In most cases, whether or not they actually feed on the host or reduce host fitness has not been documented (Eveleigh, 1974). I attempt to differentiate phoretic organisms from the other symbionts because their numbers were generally low and the taxonomic groups to which they belonged generally include widely-occurring, soil-dwelling arthropods.

Sampling technique

Part of the difficulty associated with quantifying ectoparasite communities lies in the shortcomings of the available sampling techniques (Eveleigh and Threlfall, 1974; Choe and Kim, 1987). A variety of techniques have been in use, all of which have their own series of advantages and drawbacks. Removing parasites from the hosts' feathers can be difficult or impossible in some cases. For example, Ixodid ticks secrete cement around their mouth-parts while feeding, which prevents them from being dislodged (Arthur, 1970; Sonenshine, 1991). Mechanical removal might result in the hypostome (mouth-part associated with suction) being retained in the host's skin, causing an intense localized reaction at the site of attachment (Eveleigh, 1974). Wheeler and Threlfall (1986) introduced the application of an anesthetic to the skin surface of birds to remove ectoparasites. However, this method would not dislodge Ixodid ticks if the feeding process had already been initiated (Sonenshine, 1991). Furthermore, these, and a variety of other technique limitations were likely to cause unrepresentative sampling of different

seabird parasite taxa. In my study, I was limited to techniques harmless to the host species because I was working on a Provincial Ecological Reserve where killing birds was prohibited. Dead birds can be useful for documenting ectoparasite fauna and earlier studies have relied on euthanizing wild birds (e.g. Eveleigh and Threlfall, 1976; Fitzpatrick and Threlfall, 1977). However, extremely small nymphal stages of mites are difficult to see, even under a stereoscope, and these are typically under-represented in the samples when using Eveleigh and Threlfall's (1976) method. Choe and Kim (1987) probably used the most accurate technique to collect ectoparasites. They separated whole bird skins, cut them into small pieces and boiled them in Potassium Hydroxide for several hours. This dissolved the feathers and the skin, but left the exoskeletons of the ectoparasites intact allowing enumeration and identification. The invasive nature and the extended time period required for this protocol, made its use unsuitable for my study.

In summary, the objectives of this chapter are:

- 1) to summarize the protocol of my improved seabird ectoparasite sampling technique,
- 2) to provide a review of the ectoparasites living in association with four Atlantic auk species - Atlantic Puffins, Razorbills, Thick-billed Murres and Common Murres, at the Gannet Islands, Labrador.
- 3) to compare the occurrence of each ectoparasite taxon recorded to the existing literature on alcid ectoparasites and
- 4) to investigate the nature of the symbiotic associations of the ectoparasites recorded with their respective hosts (i.e., parasitic, mutualistic, commensal or phoretic).

2.2 Materials and Methods

2.2.1 Study Area

My study was conducted at the Gannet Islands, which consists of a group of small islands about 29 km off the coast of southern Labrador (54°00'N, 56°30'W; Fig. 2.2.1). A cluster of 6 islands are referred to individually as Gannet Clusters 1 through 6 (GC1-6). Five islands (GC1-5) are located within 500m of one another, with GC6, the largest of the cluster located 1.5 km west of the GC1. In addition to the cluster there are Outer Gannet (54°00'N, 56°32'W) lying 5 km to the north of GC2 and two small outlying rocks, called East Gannet Rock and West Gannet Rock, which lie 4 km southeast of the Gannet Clusters.

The Gannet Islands are situated 29 km northeast of Packs Harbor on the south Labrador coast. The islands are low lying, reaching a maximum height of 66 m above sea level. They are composed primarily of metamorphic rock, and are mostly covered by dwarf heath shrub vegetation. Highest seabird densities occur during the summer breeding season on GC1-4 and Outer Gannet. Table 2.1.1 provides a summary of the breeding populations of the four auk species at the Gannet Islands (Lock et al., 1994).

2.2.2 Materials and Methods

Seabird adults and chicks were captured from GC2 and GC4 between July 12 and August 5, 1998. A total of 176 birds belonging to four species were captured by a variety of methods (Table 2.2.1). Most adult Atlantic Puffins, Razorbills, and Common Murres and some Thick-billed Murres were "fleyged" using a large dip net with a circular frame (about 70cm across) swept in the flight path of birds. A noose pole (with a single nylon noose) was used to catch most of the adult Thick-billed Murres from cliff edges. Adult Razorbills were captured using a Noose Carpet (a rectangular galvanized chicken-wire

screen with numerous nylon monofilament nooses attached) set on a rock where Razorbills had been previously seen to loaf.

I also captured chicks of Puffins, Razorbills and Common Murres. Thick-billed Murre chicks were not captured because of the inaccessibility of their nest sites and the danger of losing chicks and field assistants during capture efforts. Puffin chicks were captured by grubbing, which involved reaching into burrows and pulling out chicks by hand. Razorbill chicks were captured from their nesting sites at accessible crevices. A blunt wire hook was used to capture some Razorbill chicks from their crevices. Common Murre chicks were captured from two sites that were relatively sparsely occupied and thus could be approached without causing excessive panic among the breeding adults.

After capture, anatomical measurements were recorded, following which the birds were individually marked using stainless steel US Fish and Wildlife Service bands. Ectoparasites were sampled from adults and chicks using a 'delouser' plastic bucket (height 40 cm, diameter 30 cm; Fig. 2.2.2), specifically designed for this purpose. The delouser was equipped with a wire mesh platform, upon which the host stood, to act as a sieve, and a plastic tupperware container at the bottom to collect ectoparasites that fell from the captive host. Each bird was dust-ruffled (modified from Clayton and Moore, 1997) with a commercial cat flea powder (Brand name: Quick2kill-Hagen) and placed in the delouser (with the porous lid on) for 10 minutes. The flea powder used was a combination of Carbaryl, Pyrethrin and Piperonylbutoxide - which is widely used because it breaks down rapidly in the environment and is generally harmless to vertebrates (Casidia and Quistad, 1995; Clayton and Walther, 1997). Parasites falling off the bird went through the sieve and were collected in the container at the bottom. After the bird was released (or returned to its nesting site or burrow, in the case of chicks), all the contents of the container were placed into a labeled plastic bag and preserved in 70% ethanol. The collected parasites were later sorted under a dissecting microscope in the laboratory, identified and

enumerated. Identifications were based on the following references: Timmermann (1954, 1957, 1963), Clay(1959), Emerson (1972), Balogh (1972), Eveleigh and Threlfall (1974), Krantz (1978), Keirans and Clifford (1978), Marshall (1981), Holland (1984), Emerson and Price (1985), Wheeler and Threlfall (1989), Stehr (1991), Gaud and Atyeo (1996). The sex of the specimens was also determined whenever possible. Large quantities of feces generally left behind in the delouser by the treated subjects made the sorting process in the laboratory time-consuming, mean sorting time being 4 hours per sample.

2.3 Results

A total of 28 different taxa of ectoparasites were found to be living in association with the four species of auks. Some of these taxa were known parasites, while others lived on the host for their entire lives although whether or not they were parasites was uncertain. A considerable proportion of the arthropods collected were soil dwellers and were assumed to be phoretic. In this section I have presented semi-quantitative information on all the ectoparasitic taxa collected.

In general, ectoparasite abundance was less than 25 on most adults and less than 35 on chicks. Tables 2.3.1 and 2.3.2 summarize the total number of each ectoparasitic taxon collected from the four auk species and the chicks of three auk species. *Ixodes uriae* on both adults and chicks were very low in abundance, with only a handful of specimens being collected from all the birds. Feather lice occurred in very low densities on all the alcids (< 5 per host), although their densities were much higher on chicks (usually > 10 per host on Common Murres). The three genera of lice represented in the samples are shown in Plate 2.1. The feather mite genus *Alloptes* occurred in very high densities on adult birds (particularly Atlantic Puffins and Razorbills) with as many as 538 being recorded from one Atlantic Puffin. Feather mites were numerically the most abundant group,

although they rarely occurred on chicks. Plate 2.2 shows the *Alloptes* feather mites. Oribatid mite genera also occurred in relatively higher numbers in both chicks (between ~3 and 11 per host) and adults (between ~2 and 4 per host). Two oribatid nymphs are shown in Plate 2.3. Staphylinid beetles, springtails and thrips were also represented in the samples, also in low numbers, never exceeding 15 specimens per auk species.

2.4 Discussion

2.4.1 Sampling technique

My sampling technique was effective in collecting large numbers of ectoparasites from captive auks, yet it had two apparent shortcomings. Firstly, it almost certainly sampled ectoparasites differentially. The collection of hard ticks (Ixodida), for instance, was not 100% efficient because feeding ticks secrete a cement around the mouth parts which prevents dislodgment. The sampling technique only collected ticks that had not initiated feeding. Generally, adult *Ixodes uriae* were visible because of their large size, although nymphs and larvae were hard or impossible to see (Sonenshine, 1991). All visible adult *Ixodes uriae* were recorded prior to adding the flea-powder, but overall tick-counts (nymphs and larvae) could have been underestimated. The ten-minute time-period was an arbitrarily defined compromise between maximizing ectoparasite sampling and preventing host death due to hyperthermia (over-heating). Leaving birds for longer time periods on cold days (temperatures less than 10°C) could perhaps have increased ectoparasite removal rates, which, in turn, could be used to determine a correction factor for the ten-minute estimates (Poulin, 1991).

In spite of these shortcomings, this technique has several advantages. The procedure is non-lethal and the captive bird calms down soon after being placed in the delouser. The procedure is simple and can easily be replicated. Finally, most ectoparasites

found on auks in other studies using lethal techniques were represented in the samples collected using my technique (e.g. Choe and Kim, 1987). I therefore believe that my technique represents a satisfactory way of sampling ectoparasites from wild birds.

2.4.2 Acari

Hard ticks

In the present study, *Ixodes uriae* (Ixodida: Ixodidae) occurred on GC1 through GC4, but only a few specimens were collected from all the sampled adult birds. A maximum of three *I. uriae* were collected from a single adult Thick-billed Murre. Heavy tick infestations have been recorded from other seabird studies, particularly on chicks (Morbey, 1996; Gauthier-Clerc et al., 1998; Bergstrom et al., 1999), but this was not noted in the current study. The apparently low incidence of ticks on seabird hosts at the Gannet Islands could have resulted from the short duration of time during which they remain attached and feed on the hosts (four to eight days) or because of the seasonality of their infestations, most attacks on hosts being earlier in the season (Eveleigh, 1974; Eveleigh and Threlfall, 1975). Eveleigh and Threlfall (1975) observed very few feeding *I. uriae* late in the season on Gull Island, Newfoundland. The seabirds at the Gannet Islands breed relatively late compared to colonies further south (Nettleship and Birkhead, 1985; Gaston and Jones, 1998). Whether the low tick densities observed were a reflection of seasonality or of a lack of adaptation to colder climes associated with higher latitudes is not certain. Perhaps sampling earlier in the season (as well as later) would have yielded more information on the seasonal variation in the feeding activity of *I. uriae*, at the Gannet Islands.

Ixodes uriae is a widely occurring species known to parasitize over 50 species of seabirds (Eveleigh and Threlfall, 1974; Eveleigh and Threlfall, 1975; Mehl and Traavik,

1983; Danchin, 1992; McCoy et al., 1999; Bergstrom et al., 1999). *Ixodes uriae* is distributed throughout the subarctic and temperate regions of both the hemispheres (Mehl and Traavik, 1983; Olsen et al., 1993). The Common Murre is regarded as the preferred host (Eveleigh and Threlfall, 1974) although all four of the auks are known to be parasitized. *Ixodes uriae* feed on blood of the host through an elaborate, spasmodic suction mechanism after attachment on the host (Sonenshine, 1991). They have been demonstrated to carry *Borrelia burgdorferi* (Olsen et al., 1993; Sonenshine 1991), the spirochete responsible for causing Lyme disease in both mammals and birds (Anderson, et al., 1986). It has been suggested that seabirds play an important role in the maintenance of this spirochete through their association with this Ixodid tick (Olsen et al., 1993). Preliminary studies on seabird colonies in Newfoundland did not provide any evidence to substantiate this idea (Whitney, 1999 pers. comm.). Deer mice (*Peromyscus maniculatus*) have been shown to serve as a reservoir host in the wild (Rand et al., 1993). The Gannet Islands support fairly large deer mouse populations suggesting that they could be adequate reservoirs if an outbreak were to occur. In addition, Kemerovo group Orbiviruses have also been isolated from *I. uriae* (Oprandy et al., 1988), but their ecological and epizootiological significance has not been thoroughly investigated.

Feather mites

The present study produced some interesting data on the feather mite genus *Alloptes* (Astigmata: Allopidae). Mite densities were higher in the Atlantic Puffins and the Razorbills compared to the Thick-billed and Common Murres. The frequency distributions of the feather mites did not follow a negative binomial curve usually characteristic of parasitic arthropods. Their sex ratio was also strongly skewed towards females. Their abundance did not seem to have any effect on the numbers of the other taxa

of ectoparasites present (See Chapter-3). Taxonomic uncertainty in this genus prevented identification to the species level. *Alloptes crassipes* has been recorded from both Razorbills and Puffins by Canestrini and Kramer (1899) whereas Belopokskaya (1952; cited in Eveleigh, 1974) reported specimens of *Alloptes fraterculae* from Puffins. Choe and Kim (1989, 1991) found *Alloptes conurus* on Thick-billed and Common Murres but the species designation was only tentative.

Feather mites are numerically the most abundant group of ectoparasites living on birds (Gaud and Atyeo, 1996). They are known to occur on the surface of feathers, on feather barbs and within the quills. The entire life is spent on the host and accidental removal from the host results in mortality. Feather mites have been given relatively little attention, primarily due to the fact that they are generally considered to be benign to the host, feeding on feather fragments, desquamated skin scales and oily secretions (Krantz, 1978). Fungal spores and diatoms may also form part of their diet (Dubinin, 1951; Krantz, 1978). Large densities of feather mites may cause a depluming behavioral response due to skin irritation in some host species (Gaud and Atyeo, 1996). Heavy infestations are also correlated with a decline in weight and egg production in some hosts. Generally ranging in size from 0.3-0.7 mm, they are not eaten by the host nor do they penetrate the host's skin. Consequently feather mites are not considered to be vectors of disease. The type of relationship between feather mites and their hosts is not well documented, although it is assumed to be a host-parasite association (Fowler and Miller, 1984; Fowler and Williams, 1985; McClure, 1989). One study of the feather mite, *Gabucinia debilitata*, on Red-billed coughts (*Pyrhacorax pyrrhocorax*) suggests a mutualistic rather than a parasitic or commensal relationship (Blanco et al., 1997).

Oribatid mites

In the present study, at least five and possibly seven or more species were collected from all four auks. They occurred in fairly large and even densities, and a simple phoretic association does not fully explain their presence on the birds because of the fact that all the auks dive to depths of 20-200 meters or more for food (Gaston and Jones, 1998). Birds returning from the sea were also seen to carry oribatid mites. Studies on the feeding preference of one species of Oribatida showed that they have a distinct preference for particular types of fungi (Kaneko et al., 1995). It is possible that the oribatid mites might take advantage of this seasonal resource which harbours bacteria (Clayton, 1999; Burt and Ichida, 1999), fungi (Hubalek, 1976; Hubalek, 1978) and feather debris, all of which fall within their dietary requirements. The risk of falling off the host during a dive can potentially be overpowered by its suitability as a food source.

The suborder Oribatida represents a diverse, cosmopolitan group (Balogh, 1972; Krantz, 1978) that feed mainly on bacteria, yeasts, algae, plants, detritus or dead organic matter in the soil (Luxton, 1972). The diversity of forms in this group makes identification relatively easy but has resulted in the proliferation of higher taxonomic designations (Krantz, 1978). Consequently, the classification schemes developed are not very useful in determining relationships at the familial or superfamilial levels. Balogh (1972) provided a classification scheme that included all the Oribatid genera described but his system did not incorporate higher taxa in the form of a standard dichotomous key. Rather, it translated anatomical characteristics into code numbers that correspond to an individual genus. This system was relatively difficult to use (especially with partially preserved specimens) and precluded identification higher taxonomic levels, when the genus could not be determined. A major re-evaluation of the Oribatida is needed. Oribatid mites are frequently found on seabirds and the relationship is generally assumed to be phoretic (Ballard and Ring, 1979; Choe and Kim, 1987).

2.4.3 Mallophaga

The present study revealed all three genera of lice previously recorded from these auks (Eveleigh and Threlfall, 1976). Overall densities obtained were lower than those reported by Choe and Kim (1987), but were similar to those of Eveleigh and Threlfall (1976). This could be a reflection of sampling technique, since the technique used by Choe and Kim (1987) was more accurate. However, the technique of Eveleigh and Threlfall (1976) was repeated by Ballard and Ring (1979) at the Bamfield Marine Station, on Common Murres, and they found high densities with overall relative trends similar to Choe and Kim (1987). This suggests that the lower numbers in my study are a reflection of biogeography rather than sampling inefficiency. Louse densities are apparently higher at the study sites on the west coast of North America (Ballard and Ring, 1979; Choe and Kim 1987) and lower on the east coast (Eveleigh and Threlfall 1976; current study). Variations in density and abundance of these genera are discussed in Chapter 3.

Almost all bird species examined have one or more louse species living on them (Borror, 1981). They spend their entire lives on the host, although they are usually not detrimental (Rothschild and Clay, 1957; Marshall, 1981). Some species are known to cause a great deal of irritation, rendering their hosts emaciated and vulnerable to predation (Borror, 1981). The Mallophaga, or chewing lice, are known to occur on seabirds as well (Eveleigh 1974; Ballard and Ring, 1979), sometimes in very large numbers (Choe and Kim, 1987). The extent to which their presence on hosts affects breeding is not known. Eveleigh and Threlfall (1976) described the seasonal and overall variation in louse populations (representing three genera: *Saemundssonina*, *Quadraceps* and *Austrorhynchus*) in the alcids of Newfoundland. Species of *Austrorhynchus*, have been

shown to act as a vector of the filarial worm genus *Eulimdana* in charadriiform hosts but long term effects of this agent on the host life cycle has not been studied (Bartlett, 1993).

2.4.4 Diptera

In my study at the Gannet Islands, Diptera were rather scarce with two genera of larval flies obtained from Atlantic Puffin chicks, along with a single specimen (of one of the two genera) from a Razorbill adult. They were generally seen crawling over the skin surface, but some specimens were also seen to be partially imbedded in the skin, suggesting that they might be feeding on tissue fluid or blood (Stehr, 1991). The identity of these two genera could not be determined, although they were narrowed down to the suborder Muscomorpha (also cyclorhaphous Brachycera), an extremely diverse group with more than 8000 species ranging in feeding habits from scavengers to parasites that burrow in skin (Stehr, 1991).

Certain Diptera larvae are known to be hematophagous parasites of birds (Sabrosky et al., 1989; Stehr, 1991). Numerous genera of Calliphoridae have been recorded from a wide range of birds (Sabrosky et al., 1989), but none have been recorded from seabirds (Wheeler and Threlfall, 1989). The Hippoboscidae species *Icosta americana*, has been recorded from Thick-billed Murres (Wheeler and Threlfall, 1989).

2.4.5 Siphonaptera

In the present study, only one flea specimen was found from an adult Thick-billed Murre, along with four specimens from Atlantic Puffins (three from adults). The flea from the Thick-billed Murre was identified to be *Orchopeas leucopus*, a very common ectoparasite of deer mice, *Peromyscus maniculatus*. The fleas collected from the puffins

were all immature and hence could not be identified. It was assumed that these fleas were also *O. leucopus* and were phoretic.

Holland (1984) has reviewed the North American fleas and the hosts on which they live. One flea species (*Actenopsylla suavis*) has been recorded from two burrow-nesting Alcids: the Cassin's Auklet (*Ptychoramphus aleuticus*) and the Tufted Puffin (*Fratercula cirrhata*) (Holland, 1985).

2.4.6 Coleoptera

Staphylinids in this study were classified to the suborder Aleocharinae which contains about 1300 species in 200 genera (Seevers, 1978). The taxonomic uncertainty of this diverse suborder has prevented proper identification from the existing literature and major revisions are therefore necessary (Arnett, 1993). The group thrives in a range of microhabitats, feeding on decomposing animal and plant remains, along with soft bodied arthropods and fungi. They are particularly common in decomposing animal carcasses where larval Diptera abound. Their presence on Atlantic Puffins and Thick-billed Murres could be phoretic. Larval Diptera (not identified) in the guano of Common and Thick-billed Murres (personal observation) may also have been a target prey item. Beetles are representatives of the largest order of insects (Borror, 1981) but only about 71 species are considered to be ectoparasitic on mammals (Marshall, 1981). The tribe Amblyopini of the family Staphylinidae includes some ectoparasitic species but most await description.

2.4.7 Collembola

Collembola, or springtails, are soil dwelling insects that feed on bacteria, fungi and dead organic matter (Hopkin, 1997). Some are carnivorous, feeding on soil nematodes and other Collembola. None of the species are known to be parasitic to animals, but some are

known to infest and feed on wounds of amphibians. Their presence on the alcids could be phoretic, although attraction to the microbial flora of the birds (Hubalek, 1976; Hubalek, 1978; Clayton, 1999; Burt and Ichida, 1999), as suggested earlier for Oribatids, could be a possible reason for their presence. There is evidence indicating that lice might feed facultatively on Collembola (Oniki and Butler, 1989).

2.4.8 Thysanoptera

Thrips are very small terrestrial insects occurring in a wide range of habitats (Lewis, 1973; Arnett, 1993). Their feeding habits are also very diverse, including predation, fungivory, phytophagy. Many are known to feed primarily on pollen and spores. Others feed on the eggs and larvae of a variety of insects, mites and nematodes, but no parasitic forms have been recorded (Arnett, 1993). Several specimens of immature thrips were found (mainly on Atlantic Puffins, and one from a Thick-billed Murre), and they were assumed to be phoretic.

2.5 Summary

All the organisms described above formed part of a complex community of arthropods living on the auks of the Gannet Islands, Labrador. The parasitic species were of special interest because they may lower reproductive success and represent a means of disease transmission in some of their hosts. Many, however, have become specialized in living on their host without causing debilitation. The benign and apparently harmless taxa may form an indirect mutualistic association with the host by competing with some of the more harmful taxa. The next chapter examines some of these ideas and summarizes the data obtained on the more numerous ectoparasite taxa living on Alcids.

Table 2.1.1 Abundance estimates of breeding pairs of the four auk species at the Gannet Islands, Labrador (data from Lock et al., 1994)

Name	Atlantic Puffin	Razorbill	Thick-billed Murre	Common Murre
Outer Gannet	6300	620	320	26000
Gannet Clusters	33000	5800	950	21000
Total	39300	6420	1270	47000

Table 2.2.1 Sampling technique and the number of auk species sampled at the Gannet Islands, Labrador, 1998

Species	Age	Number sampled	Capture technique
Atlantic Puffin <i>Fratercula arctica</i>	Adult	32	Fleyging
	Chick	25	Grubbing
Razorbill <i>Alca torda</i>	Adult	18	Fleyging, Noose carpet
	Chick	30	By hand
Common Murre <i>Uria aalge</i>	Adult	29	Fleyging
	Chick	13	By hand
Thick-billed Murre <i>Uria lomvia</i>	Adult	29	Fleyging Noose pole

Table 2.3.1 Total abundance of ectoparasites collected from the adults of four species of auks*

	Atlantic Puffin (N=32)	Razorbill (N=18)	Common Murre (N=29)	Thick- billed Murre (N=29)
INSECTA (Insects)				
Mallophaga (Chewing lice)				
<i>Saemundssonina calva</i>			9	11
<i>Saemundssonina fraterculae</i>	15			
<i>Saemundssonina celidoxa</i>		6		
<i>Quadraceps obliqua</i>			9	5
<i>Quadraceps helgovauki</i>	6			
<i>Quadraceps alcae</i>		4		
<i>Austromenopon uriae</i>			2	2
<i>Austromenopon nigropleurum</i>	1	9		
Coleoptera (Beetles)				
Aleocharinae (Rove beetles)		1	3	3
Thysanoptera (Thrips)	6		1	
Diptera (Flies)				
Muscomorpha		1		
Collembola (Springtails)	8	15	6	
Siphonaptera (Fleas)				
<i>Orchopeas leucopus</i>	3			1
ACARI (Ticks and mites)				
<i>Ixodes uriae</i> (Hard ticks)	4	1	4	8
<i>Alloptes</i> sp. (Feather mites)	1179	644	32	177
Oribatida (Oribatid mites)	80	71	54	56
unknown Acari	16	14	3	8

*see Appendix I for a more detailed classification scheme.

Table 2.3.2 Total abundance of ectoparasites collected from the three species of auk chicks*

	Atlantic Puffin (N=25)	Razorbill (N=30)	Common Murre (N=13)
INSECTA			
Mallophaga (Chewing lice)			
<i>Saemundssonina calva</i>			2
<i>Saemundssonina fraterculae</i>	1		
<i>Quadraceps obliqua</i>			70
<i>Quadraceps helgovauki</i>	4		
<i>Quadraceps alcae</i>		24	
<i>Austromenopon uriae</i>			156
<i>Austromenopon nigropleurum</i>		39	
Thysanoptera (Thrips)	1		
Diptera (Flies)			
Muscomorpha	40		
Collembola (Springtails)	1		3
Siphonaptera (Fleas)			
<i>Orchopeas leucopus</i>	1		
ACARI (Ticks and mites)			
<i>Ixodes uriae</i> (Hard ticks)	1	1	
<i>Alloptes</i> sp. (Feather mites)	9	14	1
Oribatida (Oribatid mites)	289	100	45
unknown Acari	1	15	3

*see Appendix I for a more detailed classification scheme.

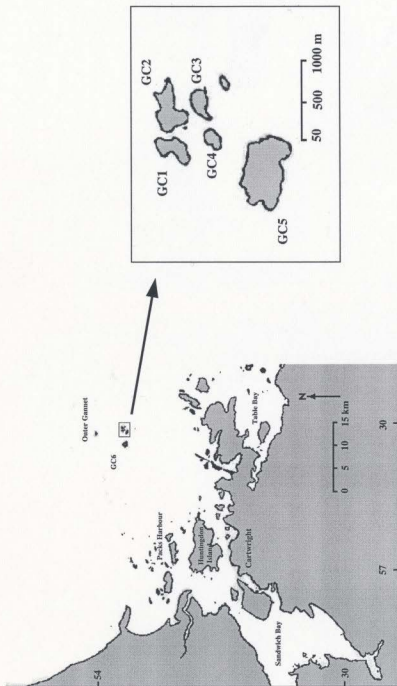


Figure 2.2.1 Map of the Gannet Islands, Labrador

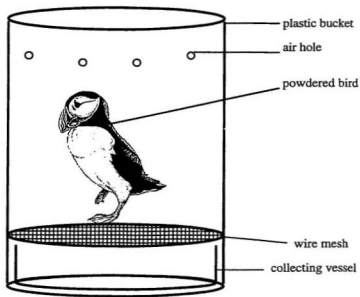


Fig. 2.2.2 : The delouser used for the removal of ectoparasites of auks

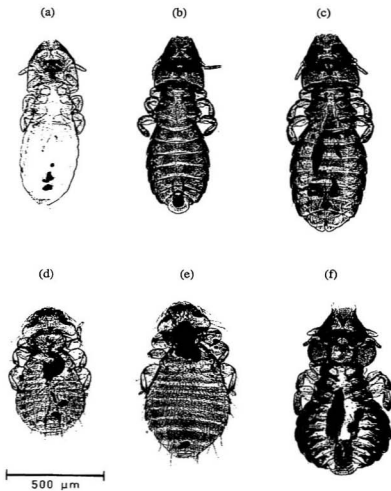


Plate 2.1 Louse genera collected from the four auks - a) *Quadriceps* (nymph); b) *Quadriceps* (male); c) *Quadriceps* (female); d) *Austromenopon* (male); e) *Austromenopon* (female); and f) *Saemundssonina* (male)

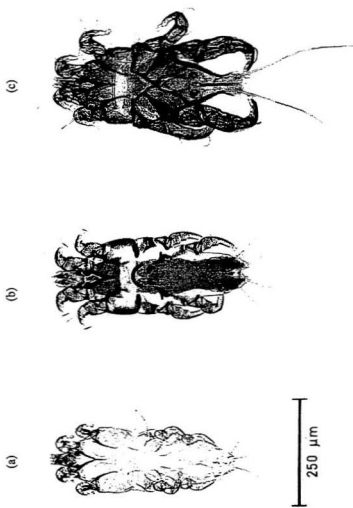


Plate 2.2 Feather mites of the genus *Alloptes* collected from the four auks - a) nymph, b) female and c) male.

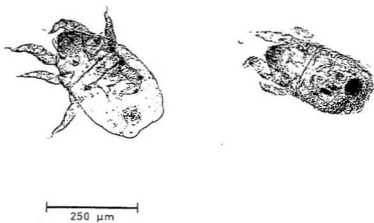


Plate 2.3 Unclassified oribatid mite nymphs collected from the four auks.

Chapter 3

Does host coloniality influence the population structure of ectoparasites of four auk species (Alcidae)?

Abstract

Host-parasite interactions are complex and a wide range of factors may influence their maintenance. One such factor, coloniality of hosts, has been shown to structure patterns of ectoparasite abundance among individual avian hosts. I investigated the role of colonial aggregations of four auk hosts (Atlantic Puffin, *Fratercula arctica*; Razorbill, *Alca torda*; Thick-billed Murre, *Uria lomvia*; and Common Murre, *Uria aalge*) in determining aggregation, prevalence and relative abundance of their ectoparasites at the Gannet Islands, Labrador. Aggregation, as measured by the k parameter, variance-to-mean ratio and Green's index showed that pooled ectoparasite distributions were aggregated. Selected ectoparasitic taxa had uniform, random and aggregated distributions. Taxa that were aggregated, however, showed low levels of aggregation with Green's indices ranging from 0.012 to 0.396. Prevalence and relative abundance were compared for selected ectoparasitic taxa among the four hosts. Prevalence of ectoparasites were generally low for most taxa, values ranging from 0 to 20%. Prevalence of *Quadraceps* and *Austromenopon* were high (76.9 and 100% respectively) on Common Murre chicks. Chicks of Atlantic Puffins and Razorbills (less aggregated hosts) had much lower prevalence of these two louse genera (4.87 and 33.3% for *Quadraceps*; 0 and 43.33% for *Austromenopon*, respectively). Relative abundance of the same genera on chicks showed a similar pattern, with the Common Murre chicks harbouring significantly more lice than Atlantic Puffin and Razorbill chicks. Feather mite prevalence was significantly higher on adult Atlantic Puffins

and Razorbills (less aggregated hosts) (93.3 and 83.3%, respectively) compared to the two murre (44.8% in both cases). Relative abundance showed the same pattern with Atlantic Puffins and Razorbills harbouring 39.3 and 35.8 feather mites/bird, respectively, which was significantly higher than the relative abundance of feather mites of Thick-billed and Common Murres (1.1 and 6.1 feather mites/bird, respectively). A hypothetical framework for the observed feather mite and louse distributions is presented based on the assumption that high louse and feather mite loads reduce reproductive success of hosts. Coloniality was related to distributions of some ectoparasitic taxa, but it apparently did not play a uniform role in generating most ectoparasitic distributions at the Gannet Islands.

3.1 Introduction

Host-parasite interactions are generally studied from the host's perspective, with emphasis being placed on the influence of the parasite on the behavior, ecology, and physiology of the host. My study approaches this subject from a different viewpoint: it regards seabirds as mobile islands supporting a diverse community of arthropods. Others have also looked at seabirds as islands (e.g. Eveleigh and Threlfall, 1976; Choe and Kim, 1987) and have recognized the difficulty associated with quantifying and interpreting patterns in ectoparasite assemblages. Nevertheless, such an approach will be necessary if we are to understand the forces molding the structure of ectoparasite communities. A better understanding of ectoparasite communities will also provide a better understanding of how the seabird host populations are affected by ectoparasitism (Holmes and Price, 1986).

Several ecological terms have been used to conceptualize and quantify ectoparasite populations (Margolis et al., 1982; Holmes and Price, 1986; Bush et al., 1997). Conspecific parasite individuals on a given host individual constitute the *infrapopulation* (Holmes and Price, 1986). Infrapopulations are regarded as subsets of the *suprapopulation* - the entire parasite population of a species distributed among the host population (Holmes and Price, 1986). The *infracommunity* is the assemblage of all parasitic species living on an individual host and it forms a subset of the larger *component community* consisting of all parasitic species exploiting the host population (Holmes and Price, 1986).

Parasites tend to be aggregated (or overdispersed) among their host population, with most individuals of the host species harboring few or no parasites (small infrapopulations) and relatively few host individuals with high infestations (large infrapopulations; Crofton, 1971). This presents a challenge to statistical analyses of host-parasite interactions (Krebs, 1989; Shaw and Dobson, 1995; Poulin, 1998). The most

commonly used index that characterizes aggregation is the index of dispersion (or the variance to mean ratio; Taylor, 1961). Ratios significantly higher than unity suggest an aggregated distribution pattern and as values increase, the levels of aggregation increase. The reliability of this aggregation index has been challenged, but it continues to be commonly used because it is easy to compute (Poulin, 1998).

The vast majority of natural host-parasite systems show varying degrees of aggregation (Taylor, 1961; Crofton, 1971; Anderson et al., 1982; Poulin, 1998). It has been hypothesized that aggregation patterns may result from similar processes in different biological systems (Poulin, 1998). Heterogeneity in the rates of parasite acquisition (Anderson et al., 1982); differential rates of birth, growth and death on different individuals; genetic control of the susceptibility of hosts (Wassom et al., 1986); and host coloniality (Rosza, et al., 1996; Rozsa, 1997; Rekasi, et al. 1997) have all been determined to be factors that produce aggregated distributions in parasites. Rosza et al. (1996) demonstrated that aggregation levels of chewing lice were higher in territorial Hooded Crows (*Corvus corone*) than in colonial Rooks (*Corvus frugilegus*). Group-living caused enhanced horizontal ectoparasite transmission, which in turn, decreased aggregation levels of infracommunities. This study also showed that some ectoparasite taxa showed similar patterns of aggregation at the infrapopulation levels in these two corvid species.

Other standard measures in parasitology that characterize parasite populations include 1) prevalence, 2) mean intensity and 3) relative abundance, each of which provides different information about the parasitic communities (Margolis et al., 1982; Bush et al., 1997). The prevalence is the percentage of hosts in a sample infected by a particular parasite species. Mean intensity is measured as the mean number of parasites of a species in a sample of infected host species. Relative abundance is a measure of mean parasite load of a species in a sample of host species. All these measures of parasite populations

characterize the extent of infection by a certain parasite species (Margolis et al., 1982; Holmes and Price, 1986; Poiani 1992).

Poulin (1991) showed that colonial species of passerine hosts had higher prevalence of feather mites than did solitary species. Avian lice of colonial corvid hosts also occur with higher prevalence than in solitary corvids (Rozsa et al., 1996). In another study, higher louse prevalence was also documented in colonial than solitary avian hosts but suprapopulation size (relative abundance) did not vary between the two social systems (Rekasi et al., 1997). In contrast, Poiani (1992) found that relative abundance was higher in cooperatively breeding passerine genera than in non-cooperatively breeding hosts, although the relationship was reversed in migratory genera.

I herein investigate the role of seabird host species coloniality in determining aggregation, prevalence and relative abundance of ectoparasites on a finer scale. I chose four auk species (Alcidae) : Atlantic Puffin, *Fratercula arctica*; Razorbill, *Alca torda*; Thick-billed Murre, *Uria lomvia*; and Common Murre, *Uria aalge* for this study because they vary considerably in breeding habitat selection and density at their breeding colonies (Gaston and Jones, 1998). These alcid species breed on headlands and small offshore islands of the Atlantic coast (Lock et al., 1994; Gaston and Jones, 1998).

Atlantic Puffins nest in burrows (varying in length from 70 to 110 cm) on grassy slopes (Harris, 1984; Gaston and Jones, 1998). Densities of 3 burrows/m² are typical although the average number of occupied burrows range from 0.4-0.6 burrows/ m² (Harris, 1984) Each burrow is occupied by only one pair of Puffins and hence direct contact between individuals (other than mates) in a colony normally occurs outside of the nest. The population estimate for Atlantic Canada is about 350 000 pairs (Nettleship and Evans, 1985; Gaston and Jones, 1998).

Razorbills nest on crevices among boulders and on cliff-edges (Cramp et al., 1985; Gaston and Jones, 1998) and breeding sites are separated by at least 10 cm, but typically by more than 30 cm, with densities reaching 4 pairs/m² (Cramp et al., 1985). In some populations, many nest sites are located 10m or more from the nearest neighbour (Lloyd et al., 1991). Estimates on the world population range from 500 000 - 700 000 pairs (Lloyd et al., 1991) out of which only about 4% breed in Eastern Canada (Gardarsson, 1985). The largest Razorbill colony on the east coast of North America is located in the Gannet Islands, Labrador (Birkhead and Nettleship, 1982).

Thick-billed and particularly Common Murres nest in the densest aggregations of any auk species (Gaston and Nettleship, 1981; Nettleship and Birkhead, 1985; Gaston and Jones, 1998). Thick-billed Murres nest in dense clumps and their nesting sites are typically located on narrow ledges (as little as 10 cm wide) along steep cliffs directly adjacent to the sea (Gaston and Nettleship, 1981; Gaston et al., 1985) with individuals usually remaining in contact with up to two neighbours from the sides on their nesting sites (Birkhead et al., 1985). Densities vary between 1 and 37 pairs/m² (Cramp et al., 1985).

Common Murres typically nest on broad, flat, rocky outcrops on headlands and offshore islands (Nettleship and Birkhead, 1985; Gaston and Jones, 1998). Birds clump next to one another with about a third of the birds being in physical contact with neighbors (Birkhead et al., 1985), with mean densities of 20 breeding pairs/m², although densities as high as 70 pairs/m² have been recorded (Cramp et al., 1985; Nettleship and Birkhead, 1985). This may perhaps be the densest nesting aggregations of any bird in the world (Nettleship and Birkhead, 1985) with breeding colonies being the largest among all the Atlantic auk species (e.g. 500 000 breeding pairs in Funk Island, Newfoundland; Nettleship and Evans, 1985).

In summary, Razorbills are less aggregated than Murres, both species of which are highly aggregated on their nesting sites; Thick-billed Murres are slightly less aggregated than Common Murres. Aggregation among individual Puffins is lower than Razorbills.

The objectives of this study were :

- 1) to determine the relationships of host coloniality to aggregation, prevalence and relative abundance of ectoparasites; and
- 2) to relate the observed patterns to existing hypotheses on parasite aggregations

3.2 Quantification and Statistical Analyses

The ectoparasites collected from the four auk hosts were enumerated and quantified (See Chapter 2 for study site and ectoparasite extraction methods). To characterize aggregation, I used two standard aggregation indices, namely the k parameter (exponent k or parameter k) and the variance to mean ratio (s^2/\bar{x}). The negative binomial distribution, defined by the k parameter, is a useful way of characterizing parasite distributions and has been used since its introduction in parasitology by Crofton (1971). The k parameter was calculated using the maximum likelihood method (Bliss and Fisher, 1953; reviewed by Krebs, 1989). As values of k approach zero, the populations and communities in question become more and more aggregated. Aggregation decreases as k increases and values ≥ 8 are unreliable because the negative binomial distribution converges with the Poisson series rendering the parasite distributions random in space (Southwood, 1978; Krebs, 1989; Poulin, 1998). The reliability of k as a descriptor of the observed aggregations was tested using Chi Square analyses reviewed by Krebs (1989).

The variance to mean ratio (s^2/\bar{x}) was calculated for all the parasites (infracommunities) on the four hosts and for selected parasite taxa (intrapopulations). Chi-

square analysis was used to determine statistically significant deviations of the calculated indices from unity (Ludwig and Reynolds, 1988):

$$\chi^2 = \frac{s^2}{\bar{x}(N-1)}$$

where N = number of hosts sampled,

s^2 = sample variance

and \bar{x} = sample mean

The values obtained by this method could not be compared among species because their computation is directly related to the number of parasite specimens collected (Ludwig and Reynolds, 1988). They only provide evidence of significant aggregation. Green (1966) modified the variance to mean ratio to derive the Green's index which is independent of the number of parasites collected:

$$\text{Green's Index} = \frac{(s^2/\bar{x}) - 1}{n - 1}$$

where n = number of parasite individuals collected.

The values of the Green's Index generally range from zero (perfectly random) to one (highly aggregated), whereas values below zero indicate a uniform distribution. The calculated values of the Green's Index were compared between species. If large differences occurred between species, Monte Carlo methods (Manly, 1991), based on 1000 randomizations, were used to determine statistical significance.

I also calculated two commonly-used and informative variables in parasitology, namely prevalence and relative abundance of ectoparasites, each of which gives slightly different information on the parasite distributions and abundance (Margolis et al., 1982; Bush et al., 1997). Inter-host differences in prevalence and relative abundance of lice and

feather mites were compared among species using Monte Carlo methods based on 1000 randomizations (Manly, 1991).

3.3 Results

3.3.1 Aggregation

The negative binomial model

Aggregation of infracommunities was evident in all four host species, as indicated by the variance to mean ratios (Table 3.3.1) and the k exponents (Table 3.3.2). The estimated k values of different arthropod taxa also revealed aggregated infrapopulations (Table 3.3.3). However, chi square analyses indicated that the observed frequency distributions differed significantly from the expected frequencies predicted by the negative binomial model, in many cases (Table 3.3.2). Fig. 3.3.1 illustrates an example of the discrepancy between the observed frequency distribution and the expected negative binomial distribution. These discrepancies made k a poor estimator of the observed aggregation and no further analyses were done with the k parameter (Krebs, 1989).

Variance-to-mean ratio

Analyses of the variance-to-mean ratios at the infrapopulation level showed that feather mites and oribatid mites were significantly aggregated in adults of all the hosts. The lice and unclassified Acari, were significantly aggregated only in some host species .

Oribatid mites and *Quadraceps* spp. were significantly aggregated in the chicks of the three species collected (Table 3.3.4), while *Austromenopon* spp. were significantly aggregated on Razorbill and Common Murre chicks, but not on Atlantic Puffins. Neither *Quadraceps* spp. nor *Austromenopon* spp. were significantly aggregated on any of the

adult hosts (Tables 3.3.1). The total parasite infracommunities were also significantly aggregated on chicks.

Green's index

The values of the Green's Index for most parasite species indicated relatively low levels of aggregation on adults (Table 3.3.5). Aggregation of oribatid mites and feather mites was higher than most other taxa. The values of the Green's index were compared between the four hosts using randomization methods (Manly, 1991); the differences in levels of aggregation were not significant ($P \gg 0.05$, in all cases; Table 3.3.5).

3.3.2 Prevalence and Relative abundance

Prevalence and relative abundance of the various ectoparasites collected were generally low (Table 3.3.6). Only two louse genera and the feather mite genus occurred in high enough numbers to allow meaningful randomizations of the prevalence and relative abundance.

Lice

The prevalence and relative abundance of two lice genera did not differ among adult host species with one exception ($P \gg 0.05$, in all cases; Tables 3.3.7 and 3.3.8). Prevalence and relative abundance of *Austromenopon* on adult Atlantic Puffins were lower than Razorbills. Prevalence and relative abundance of *Austromenopon* and *Quadraceps* varied considerably between the adults and chicks within each auk species but no clear trend was evident (Tables 3.3.7 and 3.3.8). However, comparison across species showed that the two louse genera were significantly more prevalent and had higher relative

abundance on the chicks of Common Murres than those of Razorbills or Atlantic Puffins ($P < 0.002$ in all cases; Tables 3.3.7 and 3.3.8).

Feather mites

Prevalence and relative abundance of feather mites were similar in Razorbills and Puffins ($P = 0.251$ and 0.523 for prevalence and relative abundance, respectively; Tables 3.3.7 and 3.3.8). Razorbills had significantly higher prevalence and relative abundance of feather mites compared to both the Murre species ($P < 0.001$ in all cases for prevalence; $P < 0.01$ in all cases for relative abundance). Prevalence and relative abundance were not compared between adults and chicks because they were essentially absent from the chicks.

3.4 Discussion

3.4.1 Aggregation

All parasite infracommunities showed significant aggregations on their hosts. However, variation in the degree of aggregation of parasite infracommunities did not differ significantly among host species. Although aggregation at the intrapopulation level was significant in most cases, levels of parasitic aggregation did not differ across hosts. Coloniality of hosts, therefore, had no apparent influence on levels of aggregation of ectoparasites, contrary to the findings of Rozsa et al. (1996) and Rekasi et al. (1997). The latter studies investigated aggregation in a wide range of avian hosts. They concluded that social systems of host species strongly influenced aggregation of ectoparasites, with higher aggregation levels occurring in less social host species. However, some of the host species they examined were behaviourally and phylogenetically very different. In addition, the comparisons were made on a rather crude scale defining host aggregation (e.g., colonial versus solitary).

Aggregation of parasites is a dynamic attribute, with many factors affecting its existence and maintenance (Poulin, 1998). Some of these factors may increase the level of aggregation whereas others may produce evenness in parasite distributions (Anderson et al., 1982).

The benefits and disadvantages of group living in the Atlantic alcid has been reviewed in detail by Birkhead (1985), who identified increased parasites and disease transmission as a potential cost of coloniality. Nevertheless, the roles of parasite and disease transmission on the regulation of populations and behaviour have not been investigated in auks. Coloniality of hosts, in general, would be expected to increase transmission of ectoparasites, in turn reducing parasite aggregation (Rozsa et al., 1996; Rekasi et al., 1997; Poulin, 1998). This could be favored by individual natural selection on both parasites and hosts. It could give the heavily infested host individuals an opportunity to relieve themselves of some of their parasite burden through enhanced contact transmission. The parasite could explore more suitable hosts for infestation. The fact that ectoparasites were not evenly distributed across host populations suggests that aggregated parasite distributions are a result of complex processes and coloniality may only be one of several factors influencing aggregation patterns. In auks, the influence of coloniality in causing varied aggregation patterns may not be very intense.

The negative binomial distribution did not describe most parasite distributions indicating that aggregation patterns were different from those observed in some other host-parasite systems (Krebs, 1989). Aggregated distribution patterns can occur in an infinite number of forms and the k parameter is a descriptor of only one of them. Aggregation of ectoparasites that is not well described by the negative binomial distribution has also been observed in other studies of avian host-parasite models (Rekasi et al., 1997). Mechanisms that generate specific aggregation patterns could be better understood by measuring parasite

aggregations at different hierarchical levels (e.g. Boulinier et al., 1996). For instance, aggregation of ticks (*Ixodes uriae*) may occur between Black-legged Kittiwake (*Rissa tridactyla*) chicks in different nests but not among chicks within the same nest (Boulinier et al., 1996). Whether there was aggregation at one hierarchical level and no aggregation or less aggregation at a different level could not be determined in the present study.

3.4.2 Prevalence and relative abundance

Prevalence and relative abundance of ectoparasites showed varied trends across auk host species at the Gannet Islands. Less aggregated hosts (Atlantic Puffins and Razorbills) had higher prevalence and relative abundance of feather mites than Murres, in agreement with the findings of Poulin (1991), Rozsa (1996) and Rekasi et al.(1997). Feather mites have received little scrutiny in spite of their large numbers perhaps because of their assumed benign role (Eveleigh, 1974; Choe and Kim, 1987; Gaud and Atyeo, 1996). Nevertheless, heavy feather mite infestations can cause weight loss and a decline in egg production in some host species (Gaud and Atyeo, 1996). The intrapopulation size of feather mites, therefore, may sometimes correlate negatively with reproductive success (the proportion of eggs laid that result in a successfully fledged chick). However, it would be difficult to experimentally demonstrate whether feather mites reduce reproductive success because feather mites cannot be cultured without their specific hosts (Gaud and Atyeo, 1996). This precludes the possibility of manipulating wild-host feather mite loads to investigate their effect on reproductive success. Herring Gulls (*Larus argentatus*) also carry *Alloptes* feather mites and captive gulls could potentially be used to elucidate the link between reproductive success and feather mite abundance.

Common Murre chicks had significantly higher prevalence and relative abundance of two of the three chewing louse genera, implying that chicks provide more suitable

habitat for lice than do adults. Razorbill and Puffins chicks had very few lice, and their prevalence and relative abundance were similar to those of adults. These observations illustrate the link between host aggregation and louse transmission, the more aggregated host species being more likely to have chicks with high louse loads. Part of the reason for higher louse abundance on murre chicks is that most louse reproduction takes place on the chicks (Eveleigh, 1974). Heavy louse infestations may reduce reproductive success in their hosts, either by transmitting disease causing agents or by altering behavioral responses relating to reproductive success (Clayton, 1990; Borgia and Collis, 1990; Bartlett, 1993). Several chewing louse genera, including *Austromenopon*, transmit species of the filarial worm, *Eulimdana*, in charadriiform hosts (Bartlett, 1993). Experimentally enhanced chewing louse-loads lower reproductive success by reducing courtship displays in male Rock Doves, resulting in females choosing less-parasitized mates (Clayton, 1990).

Assuming that both feather mite and louse abundance reduce host reproductive success in the four auks in this study, the following hypothetical mechanism (summarized in Fig. 3.3.2) explaining the distribution of these ectoparasites is proposed. The pattern can be interpreted as a trade-off between coloniality and adult reproductive success. Chicks of aggregated host species (murres) have high louse loads due to enhanced horizontal transmission expected in dense nesting conditions characteristic of the murres. However, this enhanced louse loads could be of benefit to the chicks since they might prevent the build-up of feather mite loads as they grow older. In less aggregated species, such as Atlantic Puffins and Razorbills, the chicks are more isolated from other chicks and adults and hence they have much lower louse loads compared to the murres. This could be beneficial to the chicks since high louse loads could be harmful. However, low louse loads may allow the build-up of feather mites as the chicks grow older, causing the adults to be heavily infested with feather mites, which are hard to eliminate by preening because of their

small size (Gaud and Atyeo, 1996). The compromise, then lies in the level of coloniality of the host species. A high degree of aggregation may jeopardize chick fledging success because of high louse loads, but may enhance long-term reproductive success since adults are relatively healthy.

Adult Common Murres nest at high density and thereby expose chicks to the risk of obtaining high louse loads from conspecific individuals. However, the adult Murres have the benefit of having lower feather mite loads which might enhance reproductive success. Puffins and Razorbills nest in more dispersed colonies and even though they have higher feather mite abundance per adult, their chicks have a lower risk of attaining contact-transmitted lice from conspecific neighbours, enhancing their fledging success.

The validity of this conceptual framework for transmission and relative abundance of lice and feather mites needs to be tested experimentally, even though it is supported by some evidence from other studies. Pacific breeding populations of Common and Thick-billed Murre colonies have relatively lower breeding success relative to Atlantic populations (Gaston and Nettleship, 1981; Byrd et al. 1993; Gaston et al., 1994; Gaston and Jones, 1998), with most failures occurring at the egg stage (Gaston and Jones, 1998). Common and Thick-billed Murres on the Pribilof Islands, Alaska have extremely high relative abundance of feather mites (Choe and Kim, 1987). I found much lower relative abundance of feather mites in my study, in agreement with another study on auks at Gull Island, Witless Bay, Newfoundland, (Eveleigh, 1974) in which no feather mites were found from Common or Thick-billed Murres, and only low numbers were found on Puffins and Razorbills (Eveleigh, 1974). The lower overall abundance of feather mites is associated with, and could be partially responsible for, the higher reproductive success observed in the Atlantic Murres. The abundance of lice on Common and Thick-billed Murres was also much higher in the Pacific (Choe and Kim, 1987) compared to those in

the Atlantic (Eveleigh, 1974; present study). The difference between louse loads of Common Murres in the Atlantic and Pacific was noted by Ballard and Ring (1979) who suggested that variation in habits and habitats of the murres could play a causal role.

Colony size may have important effects on parasite suprapopulations (Davis and Brown, 1999). The relative abundance of mite mites (*Dermanyssus prognepphilus*) on Purple Martins (*Progne subis*) increases with colony size up to a certain level and remains stable. If feather mites and lice of auks varied with colony size, then similar patterns in their prevalence and relative abundance might be expected. Overall populations of murres on the east coast of North America are lower than on the west coast (Gaston and Jones, 1998). Furthermore, the murre colonies (especially Thick-billed Murres) at the Gannet Islands are relatively small compared to other areas in Atlantic Canada (Lock et al., 1994). Differences among the observed relative loads of feather mites (Eveleigh, 1974; Choe and Kim, 1987; present study) and lice (Eveleigh, 1974; Ballard and Ring, 1979; Choe and Kim, 1987; present study) could have been caused partly by the effect of increasing abundance with increasing host colony size.

3.5 Conclusion

My study provided evidence that the degree of aggregation in ectoparasites of auks did not vary with degree of aggregation of their hosts at the Gannet Islands, Labrador. Interesting patterns of prevalence and relative abundance of feather mites and lice were noted. Feather mites were more abundant in less-aggregated hosts whereas abundance of lice was similar across hosts. A dynamic interaction between chicks, adults, and level of host coloniality is proposed as a mechanism for explaining these observations. Coloniality seems to play a role in shaping distributions of certain ectoparasitic taxa. More empirical evidence is required to establish mechanisms that might generate such distribution patterns

in parasitic taxa. Care should be taken to consider factors such as colony size when designing these studies.

Table 3.3.1 Variance-to-mean (s^2/\bar{x}) ratios for selected infrapopulations and infracommunities for adults of the four host species.

	Atlantic Puffin	Razorbill	Thick-billed Murre	Common Murre
<i>Alloptes</i> spp.	253.85*	1191.47*	46.59*	2.61*
Oribatida	24.97*	15.25*	1.50*	4.32*
Other Acari	1.39	2.05*	4.17*	0.93
Collembola	2.31*	6.10*	1.62*	1.17
<i>Saemundssonina</i> spp.	2.03*	1.05	1.51*	1.41
<i>Quadriceps</i> spp.	1.17	0.82	0.86	1.17
<i>Austrorhenopon</i> spp.	1.00	3.59	0.92	0.96
Infracommunities	227.11*	1721.61*	37.45*	3.23*

* indicate values that are significantly larger than one at $\alpha = 0.05$ (Chi square analysis)

Table 3.3.2 Summary of the values of the k parameter calculated for all ectoparasite species collected from the four auk species. χ^2 and P values indicate the statistical significance of the discrepancies between observed frequency distributions and expected negative binomial distributions based on the estimated k values.

Host Species	k	χ^2	P
Atlantic Puffin	0.378	2530.6	<0.005
Razorbill	0.476	328.5	<0.005
Thick-billed Murre	0.302	208.5	<0.005
Common Murre	1.788	35.6	<0.005

Table 3.3.3 k values of eight ectoparasite taxa. Values between zero and eight represent aggregated distributions.

	Atlantic Puffin	Razorbill	Thick-billed Murre	Common Murre
<i>Ixodes uriae</i>	$\rightarrow\infty$	$\rightarrow\infty$	0.547*	--
<i>Alloptes</i> spp.	0.316**	0.331**	0.152**	0.699*
Oribatida	0.187**	1.729	1.057*	0.669*
Other Acari	1.378	0.641	0.102**	--
Collembola	0.213	0.023**	0.153*	0.446
<i>Saemundssonina</i> spp.	0.524*	5.639	0.484	0.738**
<i>Quadriceps</i> spp.	0.940	--	--	1.774
<i>Austromenopon</i> spp.	$\rightarrow\infty$	0.319*	--	--

* and ** indicate significant differences between observed frequencies and expected negative binomial distributions at $\alpha = 0.05$ and 0.005 respectively. -- indicate parameters that could not be calculated due to the inadequacy of the data.

Table 3.3.4 s^2/\bar{x} ratios for selected infrapopulations for the chicks of three host species. Values significantly greater than zero indicate aggregated distribution.

	Atlantic Puffin	Razorbill	Common Murre
Oribatida	29.8*	11.2*	17.6*
<i>Quadraceps</i> spp.	2.5*	4.2*	5.7*
<i>Austromenopon</i> spp.	0.9	3.2*	6.0*
Total	26.5*	9.1*	14.2*

* indicate values that were significantly larger than one at $\alpha = 0.05$ (Chi square analysis)

Table 3.3.5 Variation in the values of Green's Index of aggregation for selected ectoparasitic taxa on the four host species. Negative values indicate a uniform distribution; values close to zero indicate a poisson distribution and values greater than zero but below one indicate an aggregated distribution. * indicates incalculable Green's Indices due to inadequacy of the data

Parasites	Atlantic Puffin	Razorbill	Thick-billed Murre	Common Murre
<i>Ixodes uriae</i>	-0.034	*	0.075	-0.036
<i>Austromenopon</i> spp.	*	0.324	-0.036	-0.036
<i>Saemundssonina</i> spp.	0.074	0.012	0.056	0.051
<i>Quadriceps</i> spp.	0.034	-0.059	-0.036	0.022
Oribatida	0.303	0.204	0.033	0.063
Feather mites	0.215	0.156	0.259	0.052
Acari	0.026	0.081	0.396	-0.036
Collembola	0.187	0.365	0.310	0.033
Thrips	0.172	*	*	*
Fleas	0.310	*	*	*

Table 3.3.6 Prevalence (P; percentage of birds that are infested) and relative abundance (RA; mean number of ectoparasites /bird) of selected infrapopulations on the four host species.

	Common Murre N=29		Thick-billed Murre N=29		Razorbill N=18		Atlantic Puffin N=30	
	P	RA	P	RA	P	RA	P	RA
<i>Ixodes uriae</i>	13.79	0.14	20.69	0.28	5.56	0.06	13.33	0.13
<i>Austromenopon</i> spp.	6.90	0.07	10.34	0.10	16.67	0.50	3.33	0.03
<i>Saemundsson</i> spp.	20.69	0.31	24.14	0.35	27.78	0.33	33.33	0.50
<i>Quadraceps</i> spp.	24.14	0.31	17.24	0.17	22.22	0.22	16.67	0.20
Oribatida	58.62	1.86	34.48	0.55	77.78	3.94	33.33	2.67
Feather mites	44.83	1.10	44.83	6.10	83.33	35.78	93.33	39.30
Acari	10.34	0.10	13.79	0.31	44.44	0.78	26.67	0.53
Collembola	17.24	0.21	6.90	0.10	22.22	0.83	16.67	0.27

Table 3.3.7 Prevalence (%) of two louse genera and a feather mite genus on adults and chicks of the four host species. Values in parentheses indicate standard errors of the mean, estimated by bootstrap methods.

		<i>Austromenopon</i> spp.	<i>Quadraceps</i> spp.	<i>Alloptes</i> spp.
Atlantic Puffin	Adult N=30	3.33 (± 3.25)	16.67 (± 7.88)	93.33 (± 4.70)
	Chick N=25	0.00 (± 0.00)	4.87 (± 3.54)	
Razorbill	Adult N=18	16.67 (± 8.24)	22.22 (± 9.92)	83.33 (± 8.94)
	Chick N=30	43.33 (± 9.19)	33.33 (± 8.34)	
Common Murre	Adult N=29	6.90 (± 4.74)	24.14 (± 7.89)	44.83 (± 9.04)
	Chick N=12	100.00 (± 0.00)	76.92 (± 11.84)	
Thick-billed Murre	Adult N=29	10.34 (± 5.77)	17.24 (± 6.89)	44.83 (± 9.33)

Table 3.3.8 Relative abundance (Numbers/bird) of two louse genera and a feather mite genus. Values in parentheses indicate standard errors of the mean, estimated by bootstrap methods.

		<i>Austromenopon</i> spp.	<i>Quadraceps</i> spp.	<i>Alloptes</i> spp.
Atlantic Puffin	Adult N=30	0.03 (± 0.03)	0.20 (± 0.09)	39.30 (± 18.25)
	Chick N=25	0.00 (± 0.00)	0.10 (± 0.07)	
Razorbill	Adult N=18	0.50 (± 0.33)	0.22 (± 0.10)	35.78 (± 13.35)
	Chick N=30	1.30 (± 0.36)	0.80 (± 0.32)	
Common Murre	Adult N=29	0.07 (± 0.05)	0.31 (± 0.11)	1.10 (± 0.31)
	Chick N=12	12.00 (± 2.33)	5.38 (± 1.48)	
Thick-billed Murre	Adult N=29	0.10 (± 0.06)	0.17 (± 0.07)	6.10 (± 3.10)

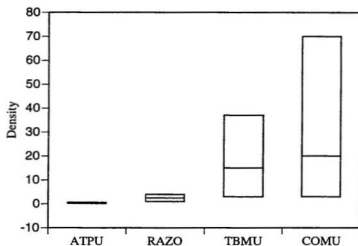


Fig. 3.1.1 Densities of individuals (numbers/m²) at nesting sites recorded for the four auk species. Each bar shows the maximum, mean and minimum density of an auk species. ATPU=Atlantic Puffin; RAZO=Razorbill; TBMU=Thick-billed Murre and COMU= Common Murre (Data derived from Cramp et al., 1985).

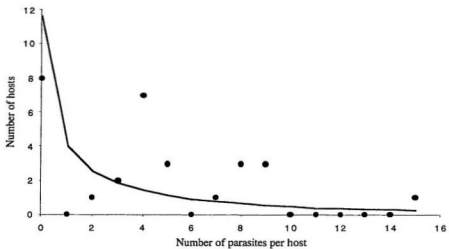


Fig.3.3.1 Frequency distribution of ectoparasites on adult Common Murres (circles) in relation to the frequency distribution predicted by the negative binomial model (line).

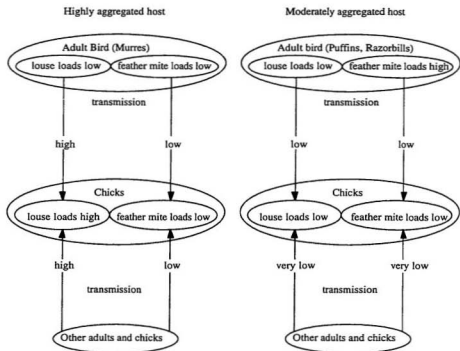


Fig. 3.3.2 The hypothetical link between transmission of lice and feather mites and seabird host aggregation

Chapter 4

Species-richness and nestedness in ectoparasite communities of four auks (Alcidae) -- evidence of structuring forces?

Abstract

Ectoparasite communities are often very diverse and they are made up of individuals and species that interact with one another. I determined the species-richness and community structure of the ectoparasites of four auk species (Atlantic Puffin, *Fratercula arctica*; Razorbill, *Alca torda*; Thick-billed Murre, *Uria lomvia*; and Common Murre, *Uria aalge*) at the Gannet Islands, Labrador. Mean species-richness of the ectoparasites of Razorbills (4.1 species/host) was significantly higher than puffins (3 spp/host), Common Murres (2.3 spp/host) and Thick-billed Murres (1.6 spp/host). Mean species-richness was also significantly higher in puffins than in Thick-billed Murres and Common Murres which were not significantly different from each other. I also investigated nestedness of ectoparasitic infracommunities to reveal non-random patterns in their assemblages. Values of relative nestedness (C) ranged from 0.123 to 0.298 for the four auk species. These values were significantly higher than zero indicating that the ectoparasite infracommunities were nested and were not merely random assemblages of arthropods. Many theories have been proposed to explain nestedness of communities. The observed species-richness and nestedness patterns seem to be a product of varied host habitat diversity, foraging and preening behaviour.

4.1 Introduction

Parasite communities are often very complex and interactions between different parasitic species within the same host may not be evident (Poulin, 1998). Understanding complex parasitic interactions may require treating parasitic communities as ecosystems on mobile islands. The study of insular communities entails the identification of different taxonomic groups and the analysis of patterns that reveal their interactions with one another (MacArthur and Wilson, 1967; Wilson, 1986; Krebs, 1989; Worthen, 1996). Substantial information on community structure can be obtained from insular communities by measuring species-richness, isolation and size of islands (Simberloff and Moore, 1997; Poulin, 1996, 1997, 1998). In more recent years, nestedness has been identified as a basic descriptor of community structure and has been used in studying fragmented communities and island ecosystems (Patterson and Atmar, 1986; Worthen, 1996). Parasite communities often have similar properties to island communities and island biogeography models may help elucidate patterns in community structure that are otherwise hard to perceive.

The theory of island biogeography predicts that smaller, more isolated islands are expected to have less species-rich communities compared to larger islands that are less isolated (MacArthur and Wilson, 1967). Species-richness of island communities is often correlated with island size, since the number and variety of available niches increase on larger islands. Monogenean gill parasites of cyprinid fishes illustrated a clear relationship between host size and species-richness (Guegan and Hugueny, 1994). Isolated islands often have lower species-richness since immigration rates of less dispersive species are low (MacArthur and Wilson, 1967). Applying these ideas to bird populations, Rozsa et al. (1996) found that group-living corvids harboured more species-rich louse loads compared to territorial species.

Analysis of species-richness in relation to size and social systems (colonial versus territorial) of hosts fails to provide sufficient information on the structure and composition

of communities (Worthen, 1996). Pairwise analysis of co-occurrences of different taxa may help elucidate competition (Connor and Simberloff, 1984) and guild structure (Worthen and McGuire, 1988). Many mathematical models that quantify community-level patterns have been proposed. In recent years, the analysis of nestedness or nested subset structure has become increasingly important for understanding communities (Patterson and Atmar, 1986; Cook, 1995; Worthen, 1996; Poulin, 1998). A community or assemblage forming structured, non-random subsets of more species-rich communities is said to be nested (Patterson and Atmar, 1986). Nestedness of parasite infracommunities would suggest that species-poor or depauperate infracommunities form distinct subsets of progressively richer infracommunities (Fig. 4.1.1). Analysis of nestedness may illuminate processes that shape infrapopulations and infracommunities of parasites.

Several hypotheses have been proposed to explain nestedness. Differential colonization rates of insular species may generate nested subset patterns (Patterson, and Atmar, 1986; Worthen, 1996; Wright et al., 1998). Species with good dispersal capabilities can colonize isolated islands; islands that are easier to colonize could be populated by both good and poor dispersers alike. Certain parasites of auks, like lice of the genus *Austromenopon*, could be regarded as good dispersers because of their ability to readily detach and seek new hosts (Eveleigh, 1974). Other louse genera found on auks, like *Quadraceps* and *Saemundssonina*, are relatively poor dispersers because they are not very mobile and are restricted to specific microhabitats on the host (Eveleigh, 1974; Choe and Kim, 1987). This difference in dispersal ability could be one of the several reasons responsible for nestedness in parasite infracommunities. Coloniality or gregariousness in hosts enhances transmission of ectoparasites (Rozsa et al., 1996) thereby potentially contributing to nestedness.

Extinction rates of insular species may also produce nested subset patterns (Patterson, and Atmar, 1986; Worthen, 1996; Wright et al., 1998). Decreasing population size usually increases the rate of extinction in ectoparasite communities (Pimm et al., 1988; Guegan and Hugueny, 1994). In addition, rates of extinction in avian ectoparasite communities may also be increased by preening (Hart, 1997). Forces causing or preventing extinction may generate patterns of nestedness.

Nested subsets of habitat types could lead to nestedness of communities (Wright et al., 1998). Specialists with restricted needs are expected to occur in particular habitat patches while generalists can be found in almost all habitats available (Worthen, 1996). Auks are known to harbour several specialist and generalist ectoparasites. *Saemundssonina* sp., for instance, occur primarily on the head region (Eveleigh, 1974; Choe and Kim, 1987) whereas the feather mites prefer the wings, although they can occur on other habitats as well (Choe and Kim, 1988). *Austromenopon* sp., on the other hand occur throughout the body with no particular preference for any specific microhabitat (Eveleigh, 1974; Choe and Kim, 1987). The nestedness of niche space and the requirements of infrapopulations may be important in creating nested subset structure in these ectoparasites. Heterogeneities in different habitats have also been shown to affect nested subset patterns in fish ectoparasites (Guegan and Hugueny, 1994).

Habitat diversity, diet and foraging strategies of hosts can generate nestedness in parasite communities (Guegan and Hugueny, 1994). Small cyprinid fish, for example, utilize habitats with higher current velocity than larger fish, making movement of gill parasites between small fish a function of water currents (Guegan et al., 1992). Similar variations in habitat utilization and foraging may influence ectoparasite community composition in the auks. Choe and Kim (1987) documented more species-rich ectoparasite infracommunities in Black-legged Kittiwakes (*Rissa tridactyla*) and Red-legged

Kittiwakes (*Rissa brevirostris*) compared to Thick-billed and Common Murres. They partly attributed these differences to a difference in nesting habits (kittiwakes are individual nest builders whereas murres nest in dense aggregations on cliffs) and foraging behavior (kittiwakes are surface feeders whereas murres are divers).

Nestedness has been investigated in relatively few parasite communities and documented nested patterns in the distributions of infracommunities are rare (Worthen and Rohde, 1996; Rohde et al., 1998; Poulin, 1998; Morand et al., 1999). Studies that have investigated nested structures have dealt primarily with ecto- and endoparasites of fish (Worthen and Rohde, 1996; Rohde et al., 1998; Morand et al., 1999) and endoparasites of birds and mammals (Poulin, 1996). Nestedness in ectoparasites of birds has not been investigated before (Worthen, 1996).

I selected four related host species of auks (Alcidae) in order to investigate ectoparasite species-richness and composition. The auk species (Alcidae) : Atlantic Puffin, *Fratercula arctica*; Razorbill, *Alca torda*; Thick-billed Murre, *Uria lomvia*; and Common Murre, *Uria aalge* vary considerably in breeding habitat selection and density at their breeding colonies (Gaston and Jones, 1998). These alcid species breed on headlands and small offshore islands of the Atlantic coast (Lock et al., 1994; Gaston and Jones, 1998).

Atlantic Puffins nest in burrows (varying in length from 70 to 110 cm) on grassy slopes (Harris, 1984; Gaston and Jones, 1998). Densities of 3 burrows/m² are typical although the average number of occupied burrows range from 0.4-0.6 burrows/ m² (Harris, 1984) Each burrow is occupied by only one pair of Puffins and hence direct contact between individuals (other than mates) in a colony normally occurs outside of the nest. The population estimate for Atlantic Canada is about 350 000 pairs (Nettleship and Evans, 1985; Gaston and Jones, 1998).

Razorbills nest on crevices among boulders and on cliff-edges (Cramp et al., 1985; Gaston and Jones, 1998) and breeding sites are separated by at least 10 cm, but typically by more than 30 cm, with densities reaching 4 pairs/m² (Cramp et al., 1985). In some populations, many nest sites are located 10m or more from the nearest neighbour (Lloyd et al., 1991). Estimates on the world population range from 500 000 - 700 000 pairs (Lloyd et al., 1991) out of which only about 4% breed in Eastern Canada (Gardarsson, 1985). The largest Razorbill colony on the east coast of North America is located in the Gannet Islands, Labrador (Birkhead and Nettleship, 1982).

Thick-billed and particularly Common Murres nest in the densest aggregations of any auk species (Gaston and Nettleship, 1981; Nettleship and Birkhead, 1985; Gaston and Jones, 1998). Thick-billed Murres nest in dense clumps and their nesting sites are typically located on narrow ledges (as little as 10 cm wide) along steep cliffs directly adjacent to the sea (Gaston and Nettleship, 1981; Gaston et al., 1985) with individuals usually remaining in contact with up to two neighbours from the sides on their nesting sites (Birkhead et al., 1985). Densities vary between 1 and 37 pairs/m² (Cramp et al., 1985).

Common Murres typically nest on broad, flat, rocky outcrops on headlands and offshore islands (Nettleship and Birkhead, 1985; Gaston and Jones, 1998). Birds clump next to one another with about a third of the birds being in physical contact with neighbors (Birkhead et al., 1985), with mean densities of 20 breeding pairs/m², although densities as high as 70 pairs/m² have been recorded (Cramp et al., 1985; Nettleship and Birkhead, 1985). This may perhaps be the densest nesting aggregations of any bird in the world (Nettleship and Birkhead, 1985) with breeding colonies being the largest among all the Atlantic auk species (e.g. 500 000 breeding pairs in Funk Island, Newfoundland; Nettleship and Evans, 1985).

In summary, Razorbills are less aggregated than Murres, both species of which are highly aggregated on their nesting sites; Thick-billed Murres are slightly less aggregated than Common Murres. Aggregation among individual Puffins is lower than Razorbills.

The objectives of this study were:

- 1) to determine the relationship of species richness of ectoparasite infracommunities to coloniality in host species
- 2) to determine the relationship of host size on the infracommunity species-richness of ectoparasites
- 3) to detect interactions between parasites by measuring nested subset structures in ectoparasite infracommunities
- 4) to determine if host coloniality affects the degree of nestedness and
- 5) to review the theories that explain nestedness of parasite infracommunities.

Based on the island biogeography model, it can be predicted that the murre species would have the most species-rich ectoparasite infracommunities whereas the Razorbills and puffins would have progressively less species-rich infracommunities. This outcome could be expected because of both size as well as coloniality of the host species. Within a given host species, larger hosts are expected to have richer ectoparasite infracommunities compared to smaller hosts. Nestedness, on the other hand, would be expected to increase with increasing similarity of communities. Since the murres are more aggregated and horizontal transmission of ectoparasites is high, the degree of nestedness is expected to decrease moving from murres to Razorbills to puffins.

4.2 Quantification and Statistical Analyses

The ectoparasites collected were identified and their presence in samples recorded (See Chapter 2 for details of study area and sampling technique). Species-richness was

compared among the four host species using Monte Carlo methods, based on 1000 randomizations. Within each host species, relationships between species richness and mass were compared using standard linear regression techniques and correlation coefficients.

The presence of nestedness in the four auk infracommunities was estimated using the following equation (Wright and Reeves, 1992):

$$C = \frac{N_c - E\{N_c\}}{\max\{N_c\} - E\{N_c\}}$$

where C = the index of relative nestedness

N_c = index of nestedness

$E\{N_c\}$ = expected value of nestedness

$\max\{N_c\}$ = maximum attainable value of N_c

The nestedness index (N_c) is directly proportional to the conditional probability that a given species is present in an infracommunity on a host, given that it is present on a more depauperate (species poor) infracommunity. The calculation of N_c allows the calculation of the relative nestedness index, C , which can be tested statistically with relative ease.

Values of C range from 0 (randomly distributed) to 1 (perfectly nested). The relative nestedness indices for each species was tested for significant departures from zero by Cochran's Q test (Wright and Reeves, 1992).

The differences in calculated C values between host species were compared using z-scores (Wright and Reeves, 1992), since randomization techniques used for comparison of nestedness do not yield significantly different results from z-score analyses (Rohde et al., 1998)

4.3: Results

4.3.1: Richness

Razorbills supported richer species assemblages compared to Atlantic Puffins, Thick-billed Murres and Common Murres ($P < 0.004$ in all cases, based on 1000 randomizations; Table 4.3.1). Atlantic Puffins also had significantly higher species-richness compared to the two murre species ($P < 0.001$ in both cases). No association was found between mass of host and species richness of parasites (r^2 values not significant, $P >> 0.05$). Fig. 4.3.1 illustrates mass plotted against richness in Thick-billed Murres.

4.3.2: Nestedness

Nested subset patterns were evident in the infracommunities of all four auks because all the values of C obtained were significantly higher than zero (Table 4.3.2) illustrating non-random structure. Comparisons between the C values of the four species showed that the differences noted among host species were significant for each pairwise comparison, showing that the different values of C reflected different levels of nestedness in the ectoparasite communities of the four auk species (Table 4.3.3).

4.4: Discussion

Richness

Atlantic Puffins and Razorbills had higher richness compared to the two murres, suggesting that host aggregation could have a relationship with species-richness. However, this was contrary to the prediction of the island biogeography model in which a lower species-richness is expected in the more isolated species (puffins and Razorbills). Thus,

species-richness of ectoparasites of auks may be controlled by other factors in addition to coloniality and factors not explained by the island biogeography model may be operating.

The lack of an association between host body mass and richness also showed that richness did not covary positively with host size as one would expect from the island biogeography theory (MacArthur and Wilson, 1967). The island biogeography theory does not fully apply to ectoparasites of seabirds because the hosts are not true "islands". During the activity period of auk hosts, a less aggregated individual (e.g. a puffin) may come in physical contact with one or more individuals several times a day regardless of its otherwise isolated nesting burrow. Additionally, many parasite species, such as ticks (*Ixodes uriae*), that are parasitic to the four auks in this study spend most of their lives in the soil (Eveleigh and Threlfall, 1976). Their presence on the auks depends on the amount of time spent by the auks on the colony, providing opportunity for these ticks to find a host. Furthermore, because temporary parasites contribute considerably to species-richness of the ectoparasite infracommunities, the island biogeography theory and its assumptions may not be sufficient to explain observed patterns of parasite species-richness because it was intended to predict species-richness of resident species (MacArthur and Wilson, 1967).

Nestedness

To my knowledge, this is the first record of nested subset patterns in ectoparasite species assemblages of birds. Significant nestedness observed in the infracommunities of all four auk species examined suggests that nestedness could be a fairly common pattern in seabird ectoparasite communities. Ecto- and endoparasites of fish (Worthen and Rohde, 1996; Rohde et al., 1998; Morand et al., 1999), and endoparasites of birds and mammals (Poulin, 1996) typically have randomly distributed infracommunities in most cases.

Generalizations on the apparent rarity of nested subset patterns in parasite communities made by Poulin (1998), based primarily on studies of endoparasites, may not apply to avian ectoparasite communities, since nestedness in ectoparasite communities has never been studied.

Several mechanisms have been proposed to account for nestedness in natural communities (Patterson and Atmar, 1986; Worthen et al. 1996; Wright et al., 1998) and many of these mechanisms may operate at the parasite infracommunity level (Guegan and Hugueny, 1994). I believe that the following three mechanisms are important in determining nestedness in the ectoparasite communities of the four auk species studied.

Differential colonization rates

The importance of differential colonization in causing nestedness of species-assemblages has been emphasized in many studies (Patterson and Atmar, 1986; Worthen, 1996). The relationship between observed nestedness of ectoparasite infracommunities and ectoparasite dispersal abilities was not directly examined in this study. However, previous studies on the ectoparasites of the Atlantic auks have shown that some of their ectoparasites are acquired faster than others (Eveleigh and Threlfall, 1976). Experimental work would be required to quantify ectoparasite dispersal ability and the resulting relationship with nestedness.

Density-dependent extinction

Closely linked with differential colonization rates is the rate of extinction of species, another factor believed to create nestedness in natural communities (Patterson and Atmar, 1986). Mathematical models of free-living insular organisms indicate that the probability of extinction of a species increases with decreasing population size (Schaffer and Samson, 1985; Pimm et al., 1988). In addition, extinction rates of the ectoparasites of birds could

also be affected by behavioural responses such as preening (Cotgreave and Clayton, 1994; Hart, 1997). The four auks in the present study have very different bill morphology with Puffins having laterally compressed, deep bills; Razorbills having less compressed, longer bills; and the Murres having elongate, pointed bills (Gaston and Jones, 1998). It has been shown that variations in bill dimensions prevent adequate preening in many avian hosts (Cotgreave and Clayton, 1994). Based on Cotgreave and Clayton's (1994) study, the murres would seem to be more efficient in preening ectoparasites particularly the smaller ones taxa, such as feather mites. Puffins and razorbills would generally be expected to be less efficient in removing some ectoparasites. However, no data exists on the preening efficiency of the four host species in this study. Allopreening (preening another bird) has been observed in all four auks, although the extent to which it influences parasite extinction rates has not been determined (Gaston and Jones, 1998). Allopreening reduces ectoparasite loads considerably in certain penguin species (Hart, 1997). It seems plausible to assume that ectoparasite extinction rates resulting from behavioral adaptations of the auk hosts may have an influence on nestedness of ectoparasite infracommunities.

Host-habitat relationships

Habitat diversity and the diet and foraging strategies of hosts all affect parasite communities (Choe and Kim, 1987; Guegan et al., 1992; Guegan and Hugueny, 1994). In the present study, species richness was generally higher in Puffins and Razorbills, although it was significantly higher in the Razorbills compared to both murres. Several factors could have been responsible for this variation in richness and hence nestedness. Habitat type used by the four auks were different, the Puffins using grassy habitat and Razorbills and Murres using rocky habitat (See Chapter 3). Certain soil arthropods preferring grassy over rocky habitats would thus be unlikely to be represented in the

infracommunities of Razorbills and Murres. In addition to habitat, the aggregation in the auks could have enhanced horizontal transmission (Chapter 3), changing patterns of infracommunity richness, since both prevalence and relative abundance are highly correlated with richness (Shaw and Dobson, 1995). Increased transmission in aggregated host species could produce greater similarity among individuals, thereby increasing nestedness (see beta diversity below). The observed nestedness scores were contrary to the expectation, since nestedness was higher in the less aggregated host species which had lower horizontal transmission of ectoparasites (Chapter 3). A third factor could be responsible for this counter intuitive observation. Foraging behavior of the auks could have modified richness by selecting against ectoparasites that are not adapted to submersions during a dive (Choe and Kim, 1987). Deeper diving Murres would be expected to have different parasite infracommunities compared to Razorbills and puffins based on the adaptations of their ectoparasites (Choe and Kim, 1988; Burger, 1991). Diving behaviour and ectoparasite abundance was not investigated in this study. A combination of all of the above factors could have produced the observed patterns of nestedness of the ectoparasite infracommunities of the four auk species.

Nestedness was significantly different among the four auk species and host-coloniality had a negative relationship with observed nestedness scores. The largest differences in nestedness were observed among the puffins and the two murres, the species with the most contrasting colonial aggregations (Tables 4.3.2 and 4.3.3). Razorbills showed less, but significant, differences in nestedness scores compared to puffins and the murres, since they represented the "moderately" aggregated host species. These values implied that host coloniality had a relatively strong influence on nested subset patterns of ectoparasite infracommunities. Additionally, coloniality might also indirectly influence nestedness by altering differential colonization rates of certain ectoparasites (as noted above) when horizontal transmission is high (Rozsa et al., 1996; Rekası et al., 1997; Chapter 3).

The meaning of nestedness

The observed nested subset patterns in the ectoparasite infracommunities show that the distributions are not random assemblages. Rather, the distribution has structure that is governed by processes that affect individuals and populations of parasites as well as their hosts. Relative nestedness is strongly negatively correlated with beta diversity (a measure of the similarity of the species composition of communities ; Wright and Reeves, 1992). The beta diversity of a group of communities decreases as the similarity in the species-composition of the communities increases. An increase in nestedness correlates with a decrease in beta diversity (an increase in the similarity of the communities). The nestedness scores of the infracommunities of the four auk species were low, implying that the compositions of the different infracommunities (in a given host species) were very dissimilar. In other words, the level of exposure and/or susceptibility of individual hosts to the range of parasites differed considerably. Conversely, higher nestedness scores would suggest low beta diversity, which in turn would mean that the hosts did not vary in their exposure and/or susceptibility to infection by some of the parasites in the parasite component community.

4.5: Conclusion

Patterns of ectoparasite species-richness did not correlate positively with coloniality of hosts nor did it increase with host size within host species. Nested subset structures were evident in ectoparasite infracommunities in the four auk host species. Relative nestedness differed among the four species and this difference seemed to have a link with host coloniality. The causes of nestedness are varied and hard to isolate, but extinction rates of ectoparasites, determined by several factors including preening by the host, could

cause nestedness in the examined auk species. Habitat diversity and foraging behaviour of alcid hosts also are potential contributors to nestedness. More empirical evidence to evaluate these hypotheses is required. The observed nestedness also suggests that individuals of each of the four host species differed in their exposure and/or susceptibility to infestation by the range of ectoparasites of each host species.

Table 4.3.1 Mean species richness of the ectoparasite infracommunities from the four host species. Standard errors of the mean were estimated using bootstrap methods.

	N	Mean richness	Standard Error
Atlantic Puffin	30	3.0	0.31
Razorbill	18	4.1	0.52
Thick-billed Murre	29	1.9	0.28
Common Murre	29	2.3	0.33

Table 4.3.2 Relative nestedness indices (C) of the four Alcid species, and associated Cochran's Q , degrees of freedom, and probability values.

Host Species	C	Q	df	P
Atlantic Puffin	0.298	187.2	19	<<0.005
Razorbill	0.252	91.2	18	<<0.005
Thick-billed Murre	0.123	58.0	15	<<0.005
Common Murre	0.169	72.3	16	<<0.005

Table 4.3.3 Comparison between the relative nestedness (C) across the four auk species.

Host a	Host b	$z_{a,b}$ (based on C values)
Atlantic Puffin	Razorbill	4.9**
Atlantic Puffin	Common Murre	25.6**
Atlantic Puffin	Thick-billed Murre	36.3**
Razorbill	Common Murre	8.9**
Razorbill	Thick-billed Murre	14.2**
Thick-billed Murre	Common Murre	9.5**

** indicates $P < 0.005$. $z_{a,b}$ refers to differences between the z -scores based on the relative nestedness (C) of hosts 'a' and 'b'.

a

Infracomunities (individual birds)	Species					
	A	B	C	D	E	F
1	*	*	*	*	*	*
2	*	*	*	*	*	
3	*	*	*	*		
4	*	*	*			
5	*	*				
6	*					

b

Infracomunities (individual birds)	Species					
	A	B	C	D	E	F
1	*	*	*	*		*
2	*	*		*	*	*
3		*	*	*	*	
4				*	*	*
5		*	*			
6	*					*

Fig.4.1.1 Two hypothetical sets of infracomunities illustrating nestedness. Each row represents an infracomunity whereas the columns show the species (A-F) found in the various infracomunities (denoted by asterisks) a) shows species depauperate communities as perfectly nested subsets of species rich communities. b) shows a random pattern and species depauperate communities are not nested subsets of richer infracomunities. The average infracomunity richness and the average prevalence of each species are the same in both the examples. (Adapted from Poulin, 1998)

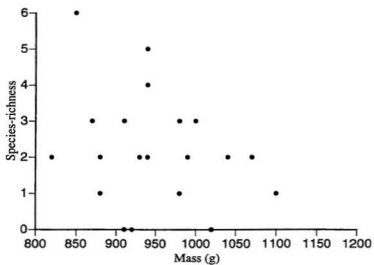


Fig. 4.3.1 Relationship between infracommunity richness and mass in Thick-billed Murres ($r^2=0.05$; $P=0.32$).

Chapter 5

General Discussion

5.1 Diversity and ectoparasite community structure

The number of species of ectoparasites found in this study were similar to those reported from auks by others (Eveleigh, 1974; Ballard and Ring, 1979; Choe and Kim, 1987). The rather high diversity of ectoparasites implies that ectoparasites have adaptations that help them cope with stresses related to the diving behaviour of their host auk species (Burger, 1991).

What processes create and maintain such diverse ectoparasite assemblages? The answer to this question lies in the analyses of the observed patterns in this study. Coloniality had been suggested as a primary agent shaping avian ectoparasitic communities (Rozsa et al., 1996). However, my study suggested that host aggregation or coloniality only affected the distribution and abundance of certain ectoparasitic taxa, with the majority of taxa being unaffected. The coloniality of hosts may be responsible for creating a balance between moderate to high loads in chicks and adults, potentially affecting lifetime reproductive success of the species.

The presence of nested subset patterns in ectoparasite communities indicated that other forces contribute to the structuring of these communities exist. One such force could be host behaviour. Preening, for example, could help reduce ectoparasite loads of certain taxa only (Eveleigh and Threlfall, 1976). Spatial distributions of ectoparasites on individual hosts could be caused by preening as well as differences in microhabitat requirements of specific ectoparasites (Choe and Kim, 1987). Individual variation among host-preening may generate differences in parasitic communities large enough to affect host fitness.

Almost nothing is known about the fate of ectoparasite communities after the hosts leave the breeding colonies and return to a pelagic existence at sea. There is a marked decline in the resident parasites in winter, but whether reproduction takes place at all during this period is not certain (Eveleigh and Threlfall, 1976). A more complete picture of the nature of these host-parasite assemblages can be obtained by investigating parasite abundance during the winter, when the auk hosts are at sea.

5.2 Future research

The ectoparasite loads of breeding auks have been quantified and compared in this study. The technique used needs modification and a correction factor for the estimates of density and species-richness needs to be determined. A small number of euthanized auks could be left in the delouser for different lengths of time and the rate of parasite removal could be tested for time dependence.

Analyses of the ectoparasitic communities of auks outside the breeding season could be challenging. Capturing live birds could be difficult, but birds taken during the Newfoundland turr hunt (Common and Thick-billed Murres are locally called turrs), open for a brief period in fall, could represent a possible source of freshly killed hosts.

Studies on breeding auks should be carried out in conjunction with studies of endoparasites to answer questions of disease transmission and prevalence. *Austromenopon* spp., for example, have been shown to carry infective and larval stages of the filarial worm genus, *Eulimdana*, in charadriiform hosts but whether *Austromenopon* spp. of auks carry *Eulimdana* is not known (Bartlett, 1993). The long-term affects of this worm on the auks, if any, should be determined. Other helminths, like *Alcataenia* spp. occur in auks (Hoberg, 1986). Some of the ectoparasites described in this

study could serve as intermediate hosts for this genus. More studies are needed to reveal such associations.

A focus should also be placed on long-term studies encompassing different colonies. Annual variations in parasite abundance could influence host reproductive success. Additional knowledge about the temporal and spatial distribution and abundance of parasites could provide information on the evolutionary history of host-parasite assemblages (Hoberg, 1986). Host-parasite coevolution may be evident in some parasitic species whereas events of host-switching may be evident in others (Rozsa, 1993). Long-term studies on entire systems covering separated geographic locations could answer questions relating to the evolution of such systems.

The study of wildlife parasitology is interesting in its own right and with every question answered, more new questions emerge. This study answered a question relating to host social systems and ectoparasite burdens. It also showed the importance of studying parasites as communities and the presence of non-random structure in the distribution of ectoparasitic communities. Both endoparasites and ectoparasites need to be studied in order to obtain a better perspective on avian parasitology.

APPENDIX I : Classification

Classification scheme of the insects collected in this study, based on Arnett, Jr. (1993) and Stehr (1987).

Class INSECTA

Order Mallophaga¹⁾

Suborder Ischnocera

Family Philopteridae

Saemundssonia calva

Saemundssonia fraterculae

Saemundssonia celidoxa

*Quadriceps obliqua*²

Quadriceps helgovauki

Quadriceps alcae

Suborder Amblycera

Family Menoponidae

Austromenopon uriae

Austromenopon nigropleurum

Order Coleoptera

Family Staphylinidae

Subfamily Aleocharinae

Order Thysanoptera

Order Diptera

Suborder Brachycera

Infraorder Muscomorpha³

Order Collembola

Order Siphonaptera

Family Ceratophyllidae

Subfamily Ceratophyllinae

Orchopeas leucopus

1. The order Mallophaga is also regarded as a suborder within the order Phthiraptera (e.g. Borror, 1981)

2. The genus *Cummingsiella* is regarded as being synonymous to *Quadriceps* by Timmermann (1957). This view is maintained in this study, although both names are used frequently in the literature. Timmermann (1957) and (1963) presented the most comprehensive work on the Charadriiform louse genera.

3. Also Cyclorrhaphous Brachycera

APPENDIX I: Classification

Classification scheme of the Acarine taxa collected in this study, based on Krantz (1978), Wheeler and Threlfall (1989), and Sonenshine (1991).

Class ARACHNIDA

Subclass ACARI (Ticks and mites)

Order Parasitiformes

Suborder Ixodida¹

Superfamily Ixodoidea

Family Ixodidae (Hard ticks)

Ixodes uriae

Order Acariformes

Suborder Acaridida²

Superfamily Analgoidea

Family Alloptidae (feather mites)

Alloptes spp.³

Suborder Oribatida⁴

unknown Acari

1. Also Metastigmata

2. Suborder was named Sarcoptiformes (Baker, 1952) and Astigmata (Krantz, 1970), both cited in Krantz(1978).

3. The subgenus *Conuralloptes* is recognized within the genus *Alloptes* of the Alcidæ

4. Also Cryptostigmata

References

- Anderson, J. F., Johnson, R. C., Magnarelli, L. A. & Hyde, F. W. 1986. Involvement of birds in the epidemiology of the Lyme Disease agent *Borrelia burgdorferi*. *Infection and Immunity*, **51**, 394-396.
- Anderson, R. M., Gordon, D. M., Crawley, M. J. & Hassel, M. P. 1982. Variability in the abundance of animal and plant species. *Nature*, **296**, 245-248.
- Arnett, R. H., Jr. 1993. *American Insects - A handbook of the insects of America north of Mexico*. Gainesville, Florida: The Sandhill Crane Press, Inc.
- Arthur, D. R. 1970. Tick feeding and its implications. *Advances in Parasitology*, **8**, 275-292.
- Baer, J. G. 1952. *Ecology of Animal Parasites*. Urbana, Illinois: University of Illinois Press.
- Ballard, J. T. & Ring, R. A. 1979. The ectoparasites of some marine birds from Bamfield Marine Station, British Columbia, with particular reference to common murre, *Uria aalge* (Pont.). *Canadian Journal of Zoology*, **57**, 1980-1984.
- Balogh, J. 1972. *The Oribatid Genera of the World*. Budapest: Akademiai Kiado.
- Bartlett, C. M. 1993. Lice (Amblycera and Ischnocera) as vectors of *Eulimdana* spp. (Nematoda: Filarioidea) in Charadriiform birds and the necessity of short reproductive periods in adult worms. *Journal of Parasitology*, **79**, 85-91.
- Bergstrom, S., Haemig, P. D. & Olsen, B. 1999. Increased mortality of black-browed albatross chicks at a colony heavily-infested with the tick *Ixodes uriae*. *International Journal for Parasitology*, **29**, 1359-1361.
- Birkhead, T. R. 1985. Coloniality and social behaviour in the Atlantic Alcidae. In: *The Atlantic Alcidae* (Ed. by Nettleship, D. N. & Birkhead, T. R.), pp. 355-383. London: Academic Press.
- Birkhead, T. R., Johnson, S. D. & Nettleship, D. N. 1985. Extra-pair matings and mate-guarding in the Common Murre *Uria aalge*. *Animal Behaviour*, **33**, 608-619.
- Birkhead, T. R. & Nettleship, D. N. 1982. Studies of the alcids breeding at the Gannet Clusters, Labrador, 1981. Nova Scotia: Canadian Wildlife Service.
- Blanco, G., Jose, L. T. & Potti, J. 1997. Feather mites on group-living Red-billed Coughs: a non-parasitic interaction? *Journal of Avian Biology*, **28**, 197-206.
- Bliss, C. I. & Fisher, R. A. 1953. Fitting the negative binomial distribution to biological data. *Biometrics*, **9**, 176-200.

- Borgia, G. & Collis, K. 1990. Parasites and bright male plumage in the Satin Bowerbird (*Ptilonorhynchus violaceus*). *American Zoologist*, **30**, 279-285.
- Borror, D. J., DeLong, D. M. & Triplehorn, C. A. 1981. *An Introduction to the Study of Insects*. Philadelphia: Saunders College Pub.
- Boulinier, T., Ives, A. R. & Danchin, E. 1996. Measuring aggregation of parasites at different host population levels. *Parasitology*, **112**, 581-587.
- Brooks, D. R. & McLennan, D. A. 1993. *Parascript, parasites and the language of evolution*. Washington: Smithsonian Press.
- Burger, A. E. 1991. Maximum diving depths and underwater foraging in alcids and penguins. In: *Studies of high-latitude seabirds. I. Behavioural, energetic and oceanographic aspects of seabird feeding ecology* (Ed. by Montevecchi, W. A. a. G., A. J.): Canadian Wildlife Service.
- Burt, E. H., Jr. & Ichida, J. M. 1999. Occurrence of feather-degrading bacilli in the plumage of birds. *Auk*, **116**, 364-372.
- Bush, A. O., Lafferty, K. D., Lotz, J. M. & Soshtak, A. W. 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. *Journal of Parasitology*, **83**, 575-583.
- Byrd, G. V., Murphy, E. C., Kaiser, G., Kondratyev, A. Y. & Shibaev, Y. V. 1993. Status and ecology of offshore fish-feeding alcids (murres and puffins) in the North Pacific. In: *The status, ecology and conservation of marine birds of the North Pacific* (Ed. by Vermeer, K., Briggs, K. T., Morgan, K. H. & Siegel-Causey, D.), pp. 176-186. Ottawa: Canadian Wildlife Service.
- Canestrini, G. & Kramer, P. 1899. Demodicidae und Sarcoptidae. *Tierreich*, **7**, 1-193.
- Casidia, J. E. & Quistad, G. B. 1995. *Pyrethrum flowers: production, chemistry, toxicology and uses*. Oxford: Oxford University Press.
- Cheng, T. C. 1986. *General Parasitology*. Orlando, Florida: Academic Press.
- Choe, J. C. & Kim, K. C. 1987. Community structure of arthropod ectoparasites on Alaskan seabirds. *Canadian Journal of Zoology*, **65**, 2998-3005.
- Choe, J. C. & Kim, K. C. 1988. Microhabitat preference and coexistence of ectoparasitic arthropods on Alaskan seabirds. *Canadian Journal of Zoology*, **66**, 987-997.
- Choe, J. C. & Kim, K. C. 1989. Microhabitat selection and coexistence in feather mites (Acari: Analgoidea) on Alaskan seabirds. *Oecologia*, **70**, 10-14.
- Choe, J. C. & Kim, K. C. 1991. Microhabitat selection and adaptation of feather mites (Acari: Analgoidea) on murres and kittiwakes. *Canadian Journal of Zoology*, **69**, 817-821.

- Clay, T. 1959. Key to the species of *Austromenopon* Bedford (Mallophaga) parasitic on the Charadriiformes. *Proceedings of the Royal Entomological Society of London (Series-B)*, **28**, 157-168.
- Clayton, D. H. 1990. Mate choice in experimentally parasitized Rock Doves: lousy males lose. *American Zoologist*, **30**, 251-262.
- Clayton, D. H. 1999. Feather busting bacteria. *Auk*, **116**, 302-304.
- Clayton, D. H., Gregory, R. D. & Price, R. D. 1992. Comparative ecology of Neotropical bird lice (Insecta: Phthiraptera). *Journal of Animal Ecology*, **61**, 781-795.
- Clayton, D. H. & Moore, J. 1997. Host-Parasite Evolution: General Principles and Avian Models., pp. 473. Oxford: Oxford University Press.
- Clayton, D. H. & Walther, B. A. 1997. Collection and quantification of arthropod parasites of birds. In: *Host-Parasite Evolution* (Ed. by Clayton, D. H. a. M., J.), pp. 473. Oxford: Oxford University Press.
- Connor, E. F. & Simberloff, D. 1984. Neutral model of species co-occurrence patterns. In: *Ecological communities: conceptual issues and the evidence* (Ed. by Strong, D. R., Simberloff, D., Abele, L. G. & Thistle, A. B.), pp. 316-331. Princeton, NJ: Princeton University Press.
- Cook, R. R. 1995. The relationship between nested subsets, habitat subdivisions and species diversity. *Oecologia*, **101**, 205-210.
- Cotgreave, P. & Clayton, D. H. 1994. Comparative analysis of time spent grooming by birds, in relation to parasite loads and other factors. *Behaviour*, **131**, 171-187.
- Cramp, S., Brooks, D. J., Dunn, E., Gillmor, R., Hollom, P. A. D., Hudson, R., Nicholson, E. M., Ogilvie, M. A., Olney, P. J. S., Roselaar, C. S., Simmons, K. E. L., Voous, K. H., Wallace, D. I. M., Wattel, J. & Wilson, M. G. 1985. Handbook of the Birds of Europe, the Middle East and North Africa: The Birds of the Western Palearctic., pp. 960. Oxford: Oxford University Press.
- Crofton, H. D. 1971. A quantitative approach to parasitism. *Parasitology*, **62**, 179-193.
- Danchin, E. 1992. The incidence of the tick parasite *Ixodes uriae* in Kittiwake *Rissa tridactyla* colonies in relation to the age of the colony, and a mechanism of infecting new colonies. *Ibis*, **134**, 134-141.
- Davis, J. A. & Brown, C. R. 1999. Costs of coloniality and the effect of colony size on reproductive success in purple martins. *Condor*, **101**, 737-745.
- Dogiel, V. A. 1964. *General Parasitology*. London: Oliver and Boyd.

- Dubinin, V. B. 1951. Feather mites (Analgesoidea). Part I. Introduction to their study. *Fauna U.S.S.R.*, **6**, 1-363.
- Duffy, D. C. 1983. The ecology of tick parasitism on densely nesting Peruvian seabirds. *Ecology*, **64**, 110-119.
- Duffy, D. C. 1991. Ants, ticks and nestling seabirds: dynamic interactions. In: *Bird-parasite Interactions: Ecology, Evolution and Behavior* (Ed. by Loye, J. E. & Zuk, M.), pp. 243-257. Oxford: Oxford University Press.
- Emerson, K. C. 1972. Checklist of the Mallophaga of North America (North of Mexico) Part IV: Bird host list. Dugway, Utah: Deseret Test Center.
- Emerson, K. C. & Price, R. D. 1985. The identity of *Quadriceps crassipedalis* (Harrison) and two new species of *Quadriceps* (Mallophaga: Philopteridae). *Proceedings of the Entomological Society of Washington*, **87**, 395-401.
- Eveleigh, E. S. 1974. A study of the ectoparasites of Alcids of Newfoundland. M.Sc. Thesis, Department of Biology, Memorial University of Newfoundland, St. John's, Newfoundland, Canada 176pp.
- Eveleigh, E. S. & Threlfall, W. 1974. A new species, and notes on a previously described species of *Austromenopon* Bedford, 1939 (Mallophaga: Amblycera) from Alcids (Aves: Charadriiformes). *Proceedings of the Entomological Society of Washington*, **76**, 271-277.
- Eveleigh, E. S. & Threlfall, W. 1975. Bionomics of *Ixodes (Ceratixodes) uriae* White 1852 on auks (Alcidae) from Newfoundland. *Canadian Journal of Zoology*, **53**, 82-86.
- Eveleigh, E. S. & Threlfall, W. 1976. Population dynamics of lice (Mallophaga) on auks (Alcidae) from Newfoundland. *Canadian Journal of Zoology*, **54**, 1694-1711.
- Fitzpatrick, C. & Threlfall, W. 1977. The ectoparasites of three species of seabirds from Newfoundland, Canada. *Canadian Journal of Zoology*, **55**, 1205-1209.
- Fowler, J. A. & Miller, C. J. 1984. Non-hematophagous ectoparasite populations of Procellariiform birds in Shetland, Scotland. *Seabird*, 23-30.
- Fowler, J. A. & Williams, R. 1985. Population dynamics of Mallophaga and Acari on Reed Buntings occupying a communal winter roost. *Ecological Entomology*, **10**, 377-383.
- Gardarsson, A. 1985. The huge bird-cliff, Latrabjarg, in Western Iceland. *Environmental Conservation*, **12**, 83-84.
- Gaston, A. J. & Jones, I. L. 1998. *The Auks*. Oxford: Oxford University Press.

- Gaston, A. J. & Nettleship, D. N. 1981. *The Thick-billed Murres of Prince Leopold Island*. Ottawa: Canadian Wildlife Service Monograph No. 6.
- Gaston, A. J., Deforest, L. N., Donaldson, G. & Noble, D. G. 1994. Population parameters of Thick-billed Murres at Coats Island, Northwest Territories, Canada. *Condor*, **96**, 935-948.
- Gaud, J. & Atyeo, T. 1996. *Feather Mites of the World (Acarina, Astigmatida): the Supraspecific Taxa Parts I & II.*: Koninklijk Museum voor Midden-Afrika Tervuren, Belgie; Annalen Zoologische Wetenschappen.
- Gauthier-Clerc, M., Clerquin, Y. & Handrich, Y. 1998. Hyperinfestation by ticks *Ixodes uriae* : a possible cause of death in adult King Penguins, a long-lived seabird. *Colonial Waterbirds*, **21**, 229-233.
- Green, R. H. 1966. Measurement of non-randomness in spatial distributions. *Researches in Population Ecology*, **8**, 1-7.
- Guegan, J. F. & Huguency, B. 1994. A nested parasite species subset pattern in tropical fish: host as major determinant of parasite infracommunity structure. *Oecologia*, **100**, 184-189.
- Guegan, J. F., Lambert, A., Leveque, C., Combes, C. & Euzet, L. 1992. Can host body size explain the parasite species richness in tropical freshwater fishes? *Oecologia*, **90**, 197-204.
- Harris, M. P. 1984. *The Puffin*. London: T. and A. D. Poyser.
- Hart, B. L. 1997. Behavioural defence. In: *Host-Parasite Evolution: General Principles and Avian Models* (Ed. by Clayton, D. H. & Moore, J.), pp. 59-77. Oxford: Oxford University Press.
- Hoberg, E. P. 1986. Evolution and historical biogeography of a parasite-host assemblage, *Alcataenia* spp. (Cyclophyllidae: Dilepididae) in Alcidae (Charadriiformes). *Canadian Journal of Zoology*, **64**, 2576-2589.
- Holland, G. P. 1984. The fleas of Canada. Alaska and Greenland. *Memoirs of the Entomological Society of Canada*, **130**, 1-631.
- Holmes, J. C. & Price, P. W. 1986. Communities of Parasites. In: *Community Ecology: Pattern and Process* (Ed. by Kikkawa, J. & Derek, A. J.), pp. 187-213. London: Blackwell Scientific Publications.
- Hopkin, S. P. 1997. *Biology of Springtails (Insecta: Collembola)*. Oxford: Oxford University Press.
- Hubalek, Z. 1976. Interspecific affinity among keratinolytic fungi associated with birds. *Folia Parasitologica*, **23**, 267-272.

- Hubalek, Z. 1978. Coincidence of fungal species associated with birds. *Ecology*, **59**, 438-442.
- Kaneko, N., McLean, M. A. & Parkinson, D. 1995. Grazing preference of *Onychiurus subtenuis* (Collembola) and *Oppeia nova* (Oribatei) for fungal species inoculated on pine needles. *Pedobiologia*, **39**, 538-546.
- Keirans, J. E. & Clifford, C. M. 1978. The genus *Ixodes* in the United States: a scanning electron microscope study and key to the adults. *Journal of Medical Entomology*, **Supplement 2**, 1-149.
- Krantz, G. W. 1978. *A Manual of Acarology*. Corvallis, Oregon: Oregon State University Book Stores, Inc.
- Krebs, C. J. 1989. *Ecological Methodology*. New York: Harper & Row.
- Lewis, T. 1973. *Thrips- their biology, ecology and economic importance*. London: Academic Press.
- Lloyd, C. S., Tasker, M. L. & Partridge, K. 1991. *The status of seabirds in Britain and Ireland*. London: T. and A. D. Ployser.
- Lock, A. R., Brown, R. G. B. & Gerriets, S. H. 1994. Gazetteer of the marine birds of Atlantic Canada - an atlas of seabird vulnerability to oil pollution.: Canadian Wildlife Service.
- Loye, J. E. & Zuk, M. 1991. Bird-parasite Interactions: Ecology, Evolution and Behavior., pp. 406. Oxford: Oxford University Press.
- Ludwig, J. A. & Reynolds, J. F. 1988. *Statistical Ecology - a primer on methods and computing*. New York: John Wiley & Sons.
- Luxton, M. 1972. Studies on the oribatid mites of a Danish beech wood soil. I. Nutritional biology. *Pedobiologia*, **12**, 434-463.
- MacArthur, R. H. & Wilson, E. O. 1967. *The theory of island biogeography*. Princeton, NJ: Princeton University Press.
- Manly, B. F. J. 1991. *Randomization and Monte Carlo Methods in Biology*. London: Chapman & Hall.
- Margolis, L., Esch, G. W., Holmes, J. C., Kuris, K. M. & Schad, G. A. 1982. The use of ecological terms in parasitology. *Journal of Parasitology*, **68**, 131-133.
- Marshall, A. G. 1981. *The Ecology of Ectoparasitic Insects*. London: Academic Press.
- McClure, H. E. 1989. Occurrence of feather mites (Proctophyllodidae) among birds of Ventura County lowlands, California. *Journal of Field Ornithology*.

- McCoy, K. D., Boulinier, T., Chardine, J., Danchin, E. & Michalakakis, Y. 1999. Dispersal and distribution of the tick *Ixodes uriae* within and among seabird host populations: the need for a population genetic approach. *Journal of Parasitology*, **85**, 196-202.
- Mehl, R. & Traavik, T. 1983. The tick *Ixodes uriae* (Acari, Ixodidae) in seabird colonies in Norway. *Fauna Norvegica Series B.*, **30**, 94-107.
- Morand, S., Poulin, R., Rohde, K. & Hayward, C. 1999. Aggregation and species coexistence of ectoparasites of marine fishes. *International Journal for Parasitology*, **29**, 663-672.
- Morbey, Y. E. 1996. The abundance and effects of ticks (*Ixodes uriae*) on nestling Cassin's Auklets (*Ptychoramphus aleuticus*) at Triangle Island, British Columbia. *Canadian Journal of Zoology*, **74**, 1585-1589.
- Nettleship, D. N. & Birkhead, T. R. 1985. The Atlantic Alcidae., pp. 574. London: Academic Press.
- Nettleship, D. N. & Evans, P. G. H. 1985. Distribution and status of the Atlantic Alcidae. In: *The Atlantic Alcidae* (Ed. by Nettleship, D. N. & Birkhead, T. R.), pp. 54-149. London: Academic Press.
- Olsen, B., Jaenson, T. G. T., Noppa, L., Bunikis, J. & Bergstrom, S. 1993. A Lyme borreliosis cycle in seabirds and *Ixodes uriae* ticks. *Nature*, **362**, 340-342.
- Oniki, Y. & Butler, J. F. 1989. The presence of mites and insects in the gut of two species of chewing lice (*Myrsidea* sp. and *Philopterus* sp., Mallophaga): accident or predation. *Rev. Brasil. Biol.*, **49**, 1013-1016.
- Oprandy, J. J., Schwan, T. G. & Main, A. J. 1988. Tick-borne Kemerovo group orbiviruses in a Newfoundland seabird colony. *Canadian Journal of Microbiology*, **34**, 782-786.
- Patterson, B. D. & Atmar, W. 1986. Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biological Journal of the Linnean Society*, **28**, 65-82.
- Pimm, S. L., Jones, H. L. & Diamond, J. M. 1988. On the risk of extinction. *American Naturalist*, **132**, 757-785.
- Poiani, A. 1992. Ectoparasitism as a possible cost of social life: a comparative analysis using Australian passerines (Passeriformes). *Oecologia*, **92**, 429-441.
- Poulin, R. 1991. Group-living and infestation by ectoparasites in passerines. *Condor*, **93**, 418-423.
- Poulin, R. 1996. Richness, nestedness, and randomness in parasite infracommunity structure. *Oecologia*, **105**, 545-551.

- Poulin, R. 1997. Species richness of parasite assemblages: evolution and patterns. *Annual Review of Ecology and Systematics*, **28**, 341-358.
- Poulin, R. 1998. *Evolutionary Ecology of Parasites: From individuals to communities*. London: Chapman and Hall.
- Rand, P. W., Lacombe, E. H., Smith, R. P., Jr, Rich, S. M., Kilpatrick, C. W., Dragoni, C. A. & Caporale, D. 1993. Competence of *Peromyscus maniculatus* (Rodentia: Cricetidae) as a reservoir host for *Borrelia burgdorferi* (Spirochaetales: Spirochaetaceae) in the wild. *Journal of Medical Entomology*, **30**, 614-618.
- Rekasi, J., Rozsa, L. & Kiss, B. J. 1997. Patterns in the distribution of avian lice (Phthiraptera: Amblycera, Ischnocera). *Journal of Avian Biology*, **28**, 150-156.
- Rohde, K., Worthen, W. B., Heap, M., Hugueny, B. & Guegan, J. 1998. Nestedness in assemblages of metazoan ecto- and endoparasites of marine fish. *International Journal for Parasitology*, **28**, 543-549.
- Rothschild, M. & Clay, T. 1957. *Fleas, flukes, and cuckoos*. New York: Macmillan Publishing Co.
- Rozsa, L. 1993. Speciation patterns of ectoparasites and "straggling" lice. *International Journal for Parasitology*, **23**, 859-964.
- Rozsa, L. 1997. Patterns in the abundance of avian lice (Phthiraptera: Amblycera, Ischnocera). *Journal of Avian Biology*, **28**, 249-254.
- Rozsa, L., Rekasi, J. & Reiczigel, J. 1996. Relationship of host coloniality to the population ecology of avian lice (Insecta: Phthiraptera). *Journal of Animal Ecology*, **65**, 242-248.
- Sabrosky, C. W., Bennett, G. F. & Whitworth, T. L. 1989. *Bird blow flies (Protocalliphora) in North America (Diptera: Calliphoridae) - with notes on the palearctic species*. Washington D. C.: Smithsonian Institution Press.
- Schaffer, M. L. & Samson, F. B. 1985. Population size and extinction: a note on determining critical population size. *American Naturalist*, **125**, 144-152.
- Schmidt, G. D. & Roberts, L. S. 1989. *Foundations of Parasitology*. St. Louis: Times Mirror/Mosby College.
- Seevers, C. H. 1978. A generic and tribal revision of the North American Aleocharinae (Coleoptera: Staphylinidae). *Fieldiana Zoology*, **71**, 1-289.
- Shaw, D. J. & Dobson, A. P. 1995. Patterns of macroparasite abundance and aggregation in wildlife populations. *Parasitology*, **111**, S111-S113.

- Simberloff, D. & Moore, J. 1997. Community ecology of parasites and free-living animals. In: *Host-Parasite Evolution: General Principles and Avian Models* (Ed. by Clayton, D. H. a. M., J.), pp. 174-197. Oxford: Oxford University Press.
- Sonenshine, D. E. 1991. *Biology of Ticks*. Oxford: Oxford University Press.
- Southwood, T. R. E. 1978. *Ecological Methods, with Particular Reference to the Study of Insect Populations*. New York: John Wiley & Sons.
- Stehr, F. W. 1991. *Immature Insects*. Iowa: Kendall/Hunt Publishing Company.
- Taylor, L. R. 1961. Aggregation, variance and the mean. *Nature*, **189**, 732-735.
- Timmermann, G. 1954. Vorläufige Übersicht über das Amblyseres-Genus *Austromenopon* Bedford, 1939 (Mallophaga). *Bonner Zoologische Beiträge*, **5**, 195-206.
- Timmermann, G. 1957. Studien zu einer Vergleichenden parasitologie der Charadriiformes oder Regenfeifervögel Teil 1. Mallophaga. *Parasitologische Schriftenreihe*, **8**, 1-204.
- Timmermann, G. 1963. Gruppen-Revisionen bei Mallophagen. VI. Die *Austromenopon* arten der Sturmvoegel. *Parasitenk.* **22**: 401-427.
- Timmermann, G. 1969. Gruppen-Revisionen bei Mallophagen. VIII. Die Formenkreise *Saemundssonina scolopacis-phaeopodis* (Schränk), 1803, *Saemundssonina platygaster* (Denny), 1842 und *Saemundssonina africana* (Timmermann), 1951. *Zoologischer Anzeiger*, **183**, 225-256.
- Wanless, S., Barton, T. R. & Harris, P. 1997. Blood hematocrit measurements in 4 species in North Atlantic seabirds in relation to levels of infestation by the tick *Ixodes uriae*. *Colonial Waterbirds*, **20**, 540-544.
- Wassom, D. L., Dick, T. A., Arnason, N., Strickland, D. & Grundmann, A. W. 1986. Host genetics: a key factor in regulating the distribution of parasites in natural host populations. *Journal of Parasitology*, **72**, 334-337.
- Wheeler, T. A. & Threlfall, W. 1986. Observations on the ectoparasites of some Newfoundland passerines (Aves: Passeriformes). *Canadian Journal of Zoology*, **64**, 630-636.
- Wheeler, T. A. & Threlfall, W. 1989. Synopsis of the parasites of Canada: Ectoparasites of birds.: Alberta Agriculture, Animal Health Division.
- Wilson, E. O. 1986. *Biodiversity*. Washington, D. C.: National Academy Press.
- Worthen, W. B. 1996. Community composition and nested-subset analyses: basic descriptors for community ecology. *Oikos*, **76**, 417-426.

- Worthen, W. B. & McGuire, T. R. 1988. A criticism of the aggregation model of coexistence: non-independent distributions of dipteran species on ephemeral resources. *American Naturalist*, **131**, 453-458.
- Worthen, W. B. & Rohde, K. 1996. Nested subset analyses of colonization-dominated communities: metazoan ectoparasites of marine fishes. *Oikos*, **75**, 471-478.
- Wright, D. H., Patterson, B. D., Mikkelsen, G. M., Cutler, A. & Atmar, W. 1998. A comparative analysis of nested subset patterns of species composition. *Oecologia*, **113**, 1-20.
- Wright, D. H. & Reeves, J. H. 1992. On the meaning and measurement of nestedness of species assemblages. *Oecologia*, **92**, 416-428.
- Zelmer, D. A. 1998. An evolutionary definition of parasitism. *International Journal for Parasitology*, **28**, 531-533.

