THE ROLE OF SCENT AND ECTOPARASITES IN THE ECOLOGY OF THE CRESTED AUKLET (AETHIA CRISTATELLA)

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THE ROLE OF SCENT AND ECTOPARASITES IN THE ECOLOGY OF THE CRESTED AUKLET (*AETHIA CRISTATELLA*)

by

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Abstract

Ectoparasites are ubiquitous, and can have negative effects on their hosts. The prevalence and intensity of ectoparasites are important in determining their effects. Prevalence can vary greatly, from near absence to all host individuals in a population being parasitized. Intensity can also vary greatly. Negative impacts of parasitizes can create the pressure required for a natural defence mechanism to evolve in hosts. Crested Auklets (*Aethia cristella*, Alcidae; Aethiini) are colonial seabirds that produce a unique tangerine-like scent. There are two hypotheses proposed for this scent's function: 1) as a pheromone; and 2) to reduce ectoparasite levels by repelling ticks and lice. My study is broken into three sections: 1) measuring the prevalence and intensity of ticks on *Aethia* auklets and determining the relationship of body condition and ornamentation to tick parasitism; 2) measuring the prevalence and intensity of lice on Least (*Aethia pusilla*) and Crested Auklets and the determining relationship of body condition and ornament expression to lice parasitism; and 3) the relationship of Crested Auklet scent to ectoparasite intensity and tick deterrence. I determined that prevalence and intensity of ticks and lice had no relationship with body condition or ornament expression on any hosts species. Lice or tick intensity were not related to naturally occurring scent levels but ticks were less likely to attach to scented objects. My study suggests that when parasitism is low in Crested and Least Auklets the need for a parasite defence is reduced and will obsure any relationship among quality and parasite load.

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Chapter 1

Introduction to Crested Auklets, their scent, and their ectoparasites

Until recently it was thought that olfaction is not a very important sense in birds. With the realization of its importance there has been growing interest in documenting avian odours and investigating their functions (Hagelin & Jones 2007). Crested Auklets (*Aethia cristatella*) produce a strong citrus-like odour with an unknown function. A number of adaptive functions have been proposed but the two that have received the most attention are intraspecific communication and chemical defence (Clayton et al. 2010; Hagelin & Jones 2007). Experimental studies (Jones et al. 2004) provided evidence that this scent plays a social role, whereas Douglas et al. (2004) suggested it could also act to repel ectoparasites. These two hypotheses are not necessarily mutually exclusive. The scent could be acting to deter ectoparasites and therefore be an honest indicator of quality that is used in mate choice. A solid description of the diversity, prevalence, intensity and ecology of ectoparasites (both for Crested Auklet and related species) is a prerequisite to understanding the function of Crested Auklet odour – this is the knowledge gap I aimed to address with my thesis.

1.1 Crested Auklets and their close relatives

Crested Auklets (Alcidae) are small, locally abundant, colonial, planktivorous seabirds occurring only in the Bering and Okhotsk Seas and adjacent parts of the North Pacific (Gaston & Jones 1998). Least Auklets (*A. pusilla*) are the smallest and most abundant of auklets that are closely related to Crested Auklets. Least Auklets forage close to their breeding colonies during summer and disperses widely at sea in winter (Jones 1993b). Crested Auklets coexist with Least Auklets at nine Alaskan breeding colonies as well as at sea during the summer and throughout the winter (Jones 1993a). Compared with other auklets, Whiskered Auklets (*A. pygmaea*, mean mass 118 g) occupy a slightly different ecological niche. They forage close to land in active tide rips, are known to roost on land during the non-breeding season, and likely remain near their breeding colonies in the Bering Sea year round (Byrd & Williams 1993; Hunter et al. 2002; Williams, Byrd, & Konyukhov 2003; Zubakin & Konyukhov 1999). In Alaska, Whiskered Auklets are rarely observed on the surface of colonies with the exception of Buldir Island where they can join aggregations of Least and Crested Auklets by day (Hunter et al. 2002). At breeding colonies (May-July) auklets congregate densely with birds in direct contact with one another on the surface and underground in their nest burrows on rocky talus slopes and lava flows. These high densities provide an ideal environment for ticks to breed and find hosts.

1.2 Crested Auklets and their scent

Crested Auklets have large crests on their forehead that are favoured by both males and females in mating selection (Jones & Hunter 1993, 1999). Both sexes also have white auricular plumes and an orange bill with accessory plates that are present during breeding but become greatly reduced after breeding (Jones 1993c).

Crested Auklets produce a citrus-like scent during the breeding season that is strongest around the bill, nape, and neck (Humphrey 1958; Jones & Hunter 1999). This strong scent is especially noticeable at nesting colonies (Kenyon & Brooks 1960). The scent was strong enough that out on the water downwind of c.10000 auklets the odour was clearly noticeable to Kenyon & Brooks (1960). Sealy (2006) reported that this scent is not present in the week before the breeding season when birds are at sea.

Using solvent extraction from three specimens the scent was found to be composed of N-hexanal, N-octanal, N-decanal, Z-4-decenal, hexanoic acid, octanoic acid, N-octanal, hexanal and a 12-carbon unsaturated aldehyde, later characterized as Z-4-dodecenal and Z-6-dodecenal (Douglas et al. 2001a; Douglas et al. 2004). In a separate study using a different scent collection method based on quantification of volatile chemicals the scent was composed of Z-4-decenal, hexanoic acid, N-octanal, octanoic acid, and decanal, as well as octanal, undecanal, tridecanal, and heptanal (Hagelin et al. 2003). Based on scent collection focusing on volatile chemical being released over a set period of time the average chemical emission for Crested Auklets was 5.7 μl octanal/50 min ±0.42 (57 individuals) with the highest levels at 19.9 μl/50 min and the lowest at 2.8 μl/50 min (Douglas 2006a) or solvent extraction, which measures chemicals found in a set mass of feathers, was 2.98 μg octanal/g of feather (Hagelin et al.

2003). There is no difference in scent chemical levels in between males and females (Douglas 2006a; Hagelin et al. 2003). The concentrations of the chemicals that make up the scent are stronger in the plumage around the crown and nape than in the mantle feathers (Douglas 2008b).

The exact origin of the scent is unknown but wick-like feathers from 25 individuals found in the interscapular region of birds had high concentrations of some of the scent's chemical constituents (Douglas 2008b), suggesting that they may be involved in scent production. The scent is not likely produced by the skin as no chemical constituents of the scent are found on the skin once feathers are removed (Douglas 2008b). The production of the scent is correlated with progesterone in males during the early chick rearing period, suggesting that hormone levels and scent production are closely linked (Douglas 2008b). Interestingly, captive birds in a zoo did not produce the odour (Douglas 2008b).

The two proposed functions of this scent are that it plays a role in social behaviour (Hagelin et al. 2003) or acts to repel ectoparasites (Clayton et al. 2010; Douglas 2006b), are not mutually exclusive. For example, scent could also have social importance if is primary role is as defence against ectoparasites. It is possible that scent could be acting to deter ectoparasites and so individuals use it as an honest indicator of quality.

1.2.1 Social Function

It has been suggested that the scent plays a social role, indicating status, condition, or being used as a measure of quality in mate choice. The ruff-sniff display (Jones and Hunter 1993) has been suggested to be a form of allopreening, and could transfer scent between individuals (Douglas 2008b). Within a t-maze adults preferentially moved towards a 1:1 mixture of octanal and Z-4-decenal but not towards feathers of Crested Auklets (Hagelin et al. 2003). Auklets in captivity are more likely to approach models with a strong Crested Auklet odour (Douglas 2008b). In a social setting with wild auklets, both male and female auklets showed attraction to scented models; birds were more likely to approach models and spent longer periods of time around them (Jones et al. 2004). Interestingly, Jones et al. (2004) did not see an increase in sexual displays towards the scented models, as had been found for models with increased feather ornament size (Jones and Hunter 1993, 1999). However, individuals can smell the primary components of the scent and are attracted towards them. Within a captive population, concentrations of Z-4 decenal and facial crest length are significant predictors of male social status and are positively correlated with rank (Hagelin 2007b). These results within wild and captive populations suggest that there is a social role for the scent, but the role may not be in mate choice.

1.2.2 Ectoparasite Defence

It has been suggested that the scent produced by Crested Auklets acts to deter ectoparasites (Clayton et al. 2010; Douglas et al. 2001a, 2001b, 2005a, 2005b; Douglas 2006b, 2008a). Studies have focused on ticks and lice the two main ectoparasites of auklets as well as mosquitoes. Studies have been conducted using both natural scent from Crested Auklets and using a mixture of synthetic chemicals that are known to be components of the scent.

Ticks are negatively affected by the chemical components of the Crested Auklet scent. Nymphs of both *Amblyomma americanum* and *Ixodes uriae* had a shorter period of attachment and moved slower when exposed to octanal and varying concentrations of a mixture of the main scent's chemical components (Douglas et al. 2004; Douglas 2008a). *I. uriae* nymphs and adults exposed to octanol had increased morbidity (Douglas et al. 2004). When exposed to fresh feathers of Crested Auklets and unscented feather *I. uriae* did not show any signs of deterrence (Hagelin 2007a). In a past study (Douglas 2006a) only two Crested Auklets of 96 had attached ticks, one of which had the lowest chemical emission rate measured in the study (Douglas 2006a).

Lice are also negatively affected by the chemical components of Crested Auklet scent. *Austromenopon* sp. had increased morbidity when exposed to the scent's chemical components (Douglas et al. 2004). The lice *Columbicola columbae* and *Campanulotes bidentatus* exposed to feather or carcasses of Crested Auklet, Least Auklet, and Rock Pigeon (*Columba livia*) did not differ in survival (Douglas et al. 2005b). Crested Auklets had a higher louse load of *Quadraceps* sp. and *Saemundssonia* sp. than Least Auklets even when body size of host was controlled for (Douglas et al. 2005b). Lice did not show any signs of detterance when exposed to feathers of Crested Auklets, Least Auklets or Parakeet Auklets (*A. psittacula*: Hagelin 2007a).

Mosquitoes do not naturally occur in most Crested Auklet colonies. *Aedes aegypti*, a commonly used mosquito in lab repellence, experiments were more likely to land on a hand with filter paper treated with just ethanol than on paper treated with a mixture of the scent's chemical components at vary concentrations (Douglas et al. 2005a). This study demonstrates that the chemical constituents of the scent of Crested Auklets acts to deter mosquitoes. The significance of these findings is not clear since wild auklets are never exposed to mosquitoes.

1.3 Ectoparasites of Auklets

Ticks (Ixodida) are a large, diverse, cosmopolitan group. They are obligate, non-permanent parasites with four life stages; egg, larva, nymph, and adult. When not attached to hosts, they live in the soil and crawl on to vertebrate hosts for blood meals. Ticks usually require a blood meal during every stage with the exeption of eggs and usually adult males (Oliver 1989). Ixodida is divided into two main families; Argasidae, the soft ticks with ~200 species in 5 genera; and Ixodidae, the hard ticks with ~700 species in 13 genera (Nava et al. 2009). Ticks can have both direct effects, such as tick paralysis and exsanguinations (Oliver 1989); and indirect effects through the transportation of disease (Nuttall 1984).

Lice (Phthiraptera) are obligate, continuous ectoparasites. They infest all orders of birds and most orders of mammals. They are highly specialized for life on their hosts with short legs and dorsal-ventrally flattened to reduce risk of detachment from preening. The two suborders that infest birds are Ischnocera and Amblycera. Ischnocera feed exclusively on feather and the debris found on the feathers. Amblycera are more agile and occur on both skin and feather, and feed on blood and feathers. Both suborders only leave their host to infest other individuals when direct contact occurs (Marshall 1981).

1.4 Purpose

In recent years there has been a debate regarding the function of the citrus-like odour produced by Crested Auklets as described above. I determined the prevalence and intensity of ticks and lice on Crested and Least Auklet. Prevalence is the number of individual birds with one or more parasite, and mean intensity is the mean number of parasites on individuals that are have at least one parasite (Bush et al. 1997; Rózsa et al. 2000). I determined whether naturally occurring levels of ectoparasites are related to body condition or ornament expression in those species, and important question to address before looking defence mechanisms. With the closely related, Least Auklet living along side Crested Auklets it is possible to examine patterns in these two species and view the unscented Least Auklet almost like a "control" next to the scented Crested Auklet. If ectoparasites are causing negative effects I would expect that Least Auklets to have higher intensities and prevalence of tick and lice, as well as more negative impacts from parasitism then the Crested Auklets. I determined the relationship between lice and tick levels and the scent in Crested Auklets in the natural environment. This is important as all work has focused on experiments, with no study examining as many individual as I have from a wild population.

Chapter 2

Tick (*Ixodes uriae*) prevalence in *Aethia* auklets on Buldir Island, Aleutian Islands, Alaska during 2009 and 2010

Abstract

Ticks (Ixodoida) are terrestrial, obligate, non-permanent ectoparasites that affect birds. Direct feeding on individual adult birds and nestlings can result in paralysis or excessive blood loss. I documented the prevalence and intensity of the tick *Ixodes uriae* on Least (*Aethia pusilla*, n=184) and Crested (*A. cristatella*, n=280) Auklets on Buldir Island, Aleutian Islands, Alaska in 2009 and 2010. I also investigated the relationship of tick intensity to body condition and ornament expression, and the relationship of tick-inflicted damage to toe webbing to body condition and ornament expression in several auklet species. Tick prevalence was low (Least Auklets, 9.2%; Crested Auklets, 5.2%) as was intensity (1.12 and 1, respectively) in parasitized individuals. I found no statistically significant relationships between ticks and body condition or ornamental traits in either Crested or Least Auklets. I also found no evidence for a relationship between web damage and body condition or ornamental traits. These results suggest that ticks had no measurable impact on body condition or ornament expression and may not play a role in auklet ecology in this colony at this time.

2.1 Introduction

Avian ectoparasites are ubiquitous and infest most bird species (Marshall 1981). The impact of these parasites can be diverse depending on type of parasite and site of infestation. Their presence can result in reduced body mass (Rózsa 1997), slower nestling growth rates (Huber 2008), or reduced breeding success (Hoodless et al. 2003). The reduction in adult health often leads to reduced fitness because of lower nestling survival (Dudaniec et al. 2006), poorer mating success (Clayton 1990), or reduced long-term survival (Hoodless et al. 2003). Though ticks have been documented on auks (Muzaffar & Jones 2004; Appendix I) the studies that have found negative impacts are limited to those focusing on condition in chicks (Mangin et al. 2003).

A common species on seabirds is *Ixodes uriae,* which parasitizes more than 50 species of seabirds (Mangin et al. 2003; McCoy et al. 1999; Muzaffar & Jones 2004). All four life stages live underground in soil and only those individuals seeking a blood meal will crawl onto a passing bird, leading to attachment and feeding lasting for 2-7 days (Finney et al. 1999). The feeding of ticks can transfer neurotoxins from their salivary glands which can result in paralysis, and occasionally excessive blood loss from the site of the bite (Oliver 1989). Indirect effects include the transmission of diseases such as Lyme disease, *Borellia* sp. (Nuttall 1984; Gylfe et al. 1999; Muzaffar et al. in press).

The impact of ticks on seabirds has been documented for a number of species (Dietrich et al. 2010; Gauthier-Clerc et al. 1998; Mangin et al. 2003;

Proctor & Owens 2000; Wanless et al. 1997). Infestation of ticks in nestlings is related to reduced feather growth rates and later chicks fledging and with shorter wings in Cassin's Auklets (*Ptychoramphus aleuticus*; Morbey 1996). High tick prevalence has been linked to reduced immune response in nestling Black-legged Kittiwakes (*Rissa tridactyla*; McCoy & Tirard 2002). Mangin et al. (2003) reported that adult King Penguins (*Aptenodytes patagonicus*) with ticks have lower success in raising chicks to one year of age. Infestation of ticks in nestlings may also have population level impacts within Black-legged Kittiwakes (Boulinier and Danchin 2008).

Ticks are commonly abundant within North Pacific seabird colonies making mixed colonies of Least (*Aethia pusilla*), Crested (*A. cristatella*), and Whiskered Auklets (*A. pygmaea*) an excellent location to document prevalence and relationships with body condition and ornament expression. Auklets (Alcidae: Aethiini) are small, locally abundant, colonial, planktivorous seabirds that occur only in the Bering and Okhotsk Seas and adjacent parts of the North Pacific (Gaston & Jones 1998). Whiskered Auklets are normally nocturnal in relation to colony surface activity but on Buldir Island some Whiskered Auklets join aggregations of Least and Crested Auklets during the day (Hunter et al. 2002). At breeding colonies (May-July) Least and Crested Auklets congregate densely (with birds often touching one another) on the surface and underground on rocky talus slopes and lava flows. These high densities appear to provide an ideal environment for questing ticks. However, auklets spend only their breeding season on land limiting the amount of time that they are exposed to ticks as they cannot pick up ticks during the winter season. These seasonal patterns allow my study to focus on the impacts of tick parasitism without having to consider tick parasitism that may occur outside of the breeding season when seabirds are difficult to study.

Douglas (2004) has suggested that chemical emissions from the feathers of Crested Auklets function to deter ectoparasites including ticks, based on the assumption that ticks have negative effects on auklet condition and ornamentation. I was also interested in testing whether Least Auklets, which lack a pungent plumage odour, have different levels of tick infestation from Crested Auklets.

The objectives of my study were to: 1) quantify prevalence of *Ixodes uriae* on Least and Crested Auklets at Buldir Island in order to establish a baseline; and 2) investigate the relationships between tick prevalence and intensity as well as foot web damage (an inferred measure of tick parasitism on nestlings) and body condition index and ornament expression in Least, Crested, and Whiskered Auklets. I focused on *I. uriae* because they are abundant in some years at Buldir Island, have been shown to affect breeding success in other seabird species (Danchin 1992; Morbey 1996) and are easily quantified.

2.2 Methods

2.2.1 Study location

I studied auklets at a colony of more than 100,000 Crested, Least, and Whiskered Auklets at Main Talus, Buldir Island, Aleutian Islands, Alaska (52°2'N 175°5'E; Byrd & Day, 1986) during early June to mid August of 2009 and 2010. Data on Whiskered Auklets were collected between 1992 and 2006 by ILJ as part of a long-term monitoring project at a smaller colony, located just west of Main Talus, also on Buldir Island.

2.2.2 Quantification of ticks

Adult Least and Crested Auklets were captured during the morning activity period 900-1300HADT (Hawaiian Aleutian daylight-savings Time: GMT-9:00) using noose carpets set on the colony surface. Birds were placed in a freshly washed cloth bag to reduce stress on birds and parasite contamination of previously caught birds. Birds were processed in the order of capture. An individual that displayed any apparent distress (hot feet, open bill breathing) was immediately released. Each captured auklet was given a numbered US FWS stainless steel leg band, and was assigned a unique combination of three Darvik plastic colour bands.

Birds were visually inspected and palpated for attached and non-attached ticks from head to toe (Clayton & Walther 1997). Crested Auklets were inspected for 5 minutes and Least Auklets for 3 minutes to account for differences in body size. The feet and area around the eyes were visually inspected. The life stage (larval, nymph, and female adult) and location of each tick was noted.

2.2.3 Condition and body ornamentation

I weighed birds to the nearest 1 g using an Ohaus electronic balance. I measured wing length (flattened and straightened on the right wing; from the wrist to the time of the longest primary, P10), and auricular plume length (from the exposed proximal end of the plumes just below the eye to the end of the longest plume: Jones et al. 2000) to the nearest 0.1 mm using calipers. Sub-adults were excluded from this study as tick prevalence found on both Least and Crested Auklets were quite low and not enough sub-adults were caught to perform a meaningful analysis.

For Crested Auklets, I measured crest length (length of the longest straightened crest feather shaft: Jones et al. 2000) and right auricular plume length. For Least Auklets, I measured bill depth (measured twice, once from the angle of the gonys to the uppermost tip of the bill knob, and a second time from the angle of the gonys to the point where the bill meets the ridge of the culmen) and mean auricular plume length.

Whiskered Auklets, were captured using mistnets as they returned to their colony at dusk (2300-0100 HADT). ILJ banded, weighed, and measured crest length from 1992 to 2006. All measurements were taken by a single observer, and followed the same protocols applied in 2009 and 2010 for Least and Crested Auklets, except some bird bags were reused before washing.

2.2.4 Foot web damage

Damage to the webbing between the toes was scored for each bird, with a scale of 0-2: 0- both feet undamaged; 1- one small hole in either foot, 2- multiple holes or tears in the webbing. These were old healed injuries that are acquired at the nestling stage when ticks attach to the chick's soft webbing (Hoberg & Wehle 1982; Morbey 1996).

2.2.5 Statistical techniques

Statistics were conducted in SPSS (version 19) or Quantitative Parasitology (Reiczigel & Rózsa 2005). Prevalence and mean intensity of tick infestation are reported with 95% confidence limits. Prevalence is the number of individual birds with one or more parasite, and mean intensity is the mean number of parasites on individuals that are have at least one parasite (Bush et al. 1997; Rózsa et al. 2000). I calculated day as the day number from January 1 of the respective year. Web damage was used as a score of impact of tick infestation that occurred as a nestling. I compared the number of ticks and foot web damage observed in Least and Crested Auklets using MANOVA. Web damage and number of ticks on an individual were the dependent variables with species, year, and day being the independent variables. All non-significant interaction terms were removed. I analyzed Least, Crested, and Whiskered Auklet data separately from this point forward as ornament measures and size differ between species.

In both species body condition index was defined as the residual mass from a linear regression of body mass against body size (with wing length as a body size proxy) expressed as the percentage of the predicted value (Janicke et al. 2008). In Crested Auklets I used body condition index, wing length, crest length, and right auricular plume length as my measures of condition and degree of ornamentation. Crest length and right auricular plume length were not correlated (Pearson correlation, $r=0.10$, $p=0.10$, $n=280$). In Least Auklets I used body condition index, wing length, bill knob height and mean auricular plume length as measures of condition and degree of ornamentation. Bill knob was not correlated with mean auricular plume length (Pearson correlation, $r=-0.10$, $p=0.19$, $n=184$) and wing length was not correlated with body condition index (Pearson correlation, $r=0.01$, $p=0.97$, $n=184$). These measures were related to number of ticks found and foot web damage with day and year of capture as covariates using MANOVA.

Tick prevalence data were available only for a small number of individuals for Whiskered Auklets so analysis focused only on web damage. Mass and crest length were related to web damage score, year of sample, and day date of sample using a MANOVA.

2.3 Results

The prevalence (95% confidence interval) of ticks on Crested Auklets 5.2% (2.9-8.7%; n=251) and on Least Auklets was 9.2% (5.6-14.3%; n=184; Figure 2.1). The mean intensity (95% confidence interval) was 1 (1-1) and 1.12 (1-1.35) for Crested and Least Auklets, respectively. In Least, Crested, and Whiskered Auklets most individuals had no visible damage to their feet (Table 2.1; Figure 2.2).

Least or Crested Auklets did not differ in number of ticks (MANOVA, F=0.99, p=0.32) or the web damage (MANOVA, F=0.217, p=0.64) when accounting for year and date of capture.

In Crested Auklets, the number of ticks and foot web score were not correlated with body condition index, wing length, crest length, or length of the right auricular plume. Body condition index was related to day of collection in the season, and year (Table 2.2: Figure 2.3). Individuals that were caught in 2010 were in better condition and had longer wings than those caught in 2009 (Figure 2.4). Body condition index decreased throughout the season (Figure 2.5).

In Least Auklets, the number of ticks found on individuals or level of damage on foot webs was not correlated with body condition index, wing length, knob height, or mean auricular plume length (Figure 2.6). Body condition varied by year (greater in 2010; Figure 2.7) and bill knob height was related to date of measurement (Table 2.2; Figure 2.8). The size of bill knobs decreased over the season (Figure 2.8).

In Whiskered Auklets, foot web score was not correlated with mass or crest length (Table 2.3; Figure 2.9). Body mass was not related to year or day of capture, but crest length varied between years (Table 2.3; Figure 2.10).

2.4 Discussion

2.4.1 Tick Prevalence and intensity

For both Least and Crested Auklets, the prevalence of ticks and mean intensity were low on Buldir Island in 2009 and 2010. There was no difference in intensity of ticks found between Least or Crested Auklets. In other studies, prevalence of ticks in alcids has ranged widely by species, locality, and year of sampling (Muzaffar and Jones 2004, Appendix I). For example, Common Murres (*Uria aalge*) have been reported to have tick prevalence range from 1% (Barton 1996) to as high as 97% of individuals (Choe & Kim 1987a). Within Crested Auklets, Engström et al. (2000) found no ticks on 131 Crested Auklets at Talan Island in the 1997 breeding season. On Buldir Island some years nearly 100% of auklet individuals have at least one tick – indicating that inter-year and inter-colony variability in prevalence are high (I.L. Jones pers. comm.).

2.4.2 Impact of ticks on body condition and ornament expression

Tick prevalence was not related to body condition or ornament expression in either species. The impact of ticks on condition may be difficult to detect when tick intensity is low, because they attach for brief period (7.7 days; Finney et al. 1999), which reduces both the chances of finding the few ticks that an individual bird attracts, and also the physiological effect of parasitism.

Ticks are known of a wide range of diseases and arboviruses (Nuttall 1984) that can cause infection at the site of attachment. These infections may have greater impacts than the impacts of direct feeding and would require monitoring of over long periods of time to examine survival and other factors throughout individuals lifetimes. Web damage was measured to address long-term negative impacts of ticks, as this damage arises when tick(s) attach to the toe webbing of seabird chicks (Hoberg & Wehle 1982; Morbey 1996). These holes are thought to be caused by infection at site of attachment. Primarily small holes in the web between toes are observed. Occasionally damage as non circular holes and loss of web is seen and could be caused by other factors. My findings are important because this measure was not be related to body condition and ornament expression later in life, perhaps because individuals that survived tick parasitism were strong fitter.

Assessing the question of tick impacts on auklet health was difficult due to the low intensity of the parasite and small number of affected birds (17 and 13 individuals ticks out of 184 and 251 Least and Crested Auklets examined respectively). These low levels require large samples sizes to achieve adequate statistical power and body condition and ornament expression are related to various other environmental factors simply adding noise to the analysis. Confounding this, many factors influence tick densities (Oliver 1989), and the impacts that ticks will have (Whiteman & Parker 2004). To address the complexity of this system a study must be carried out over numerous seasons to remove noise and quantify the impact of as many additional variables as possible.

2.5 Summary

1. Prevalence and intensity of ticks in both Least and Crested Auklets were low on Buldir in 2009 and 2010. In Crested Auklets, prevalence (95% confidence interval) was 5.2% (2.9-8.7%) in 251 individuals and in Least Auklets was 9.2% (5.6-14.3%) in 184 individuals. The mean intensity (95% confidence interval) was 1 (1-1) and 1.12 (1-1.35) Crested and Least Auklets respectively.
2. The number of ticks did not differ between Least or Crested Auklets, or on the web damage between the two species.
3. Prevalence of ticks was not related to condition or ornament expression in Crested Auklets or Least Auklets measured at Buldir Island during 2009 and 2010.
4. Foot web damage score, an indication of earlier tick parasitism at the nestling stage, was not related to condition or ornament expression in Crested or Least Auklets at Buldir.

5. Foot web damage score in Whiskered Auklets was not related to body mass or ornament expression.

Table 2.1. Most Least (*Aethia pusilla*), Crested (*A. cristatella*) and Whiskered Auklets (*A. pygmaea*) captured on Buldir Island, Alaska do not have any web damage. Individuals with scores of 0 had no holes in either foot web; 1- individuals had a single circular hole in either foot web; and 2- had greater than one hole with non-circular holes and tears in their foot webs rarely observed.

	Incidence (%)		
Foot web score	**Least Auklet N=184**	**Crested Auklet N=251**	**Whiskered Auklet N=256**
0	75%	81%	86%
1	19%	13%	13%
2	6%	6%	1%

Table 2.2. Within 184 Least Auklets (*Aethia pusilla*) and 251 Crested Auklets (*A. cristatella*) captured on Buldir Island in 2009 and 2010 there was no relationship among tick intensity, web damage, body condition, and ornament expression. The year and day of capture was included as dependent variables in MANOVA to address variation in body condition and ornament expression between and within breeding seasons.

		Overall		Body condition index		Wing length		Mean auricular plume length		Bill knob height	
	Wilks's λ	F	P	F	P	F	P	F	P	F	P
Least Auklet											
Ticks	1.0	0.8	ns	0.9	ns	0.9	ns	0.2	ns	1.0	ns
Web	1.0	0.5	ns	0.5	ns	0.1	ns	0.6	ns	0.9	ns
Year	0.9	2.3	ns	8.4	<0.01	0.6	ns	0.1	ns	0.1	ns
Day	0.8	13	<0.01	1.5	ns	2.9	ns	0.6	ns	44	<0.01
Crested Auklet								**Crest length**		**Length of right plume**	
Ticks	1.0	0.6	ns	0.1	ns	1.6	ns	0.1	ns	0.3	ns
Web	1.0	0.6	ns	0.3	ns	0.1	ns	1.8	ns	0.1	ns
Year	0.9	6.9	<0.01	11	<0.01	6.1	0.01	3.8	ns	3.4	ns
Day	0.9	5.4	<0.01	19	<0.01	0.4	ns	1.2	ns	2.5	ns

Table 2.3. Within 256 Whiskered Auklets (*Aethia pygmaea*) captured at Buldir Island, Alaska from 1992 to 2007 there was no relationship among web damage, body condition, and ornament expression. The year and day of capture was included as dependent variables in MANOVA to address variation in mass and ornament expression between and within breeding seasons.

				Mass		**Crest**	
	Wilks's λ	**F**	**P**	**F**	**P**	**F**	**P**
Web	1.0	1.6	ns	2.8	ns	0.1	ns
Year	0.8	2.7	<0.01	1.2	ns	4.4	<0.01
Day	1.0	0.1	ns	0.2	ns	1.0	ns

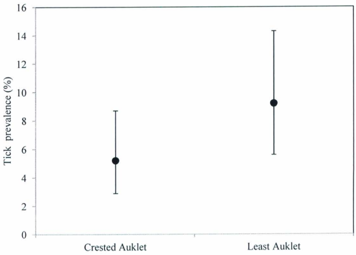

Figure 2.1 Prevalence of ticks in Least (*Aethia pusilla*) and Crested Auklets (*A. cristatella*) on Buldir Island during 2009 and 2010. Error bars represent 95% confidence limits.

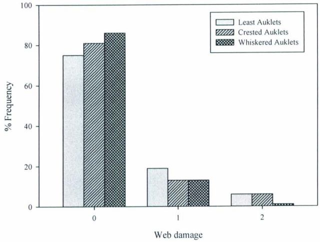

Figure 2.2 Percent frequency of web damage in Least (*Aethia pusilla*), Crested (*A. cristatella*), and Whiskered Auklets (*A. pygmaea*) caught on Buldir Island.

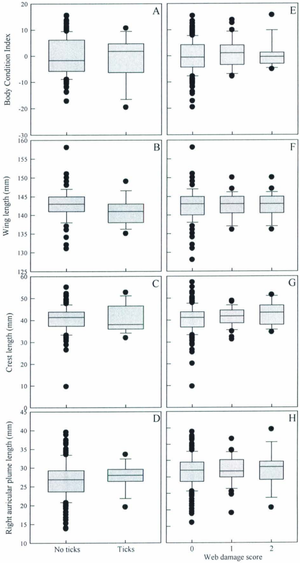

Figure 2.3 In Crested Auklets (*Aethia cristatella*; n=251), body condition index (A,E), wing length (B,F), crest length (C,G), and right auricular plume length (D,H) was not related to the intensity of ticks (A-D) or web damage score (E-H) on Buldir Island during 2009 and 2010.

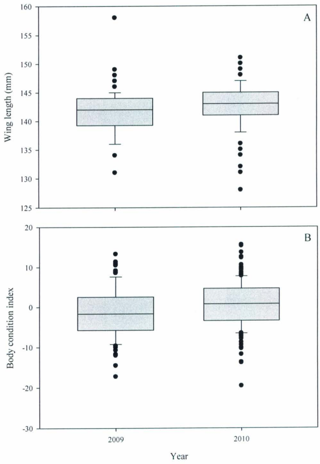

Figure 2.4 Crested Auklets (*Aethia cristatella*; 251) caught on Buldir Island in 2009 had shorter wings and lower body condition index scores than those caught during 2010.

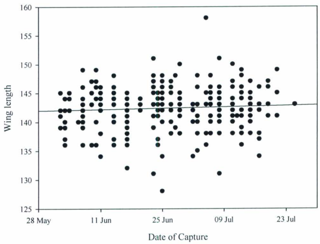

Figure 2.5 Crested Auklets (*Aethia cristatella* ; n=251) caught later in the season in both 2009 and 2010 on Buldir Island have longer wing lengths.

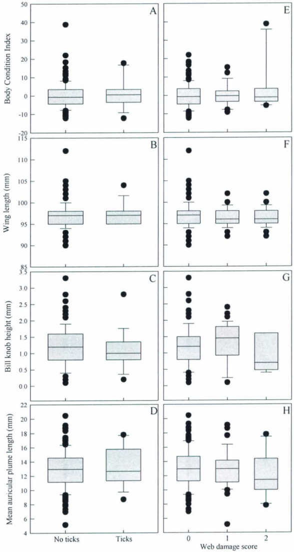

Figure 2.6 In Least Auklets (*Aethia pusilla*; n=184), body condition index (A,E), wing length (B,F), bill knob height (C,G), and mean auricular plume length (D,H) was not related to the intensity of ticks (A-D) or web damage score (E-H) on Buldir Island during 2009 and 2010.

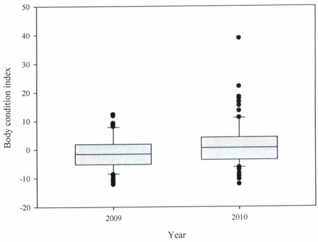

Figure 2.7 Least Auklets (*Aethia pusilla*; n=184) caught on Buldir Island in 2009 had a lower body condition index than those caught during 2010.

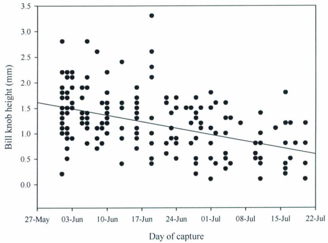

Figure 2.8 Least Auklets (*Aethia pusilla*; n=184) caught on Buldir Island had a smaller bill knobs later in the season than those caught earlier in the season in both 2009 and 2010.

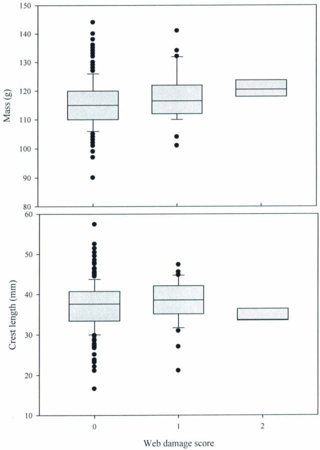

Figure 2.9 Web damage score in Whiskered Auklets (*Aethia pygmaea*, n=256) caught from 1992 to 2006 was not related to mass or crest length.

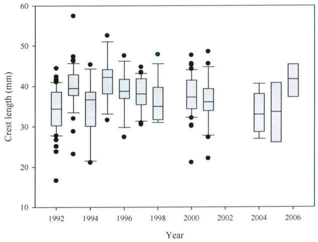

Figure 2.10 Crest length in 256 Whiskered Auklets (*Aethia pygmaea*) auklets caught from 1992 to 2006 varied significantly between years.

Chapter 3

Louse (Phthiraptera) prevalence on adult Least (*Aethia pusilla*) and Crested Auklets (*A. cristatella*) at Buldir Island, Aleutians Islands, Alaska during 2009 and 2010

Abstract

Lice are a common ectoparasites on many seabirds. The prevalence of lice can range from below 10% to as high as 100% in alcids. Lice prevalence is important to quantify before considering the negative impacts that lice may have on hosts. I caught Least and Crested Auklets on Buldir Island during the 2009 and 2010 breeding seasons, determined louse prevalence and mean intensity. Birds were caught during the breeding season and lice collected by dust ruffling with an insecticide. Louse prevalence was low (7.1%-12.9%) in Least and Crested Auklets respectively with mean intensity similarly being low at 1.20 in Least Auklets and 1.22 in Crested Auklets. In addition I investigated the relationships of prevalence to body condition and ornament expression. In both Least and Crested Auklets I found no relationship between the number of lice found on individual auklets and their body condition or ornament expression. My results provide baseline information on louse prevalence and intensity on these two seabird species which is integral to understand the impacts that lice have on their hosts.

3.1 Introduction

Bird lice are ubiquitous and infest most bird species in all habitats and regions of the world (Price et al. 2003). These parasites can have detrimental impacts when prevalence is high, e.g. reduced body mass (Booth et al. 1993), reduced body condition (Blanco et al. 2001; Calvete et al. 2003; Whiteman and Parker 2004), and reduced breeding success (Clayton 1990). Nevertheless, although lice sometimes occur in very large numbers on auks (Choe & Kim 1987), there is no published evidence that they have any negative impact in that group of seabirds (Muzaffar and Jones 2004).

In the Galápagos Hawk (*Buteo galapagoensis*), Whiteman and Parker (2004) found a negative relationship between lice abundance and body condition (Whiteman and Parker 2004). In Rock Pigeons (*Columba livia*), birds infested with high levels of lice had lower body mass and basal metabolic rate (Booth et al. 1993). Reduced body mass was thought to be the result of feather damage as those same individuals had lighter feathers, which resulted in lower minimal whole-body thermal conductance (Booth et al. 1993). A reduction in body mass, and increased energy output can result in reduced nutritional condition, e.g. in Red-legged Partridge (*Alectoris rufa*, Calvete et al. 2003) and European Magpie (*Pica pica,* Blanco et al. 2001).

Auk (Alcidae) lice have been studied in general (Muzaffar and Jones 2004), but little is known about lice of auklets (Aethiini). Lice on auklets on Buldir Island have been documented(Table 3.1) but prevalence has been reported only for Crested Auklets (*Aethia cristatella*, 4.0% at Big Koniuji Island; Douglas 2006). Prevalence and intensity of lice are variable so it is useful to document these parameters at more than one colony and across species.

Auklets are small, locally abundant, colonial, planktivorous seabirds that occur only in the Bering and Okhotsk Seas and adjacent parts of the North Pacific (Gaston and Jones 1998). The smallest and most abundant species, Least Auklet (*Aethia pusilla*, mean mass 85 g) forages close to its breeding colonies during summer and disperses widely at sea in winter (Jones 1993). Crested Auklets (mean mass 260 g) coexist at most Alaskan colony sites and at sea with Least Auklets in summer and in winter form dense concentrations near Aleutian passes (Jones 1993; Jones and Hunter 1993). Least and Crested Auklets breed at only nine colony sites in the Aleutian Islands (Williams et al. 2003). At breeding colonies (May-July) auklets congregate densely (with birds in direct contact with one another) on the surface and underground on rocky talus slopes and lava flows.

Douglas (2004) has suggested that chemical emissions from the feathers of Crested Auklets function to deter ectoparasites including lice, based on the assumption that lice have negative effects on auklet condition and ornamentation. I was also interested in testing whether Least Auklets, which lack a pungent plumage odour, have different levels of louse infestation from Crested Auklets.

In summary, the objectives of my study were: 1) to quantify the prevalence and intensity of lice on adult Least and Crested Auklets on Buldir

Island during the 2009 and 2010 breeding seasons; 2) to compare between the two auklet species; and 3) to test for relationships between louse prevalence and intensity and body condition and ornamentation.

3.2 Methods

3.2.1 Location

Fieldwork was carried out at a colony of more than 100,000 Crested, Least and other auklets at Main Talus, Buldir Island, Aleutian Islands, Alaska (52°2'N 175°5'E; (Byrd and day 1986) from early June to late August of 2009 and 2010.

3.2.2 Capture and measurement of auklets

Adult Least and Crested Auklets were captured during the morning activity period 900-1300HADT (Hawaiian Aleutian daylight-savings Time: GMT-9:00) using noose carpets set on the colony surface. Birds were placed in a washed cloth bag to reduce stress and contamination of previously caught birds. Birds were processed in the order of capture. An individual that displayed any apparent distress (hot feet, open bill breathing) was immediately released. Each captured auklet was given a numbered US FWS stainless steel leg band, and was assigned a unique combination of three Darvik plastic colour bands.

I weighed birds to the nearest 1 g using an Ohaus electronic balance. I measured wing length (flattened and straightened on the right wing; from the wrist to the time of the longest primary, P10), and auricular plume length (from the exposed proximal end of the plumes just below the eye to the end of the longest plume: Jones et al. 2000) to the nearest 0.1 mm using callipers. Sub-adults were excluded from this study as louse prevalence found on both Least and Crested Auklets were quite low and not enough sub-adults were caught to perform a meaningful analysis.

For Crested Auklets, I measured crest length (length of the longest straightened crest feather shaft: Jones et al. 2000) and the rictal plate height (on the right side, from its mid-point along the cutting edge of the bill near the gape to its highest point). For Least Auklets, I measured mean auricular plume length and quantified underpart plumage colouration (i.e., the degree of blackness in the breast plumage) on a scale of 0 – 4 (Jones 1990).

3.2.3 Louse collection and quantification

After they were banded and measured birds were dust-ruffled (Walther and Clayton 1997) using dog flea powder (Sergeant's® tick and flea power for dogs, Carbaryl 5.0%, Pyrethrins 0.1%, Piperonyl Butoxide 1.0%) to collect lice. In order to apply an equal amount of insecticide per unit area of skin surface of each species, a ratio of 1 (Least Auklet) : 2.1 (Crested Auklets) was applied (based on calculations of the relative surface area of the two species; Appendix III). Birds were held over a clear plastic Ziplock® bag with powder applied evenly across the body following the procedure described by Walther and Clayton (1997). Powder was massaged into the feathers to ensure that the insecticide reached the bird's skin. Least Auklets were ruffled for three minutes and Crested Auklets for five minutes, again to account for differences in body size. The first minute was used to distribute the powder over the bird, while the next two or four minutes were spent ruffling the powder. It took the same time to distribute the powder for both species. The Ziplock® with powder and lice were visually inspected in the lab using a dissecting microscope so that all lice could be removed and placed in 70% ethanol for later identification. Lice have previously been collected from Buldir Island and identified to species (Table 3.1). Based on these previous identifications I refer to louse taxa by genus since each auklet species had only one louse species from each of the three genera.

3.2.4 Statistical techniques

All statistics were conducted in SPSS (version 19) and Quantitative Parasitology (Reiczigel & Rózsa 2005). Prevalence and mean intensity of lice infestation are reported with 95% confidence limits. Prevalence is the number of individual birds with one or more parasite, and mean intensity is the mean number of parasites on individuals that are have at least one parasite (Bush et al. 1997; Rózsa et al. 2000). I calculated day as the day number from January 1 of the respective year. To determine if the intensity of lice on the two species of auklets differed, a generalized linear model with was used to compare individual intensities of lice. A negative binomial distribution was assumed and a log link function applied. Number of lice was the dependent variable and species the independent with day and year included to control for variation between and within season. The interactions between species and year or day were excluded as they were not significant. It was assumed that number of lice found on an individual could be directly compared as differences in body size were controlled for in sampling technique. All future analyses examined Least and Crested Auklet data separately.

In both species body condition index was defined as the residual mass from a linear regression of body mass against body size (with flatened wing length as a proxy) expressed as the percentage of the predicted value (Janicke et al. 2008). In Least Auklets I used body condition index, wing length, breast plumage score (correlated with age and social dominance; Jones 1990) and mean auricular plume length (favoured by mating preferences) as my measures of condition, body size and degree of ornamentation. Breast plumage score was not correlated with mean auricular plume length (Pearson correlation, r=0.02, p=0.79, n=140) and wing length was not correlated with body condition index (Pearson correlation, r=0.01, p=0.99, n=140). All non-significant two-way interactions were removed. In Crested Auklets I used body condition index (Janicke et al. 2008), wing length, crest length (favoured by mating preferences; Jones and Hunter 1993, 1999), and bill rictal plate height as measures of condition, body size and degree of ornamentation. Crest length and rictal plate height were not correlated (Pearson correlation, r=0.09, p=0.18, n=209). Using a MANOVA these measures were related to number of lice found on an individual with day and year of capture as covariates. All non-significant two-way interactions were removed.

3.3 Results

Austromenopon, *Quadraceps*, and *Saemundssonia* were collected from Least and Crested Auklets. Prevalence of each species was low (Table 3.2) so data were pooled (i.e. I used a total count of all lice of all genera present to quantify each individual's ectoparasite loads). In Crested Auklets 12.9% (8.2-18.0%, 95%CL) in 210 individuals and in Least Auklets the prevalence of lice was 7.1% (3.8-12.7%, 95%CL) in 140 individuals. The mean intensity was 1.22 (1.04-1.47, 95%CL) and 1.20 (1-1.6, 95%CL) and Crested and Least Auklets respectively.

Abundance of lice on individual Least Auklets did not differ significantly from the abundance on individual Crested Auklets (GlzLM, χ^2=1.36, p=0.24; Figure 3.1). With intensity of lice being low on both species, the analysis included both parasitized and non parasitized individual thus addressing abundance instead of intensity, which is a metric that accounts for both prevalence and intensity.

In Least and Crested Auklets the intensity of lice was not correlated with body condition index, wing length, plumage colour or ornament expression (Table 3.3; Figure 3.2-3.3). There were however some statistically significant relationships with day in the breeding season and year of sampling in each species.

3.4 Discussion

Least and Crested Auklets had low prevalence and low mean intensity of lice in my study area at Buldir Island during the breeding seasons in 2009 and 2010. Alcids can have variable levels of lice (Muzaffar and Jones 2004; Appendix II) with reported levels as low as 3% in Atlantic Puffins (*Fratercula arctica,* Muzaffar 2000) and as high as 100% in Dovekies (*Alle alle*; Eveleigh & Threlfall 1976). A previous study of Crested Auklets found prevalence to be 4% (Douglas 2006). This result underscores the high inter-year and inter-colony variation in ectoparasitism rates that have been previously reported (Muzaffar and Jones 2004).

I found no difference between the number of lice found on Least versus Crested Auklets. Differences in body size between the two species should not have influenced the results since I accounted for this by sampling Crested Auklets with more tick and flea powder and for a longer length of time based on calculations of body size (Appendix III). With such low prevalence's and intensities in both species it is likely that any differences would be very subtle and require large samples sizes to detect. Douglas (2005) suggested that chemical emissions from the feathers of Crested Auklets function to deter ectoparasites. If this were the case there might be a difference in prevalence or intensity between species, especially at a mixed-species colony such as Buldir Island. My results do not show this; however it is possible that plumage odour of Crested Auklets plays a role but relationship is subtle and difficult to detect. It is possible that the plumage odour of Crested Auklets reduces the pressures of parasitism to levels seen in Least Auklets and so that is why no difference was observed. One way to address the possibility of Crested Auklet scent acting to reduce lice levels would be to determine louse prevalence and intensity on unscented Crested Auklets compared to Least Auklets. Unscented Crested Auklets have not been recorded in nature, though the captive population in the Cincinnati Zoo does not produce the distinctive odour (Douglas 2008b).

The low prevalence and intensity of lice on Crested and Least Auklets observed in this study were not high enough to cause any measurable impact on body condition or ornament expression. The low prevalence and low intensity makes correlations difficult to address and likely is responsible for the lack of relationship between prevalence and condition in these two species via a sampling effect (i.e., I was unable to measure enough infested birds to provide a comparative sample for an analysis capable of detecting differences between infested and non-infested individuals). Alternatively, because the lice identified are scavengers that live principally off feather debris, it is possible that they have no effect on auklet health or viability, which is consistent with some previous suggestions about this group (Muzaffar and Jones 2004). However, my results do not exclude the possibility of a deleterious effect of these louse taxa at high levels of infestation (i.e., heavily infested birds would not have been included in my sample of healthy birds caught at a breeding colony). If at low levels parasites cause dramatic negative impacts, high levels of parasitism will rarely be observed in wild populations, as individual that become infested will quickly be lost from the population, so only these that are unparasitized, or with extremely low levels of parasitism and are healthy will be observed. It is difficult to distinguish between these two mechanisms without experimental manipulation of the system.

It is likely that my observed number of infested birds was not large enough to disentangle the multitude of factors that influence condition and ornament expression in Least and Crested Auklets. Multiple years of data, with many hundreds of birds would have to be caught in order to control for such factors. My study found variation between years and levels were higher than those reported in another colony (4%, Big Koniuji Island; Douglas 2006) suggesting that there may be considerable inter-annual and inter-colony variability in intensity and prevalence. Mean intensity and prevalence of lice infestation on both Least and Crested Auklets may have been so low enough that it did not affect body condition or ornament size. In addition, lice populations tend to be highly variable in many seabird species and the low prevalence found in these species of seabirds requires that extraordinarily large numbers of individuals be sampled over a number of breeding seasons.

The complex nature of host parasite relationships make it difficult to measure any impacts on host fitness, especially when prevalence is low and infested individuals have few parasites. The low prevalence and intensity of *Austromenopon*, *Quadraceps*, and *Saemundssonia* lice on the two alcid species, Least and Crested Auklets with high degrees of annual and seasonal variability in condition emphasize the subtleties of impact of these parasites and the need for large scale, long-term data sets as well as experimental studies to address the vital ecological questions of the impacts of parasites on their host species.

3.5 Summary

1. Lice prevalence and intensity was low in both species with Crested Auklets 12.9% (8.2-18.0%) in 210 individuals and in Least Auklets the prevalence was only 7.1% (3.8-12.7%) in 140 individuals. The mean intensity was only 1.22 (1.04-1.47) and 1.20 (1-1.6) Crested and Least Auklets respectively.
2. Intensity of lice found on individual Crested Auklets did not differ significantly from the intensity found on Least Auklets when sampling methods to control for body size were applied.
3. I was unable to detect a relationship between louse infestation and either body condition or ornament expression in Crested or Least Auklets, but the low prevalence of lice in my large sample of dust-ruffled birds may have affected my ability to detect such relationships.

Table 3.1. Summary of lice collected from Crested and Least Auklets on Buldir Island and housed at the Museum of New Zealand Te Papa Tongarewa. Specimens collected in the breeding season of 1997-1998 by Fiona Hunter on Buldir Island. The number of specimens and corresponding registration numbers (Reg. Num.) are included. Number of specimens in the collection is broken down into nymphs (N), adult males (M), and adult females (F). Lice were identified to species by Ricardo L. Palma or Roger D. Price.

		No. of specimens			Reg. Num.
Host Species	**Louse Species**	**N**	**M**	**F**	**AI.-**
Crested Auklet *Aethia cristatella*	*Austromenopon nigropleurum* (Denny, 1842)		14	12	015651 015652 015653
	Quadraceps aethereus (Giebel, 1874)		1	22	017867 017868
	Saemundssonia wumisuzume (Uchida, 1949)	5	1	7	018935
Least Auklet *Aethia pusilla*	*Austromenopon nigropleurum* (Denny, 1842)		7	22	015648 015649 015650
	Quadraceps aethereus (Giebel, 1874)	2	20	18	017863 017864
	Saemundssonia boschi (Price *et al*., 2003)	4	12	18	018741 018742

Table 3.2. Least (*Aethia pusilla*) and Crested Auklets (*A. cristatella*) dust-ruffled at Buldir Island Alaska during 2009 -2010 had *Quadraceps aethereus* while Crested Auklets also were infested with *Austromenopon nigropleurum* and *Saemundssonia wumisuzume*. Prevalence(P) and mean intensity (MI) are reported with 95% confidence limits.

	Louse species					
	Quadraceps aethereus		*Austromenopon nigropleurum*		*Saemundssonia wumisuzume*	
Host Species	**P**	**MI**	**P**	**MI**	**P**	**MI**
Least Auklet						
2009 (N=80)	10.7% (4.8-22.1%)	1.00 (1-1)	0	-	0	-
2010 (N=116)	4.8% (1.7-11.7%)	1.5 (1-2)	0	-	0	-
Total	**7.1% (3.8-12.7%)**	**1.20 (1-1.6)**	**0**	**-**	**0**	**-**
Crested Auklet						
2009 (N=66)	15.2% (8.1-25.6%)	1.3 (1-1.5)	3% (0.5-10.38%)	1.00 (1-1)	1.5% (0.08-8.07%)	1.00 (1-1)
2010 (N=206)	6.3% (3.5-10.6%)	1.00 (1-1)	1.0% (0.18-3.5%)	1.00 (1-1)	0.5% (0.03-2.79%)	1.00 (1-1)
Total	**11.0% (7.3-15.9%)**	**1.13 (1-1.3)**	**1.6% (0.6-4.1%)**	**1.00 (1-1)**	**0.8% (13.6%)**	**1.00 (1-1)**

Table 3.3. Within 140 Least Auklets (*Aethia pusilla*) and 210 Crested Auklets (*A. cristatella*) captured on Buldir Island in 2009 and 2010 there was no relationship among louse intensity, body condition, and ornament expression. The year and day of capture was included as dependent variables in MANOVA to address variation in body condition and ornament expression between and among breeding seasons.

				Body Condition Index		**Wing Length**		**Mean Auricular Plume Length**		**Breast Plumage Score**	
	Wilks's λ	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**
Least Auklet											
Lice	0.92	1.47	ns	1.3	ns	2.9	ns	0.1	ns	1.4	ns
Year	0.81	7.62	<0.01	7.4	<0.01	5.1	0.03	0.1	ns	17	<0.01
Day	0.89	4.22	0.01	15	<0.01	1.4	ns	0.2	ns	0.1	ns
Crested Auklet								**Crest Length**		**Rictal Plate Height**	
Lice	0.97	0.7	ns	0.1	ns	0.8	ns	1.34	ns	0.2	ns
Year	0.91	5.1	<0.01	13	>0.01	3.0	ns	0.01	ns	2.4	ns
Day	0.71	20	<0.01	4.3	0.04	0.2	ns	0.13	ns	72	>0.01

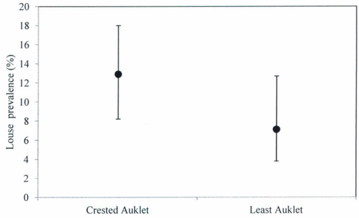

Figure 3.1 Prevalence of lice in 210 Crested Auklets (*Aethia cristatella*)and 140 Least Auklets (*A. pusilla*) captured on Buldir Island during 2009 and 2010. Error bars represent 95% confidence limits around the mean prevalence for each species.

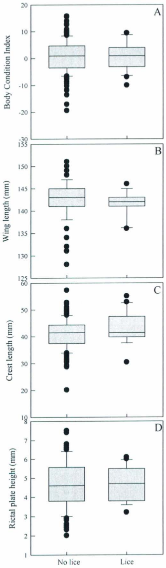

Figure 3.2 In Crested Auklets (*Aethia cristatella*; n=210), body condition index (A), wing length (B), crest length (C), and rictal plate height (D) was not related to the intensity of ticks (A-D) on Buldir Island during 2009 and 2010.

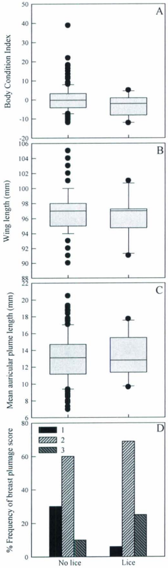

Figure 3.3 In Least Auklets (*Aethia pusilla*; n=140), body condition index (A), wing length (B), mean auricular plume length (C), and breast plumage score (D) was not related to the intensity of lice (A-D) on Buldir Island during 2009 and 2010.

Chapter 4

An experimental study of anti-parasite function for Crested Auklet (*Aethia cristatella*) feather odour

Abstract

The function of the unique tangerine-like scent produced by Crested Auklets (*Aethia cristatella*) provides an interesting Darwinian puzzle. Experimental evidence suggests a social role for the odour, but evidence that it functions to repel ectoparasites is equivocal. These two functions are not mutually exclusive. To test the ectoparasite hypothesis, at Buldir Island, Aleutian Islands, Alaska in 2009 and 2010 I investigated the relationship between tangerine odour to ectoparasite prevalence in wild caught individual Crested Auklets. I experimentally tested whether cloth treated with the two major components of the scent (Z-4-decenal and octanal), with an emission level duplicating that seen in nature, deterred questing adult ticks (*Ixodes uriae*) from attaching, compared to a scent-free control. More ticks (2.73x) were collected on unscented sheets. To examine the relationship of odour to ectoparasitism, I quantified individual birds' scent through a standard observer measure and quantified ectoparasite prevalence via collection by dust-ruffling with an insecticide. I found no relationship between odour and levels of parasitism.

4.1 Introduction

It has been traditionally assumed that olfaction plays a minor role in birds compared with other senses, so the study of avian odours and their functions has been neglected (Hagelin & Jones 2007). However, since the realization that most birds have a fully functional olfactory system there has been growing interest in birds' use of smell, avian odours, and odour functions (Balthazart & Taziaux 2009; Bonadonna & Nevitt 2004; Mínguez 1997).

Crested Auklets (*Aethia cristatella*) have a strong citrus-like odour during the breeding season (Douglas et al. 2001a; Hagelin et al. 2003; Humphrey 1958; Hunter & Jones 1999; Jones 1993a; Jones et al. 2000). Two functions have been proposed for this smell: intra-specific communication and chemical defence against ectoparasites (Clatyon et al. 2010; Hagelin & Jones 2007). Experimental evidence suggests a social role, because birds are attracted to the tangerine smell (Douglas et al. 2001a; Hagelin et al. 2003; Jones et al. 2004). Evidence for the ectoparasite repulsion hypothesis has been mixed (Douglas 2006a; Hagelin 2007; Hagelin and Jones 2007; Table 4.1). Due to the difficulty of reproducing realistic presentations of the odour to naturally occurring auklet ectoparasites in controlled experiments in the birds' remote and harsh environment. A dual function for the odour is possible, so a research priority is for more tests of the anti-parasite hypothesis.

Crested Auklets are small, locally abundant, colonial, planktivorous seabirds that occur only in the Bering and Okhotsk Seas and adjacent parts of the North Pacific (Jones 1993a). Crested Auklets coexist at most Alaskan colony sites and at sea with Least Auklets in summer and in winter form dense concentrations near Aleutian passes (Jones 1993a). They are known to only breed in nine colony sites in the Aleutian Islands (Williams et al. 2003). At breeding colonies (May-July) auklets congregate densely (with birds in direct contact with one another) on the surface and underground on rocky talus slopes and lava flows. These high densities provide an ideal environment for parasite transfer, tick attachment, and social interactions. However, auklets spend only their breeding season on land, limiting the amount of time that they are exposed to ticks. Crested Auklets have large crests on their forehead that are favoured by both males and females in mating selection (Jones & Hunter 1993, 1998). Both sexes also have white auricular plumes, and an orange bill with accessory plates that are displayed during breeding but become highly reduced after breeding (Jones 1993c; Jones & Hunter 1993). Their scent is composed of primarily short-chained, highly volatile aldehydes, alcohols and acids: N-hexanal, N-octanal, N-decanal, Z-4-decenal, hexanoic acid, octanoic acid, N-octanal, Z-4-dodecenal and Z-6-dodecenal as well as octanol, undecanal, tridecanal, and heptanal (Douglas et al. 2001a; Douglas et al. 2004; Hagelin et al. 2003). Emission rates differ depending on the measurement technique; solvent extraction: 5.7 μl octanal/50 min ±0.42 with a range of 19.9 μl/50 min to 2.8 μl/50 min (Douglas 2006a); head space analysis: 2.98 μg octanal/g of feather (Hagelin et al. 2003).The citrus-like scent is strongest during the breeding season and greatly reduced during the winter (Hagelin et al. 2003), and individuals vary in strength of the scent (IL Jones pers. com.; Douglas 2006a). The scent appears to be stronger in the plumage around the crown and nape than in the mantle feathers (IL Jones pers. comm.; Douglas 2006a). The anatomical source of the scent is unknown but Douglas (2008b) speculated that wick-like feathers in the interscapular region might be involved as some of the chemical constituents found in the scent were associated with this area (Douglas 2008b). The scent is not likely produced by the skin as no chemical constituents of the scent are found on the skin once feathers are removed (Douglas 2008b). Finally, captive birds at the Cincinnati Zoo do not produce the odour at all (Douglas 2008b), suggesting that some factors present in natural habitat are required for scent production.

Scent may play a social role, indicating status, condition, or being used in mate choice (Douglas 2006b; Jones et al. 2004). The ruff-sniff display (Jones and Hunter 1993) has been suggested to be a form of allopreening (Douglas 2008b), and transfers of scent between individuals. Douglas (2001b) speculated that the scent of the Crested Auklets acts to deter ectoparasites. Subsequent studies focusing on this role of the scent (Table 4.1) can be separated into those that used natural source Crested Auklet feather odour, and those that used a mixture of synthetic chemicals (available from commercial suppliers). These laboratory studies have focused on the two primary ectoparasites of auklets (ticks; lice) and have equivocal results (Table 4.1). Studies with natural presentation of scent did not reveal deterrence, but when synthetic chemicals were used (some with concentrations above natural levels), some results were consistent with the function of the scent as an ectoparasite repellent. Accordingly, I set out to perform more tests of the ectoparasite deterrence hypothesis with field experiments. I will: 1) test for a relationship between naturally occurring scent levels and ectoparasite prevalence on free-living Crested Auklets as predicted by the anti-parasite hypothesis; and 2) determine if a simulated odour treatment with the main components of Crested Auklet scent deterred questing ticks *(Ixodes uriae)*.

4.2 Methods

4.2.1 Study Location

Fieldwork was carried out at a colony of more than 100,000 Crested, Least other auklets at Main Talus, Buldir Island, Aleutian Islands, Alaska (52°2'N 175°5'E; Byrd & Day, 1986) during early June to late August of 2009 and 2010.

4.2.2 Capture and measurement of adults

Adult Crested Auklets were captured during the morning activity period 900-1300HADT (Hawaiian Aleutian daylight-savings Time: GMT-9:00) using noose carpets set on the colony surface. Birds were placed in a washed cloth bag to reduce stress and contamination of previously caught birds. Birds were processed in the order of capture. An individual that displayed any apparent distress (hot feet, open bill breathing) was immediately released. Each captured auklet was given a numbered US FWS stainless steel leg band, and was assigned a unique combination of three Darvik plastic colour bands.

Damage to the webbing between the toes was scored for each bird, with a scale of 0-2: 0- both feet undamaged; 1- one small hole in either foot, 2- multiple holes or tears in the webbing). These were old healed injuries that are acquired at the nestling stage when ticks attach to the chick's soft webbing (Hoberg & Wehle 1982; Morbey 1996).

Before bird were measured or sampled for parasites, I assessed their odour by smelling the nape for 5 seconds (Brattoli et al. 2011; Craven et al. 1996; Peris & Escuder-Gilabert 2009). Scent was quantified on a discrete scale of 0 to 3 (0 being unscented and 3 being highly scented).

4.2.3 Quantification of ectoparasite prevalence and intensity

Birds were visually inspected and palpated for attached and non-attached ticks from head to toe for 5 minutes (Clayton & Walther 1997). The feet and area around the eyes were visually inspected. The life stage (larval, nymph, and female adult), location of each tick was noted.

Birds were dust-ruffled (Walther and Clayton 1997) using dog flea powder (Sergeant's® tick and flea power for dogs, Carbaryl 5.0%, Pyrethrins 0.1%, Piperonyl Butoxide 1.0%) to collect lice. Birds were held over a clear plastic Ziplock® bag with powder applied evenly across the body following the procedure described by Walther and Clayton (1997). Powder was massaged into the feathers to ensure that the insecticide reached the bird's skin for five minutes. The first minute was used to distribute the powder over the bird, while the four minutes were spent ruffling the powder. The Ziplock® with powder and lice were visually inspected in the lab using a dissecting microscope so that all lice could be removed and placed in 70% ethanol for later identification. Lice have previously been collected from Buldir Island and identified to species (Table 3.1). For the purpose of this study, the level of louse prevalence was a measure by the count of individuals detected, regardless of species. Previous work indicates the taxa of lice present on Crested Auklets at Buldir are *Austromenopon nigropleurum*, *Quadraceps aethereus*, and *Saemundssonia wumisuzume* (Chapter 3).

4.2.4 Odour and tick questing experiment

To test whether questing ticks are deterred by chemicals I deployed a modification of a standard 'flagging technique' (Falco & Fish 1992), commonly used to collect ticks from the surrounding environment. I used two 1 m^2 (1.2m x 0.83m) cotton sheets, with a 1.5 cm diameter hardwood dowel supporting one side and weights applied to the opposite side to sample questing ticks. The sheets were placed on rocks throughout the colony and flipped over every minute for 30 minutes. Ticks were removed from the sheet with forceps, placed in 70% ethanol and later identified. Ticks were quantified as ticks per hour caught. Two treatments were used 1) control, the sheet was stored in a sealed container and so could not pick up the scent of auklets from any source and 2) experimental, sheet was stored in a container that had volatizing synthetic Crested Auklet scent. I restricted my experiment to a single treatment and a single control because I anticipated that few days would be suitable for sheet presentations due to the frequency of precipitation and water-soaked ground at Buldir. The scent treatment consisted of the two major components of the scent Z-4-decenal and octanal in a 1:3 ratio, the same chemicals used by Hagelin et al. (2003; presented 1:1) and Jones et al. (2004; presented 1:2) but in a ratio dominated more by octanal to replicate natural conditions as closely as possible (Douglas et al. 2004; Hagelin et al. 2003). To dose the sheet with an odour concentration similar to that emitted by wild birds I placed one drop of mixture onto a cotton ball housed inside the container 3-5 days before flagging. The container had a total volume of 2.5 L allowing the scent to reach the entire sheet. One drop contained 50 μl of mixture. Based on the density of octanal at 0.84 g/mL, sheets were exposed to 31.6 μg of octanal. An average Crested Auklet has a total feather mass of 11.9 g (Hagelin 2007a) and past estimates indicated that feathers of living wild birds have a mean of 2.98 μg of octanal per gram of feather mass (Hagelin et al. 2003). Based on these measurements an auklet would emit about 35.6 μg of octanal for its entire mass which is similar to the levels used in my experiment. At the same time two people each with one sheet walked through the colony placing a sheet on rocks and low vegetation. Sheets were never pulled through vegetation when it was raining or when the ground was water-soaked.

4.2.5 Analysis

All statistics were conducted in SPSS (version 19) and Quantitative Parasitology (Reiczigel & Rózsa 2005). Prevalence and mean intensity of tick infestation are reported with 95% confidence limits. Prevalence is the number of individual birds with one or more parasite, and mean intensity is the mean number of parasites on individuals that are have at least one parasite (Bush et al. 1997; Rózsa et al. 2000). Mean scent level is reported with 95% confidence limits. I used prevalence of lice, ticks and foot web damage as my scores of ectoparasites on individuals. I calculated day as the day number from January 1 of the respective year. These measures were related to the smell score with day and year of capture as covariates using a MANOVA. For the experiment, the number of ticks found on each sheet was related to treatment, and date of trial using a generalized linear model with a loglinear link function and a Poisson error structure.

4.3 Results

4.3.1 Tick and louse prevalence and their relation to odour

I captured individual Crested Auklets during the periods 3 June – 27 July 2009 and 2 June - 19 July 2010. Odour varied greatly across individuals, with scent score 2 individuals being the most frequent and large numbers of individuals scoring in all other categories (Table 4.2). The prevalence of ticks was 4.7% (2.4-8.2%, 95%CL) and prevalence of lice was 10.6% (7.1-15.2%, 95%CL). The mean intensity on birds that had at least one ectoparasite was 1.18 (1.00-1.36, 95%CL) and 1.20 (1.00-1.68, 95%CL) for ticks and lice, respectively. Neither the count of ticks nor count of lice found related to scent level (Table 4.3). All biologically relevant interaction terms were included, but removed from subsequent analysis when effect was not significant. Sex was removed from the analysis as there was not effect or interaction with scent and all previous studies have not reported a difference (Douglas 2006a; Hagelin et al. 2003).

4.3.2 Odour and tick questing experiment

I presented the scented and control sheets on 7 days (c. 3.5 hours of presentations) during the period 12 June – 28 July 2010. In the dragging experiment 2.73x more ticks were collected on (i.e., attached to) the unscented sheet than the scented sheet (scented=9.3±5.3, unscented=25.3±16.7, one standard deviation; χ^2=47.709, df=1, 11, p<0.001). The number of ticks collected was not related to date of season (χ^2=0.029, df=1, 11, p=0.864).

4.4 Discussion

I found no relationship between ectoparasite levels and natural scent levels on Crested Auklets. Conversely when scent levels were manipulated ticks were less likely to climb on to scented flagging cloths than unscented cloths suggesting a link between scent and tick behaviour. These results follow the pattern observed in many of the past studies (e.g., Douglas et al. 2001b; Hagelin et al. 2003; Douglas 2008), suggesting that variation at natural levels are too low to see the effect but with experimental manipulations there is an effect. It is important in scent presentation experiments is the concentration of odour presented to ectoparasites – if the odour concentration is higher than that expressed in nature on wild Crested Auklets, then any inference of repellency function is questionable. I believe my odour presentation was realistic because the sheet was dragged across Crested Auklet display rocks at a colony site during the breeding season when birds were present, and the dosed sheets emitted similar levels of chemical emissions to those found in wild Crested Auklets.

Tick and louse prevalence on Crested Auklet individuals were low, with only 4-10% of individuals having at least one ectoparasite individual detected (Chapter 2 and 3). Crested Auklets are known to have variable infestations of ectoparasites with some past studies failing to find any attached ticks (Engström et al. 2000), while in some years at Buldir, nearly every individual captured had ticks (IL Jones pers. comm.). Low ectoparasite prevalence could be attributed to the scent produced by this species, but closely related species at the same colony site including Least Auklets had similarly low levels during the same breeding seasons (Chapter 2 and 3). Low parasite levels require a large sample size to attain enough statistical power for a robust analysis and disentangle the other factors that are known to influence parasite levels including but not limited to interannual variability (T. Boulinier pers. comm.; Chapters 2 and 3) and climatic factors (Oorebeek & Kleindorfer 2008), limiting my ability to make strong inferences in this study.

Another issue concerns whether lice found on auklets are deleterious to the birds (i.e., whether they are in fact parasites as opposed to mere commensals). In a review of ectoparasites of the Alcidae, Muzaffar and Jones (2004) found no published evidence that lice (*Austromenopon* sp., *Quadraceps* sp., or *Saemundssonia* sp.) cause harmful effects. Because they feed on dead skin and feather particles, lice may perform a beneficial function, in which case it would not be expected that Crested Auklets would have chemical emissions adapted to repel them. In contrast, deleterious effects of *Ixodes* ticks on auks (both adults and nestlings) are widely known. Further research is required concerning health effects of bird lice on auklets and other seabird species to clarify this issue.

My method of scent quantification (Brattoli et al. 2011; Craven M.A. et al. 1996; Peris & Escuder-Gilabert 2009) was basic and allowed large numbers of individuals to be quickly assessed, but did not quantify the chemical components analytically using laboratory instruments. Scent is complicated, with each observer experiencing it differently, but my approach allowed all chemical components to be addressed. The disadvantage of chemical analyses previously used (Douglas et al. 2001a; Douglas 2006a; Hagelin et al. 2003) is that one is limited to quantifying a small subset of chemical components due to logistical constraints. I was able to qualify the scent addressing more components than measuring a single chemical component, e.g. octanal (Brattoli et al. 2011; Craven M.A. et al. 1996; Peris & Escuder-Gilabert 2009). This approach is limited in that year-to-year variation in criteria cannot be tested for, and it was unfortunate that I did not have the resources to compare my technique to a chemical analysis. As a result I used a 4-category scale to reduce the influences of these constraints. I do believe that this technique was robust, as human observers are commonly used in scent analyses (Brattoli et al. 2011; Craven et al. 1996; Peris & Escuder-Gilabert 2009).

The chemical components did reduce the number of questing tick collected on the experimental flagging sheets. This supports past results that the two primary chemical components do act as a defence against ticks (Douglas et al. 2001b; Douglas 2008b, 2006a). Though compelling these results are difficult to compare to natural circumstances with absolute certainty. Odours are not necessarily the sum of their parts, with the entire scent having to be considered – therefore I recommend that further attempts be made in future studies of wild birds. The most crucial further research on relationships between Crested Auklet ectoparasites and the tangerine odour would ideally take place at a colony site and in a year with high numbers of *Ixodes* ticks present. Ticks were relatively rare at Main Talus, Buldir Island in 2009 and 2010 (IL Jones pers. comm.), hampering my ability to make inferences.

4.4.1 Conclusion

Past studies have failed to find relationships between parasites and scent at natural levels acting as a defence mechanism (Douglas et al. 2005b; Hagelin et al. 2003; Hagelin 2007a). My results support the patterns found in past studies that at naturally occurring levels, with parasites at low levels, the scent produced by Crested Auklets does not act as a defence against ectoparasites. It also fits with past results that when scent is experimentally manipulated parasite levels are reduced, activity reduced, and morbidity increased. It is important to look at scent levels at natural occurring levels, with realistic environmental conditions (humidity, temperatures, wind, etc.) and understanding naturally occurring parasite levels. It will be necessary to establish natural relationships in conjunction with experimental manipulations before any conclusions can be made about whether Crested Auklet scent does act to deter parasites, or most specifically ticks.

4.5 Summary

1. Number of ticks, lice, or foot web damage was not related to the strength of scent on Crested Auklets.
2. More ticks were collected on unscented sheets than sheets with the two major components of the Crested Auklet scent, Z-4-decenal and Octanal in a dragging experiment in the breeding colony.

Table 4.1. Summary of published experimental and observational laboratory studies examining the function of Crested Auklet scent as an ectoparasite repellent. Studies are organized by parasite taxon studied, how the scent was presented, and if the study replicated natural odour emission intensity. N=natural; S=synthetic; O=observational study; E=experimental study; Yes=effect; No=no effect.

Ref.	Parasite species	Scent	Study	Results
1	*Ixodes uriae*	N	O	No. Small sample size
2	*I. uriae*	N	E	No.
3	*Amblyomma americanum*[*]	S[**]	E	Yes. Tick mobility reduced
4	*A. americanum*[*]	S[**]	E	Yes. Reduced time of attachment to artificial host
4	*I. uriae*	S[**]	E	Yes. Reduced time of attachment to artificial host
4	*I. uriae*	S[**]	E	Yes. Increased nymph and adult mortality
5	*Quadraceps aethereus*	N	O	Yes. More lice on Crested Auklets
5	*Saemundssonia wumisuzume, S. boschi, Austromenopon nigropleurum*	N	O	No. Louse prevalence similar within genus between Least and Crested Auklets
5	*Columbicola columbae*[*], *Campanulotes bidentatus*[*]	N	E	No.
5	*Co.columbae*[*]*, Ca.bidentatus*[*]	N	E	No.
4	*Q. aethereus, Au.nigropleurum*	S[**]	E	Yes. Increased nymph and adult mortality
6	*Aedes aegypti**	S	E	Yes. Reduced chances of landing on host

[*]Species not found within the range/habitat of Crested Auklets
[**]Odour concentration likely higher than that found naturally on Crested Auklet feathers

1-Douglas 2006a; 2-Hagelin 2007a; 3-Douglas 2008b; 4-Douglas et al. 2004; 5-Douglas et al. 2005b;6- Douglas et al. 2005a

Table 4.2. Most Crested Auklets (*Aethia cristatella*) caught on Buldir Island in 2009 and 2010 during the breeding season had no ticks or lice. Frequency of individuals with a scent (0- no noticeable scent; 1- lightly scented; 2- medium scent; and 3- highly scented) and parasite status (no parasites, just lice, just ticks, and both lice and ticks).

Scent level	Parasite status				
	No parasites	Lice	Ticks	Lice and ticks	**Total**
0	7	0	0	0	**7**
1	15	2	1	1	**19**
2	43	5	2	0	**50**
3	20	2	2	0	**24**
Total	**85**	**9**	**5**	**1**	**100**

Table 4.3 Within 236 Crested Auklets (*Aethia cristatella*) captured on Buldir Island in 2009 and 2010 there was no relationship among intensity of ticks, foot web damage, intensity of lice and the scent. The year and day of capture was included as dependent variables in MANOVA to address variation in body condition and ornament expression between and among breeding seasons.

				Ticks		Web damage		Lice	
	Wilks's λ	F	p	F	p	F	p	F	P
Scent	0.97	0.75	ns	0.96	ns	0.64	ns	0.87	ns
Year	0.97	2.12	ns	0.15	ns	0.39	ns	5.62	0.02
Day	0.99	0.25	ns	0.12	ns	0.01	ns	0.57	ns

Chapter 5

General Discussion

In recent years there has been a debate regarding the function of the citrus-like odour produced by Crested Auklets (*Aethia cristatella*). A number of adaptive functions have been proposed but the two that have received the most attention are intraspecific communication and chemical defence (Hagelin and Jones 2007). Jones et al. (2004) has provided evidence that this scent plays a social role, whereas Douglas et al. (2004) suggest that it acts to repel ectoparasites. These two hypotheses are not necessarily mutually exclusive.

I addressed the question: does this odour act as a chemical defence against ectoparasites and what effect do these parasites have on the birds? Before directly addressing the hypothesis it is important look at the relationship between ectoparasites and Crested Auklets. There must be negative impacts from ectoparasites for this likely energetically expensive scent to be worth producing if it simply protects these birds. In addition relationships between the intensity and body condition or ornament expression, which are related to quality can highlight the biological importance of these parasites.

I have demonstrated several points:

a) Within both Least and Crested Auklets the prevalence and mean intensity of tick were low. These intensities were not related to body condition or ornament expression in either species suggesting that they may not be biologically important to quality low levels.

b) In Whiskered, Least, and Crested Auklets there was no relationship between foot web damage and body condition or ornament expression. This further suggests that the levels of tick parasitism as a chick may not be related to adult health.

c) Louse prevalence in Least and Crested Auklets was low and mean intensity was also low. The intensity observed was not related to body condition or ornament expression suggesting that lice intensities observed in 2009 and 2010 on Buldir Island.

d) There was no relationship between ectoparasite levels and natural scent levels, but ticks are less likely to climb on to scented objects than unscented. The lack of naturally occurring relationship suggests that despite the fact that ticks may be repelled by the chemical components of the Crested Auklet scent, it may not be biologically important when ticks are in low abundance.

Literature examining the impacts of ectoparasites on the condition of individuals is quickly growing. Due to the fascinating nature of ectoparasites and interesting ecology of both host and parasite it is often difficult to determine when a relationship exists between their population level on a host and measures of condition. My findings add to the wealth of knowledge, demonstrating low levels of parasitism had no apparent negative effects on adult Least, Crested, and Whiskered Auklets.

Past studies have failed to find relationships between parasites and scent acting as a defence mechanism (Douglas et al. 2005b; Hagelin et al. 2003; Hagelin 2007a), and I believe that my results support the trend that at naturally occurring levels, with parasites at low levels, the scent produced by Crested Auklets does not act as a defence against ectoparasites. It is important that we have natural relationships in conjunction with experimental manipulations before any conclusions can be made about whether Crested Auklet scent does act to deter parasites, or most specifically ticks.

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Appendix I- Tick Prevalence in Alcids

Review of all available tick prevalence data from the literature for Alcids. Multiple entries from the same resource represent multiple colonies that were independently reported within source.

Host	Prevalence	Reference
Common Murre (*Uria aalge)*	1%	Barton 1996
	14%	Muzaffar 2000
	28%	Choe & Kim 1987a
	29%	Wanless et al. 1997
	54%	Eveleigh & Threlfall 1975
	97%	Choe & Kim 1987a
Thick-billed Murre (*Uria lomvia*)	2%	Coulson et al. 2009
	21%	Muzaffar 2000
	50%	Choe & Kim 1987a
	97%	Choe & Kim 1987a
Razorbill (*Alca torda*)	0%	Wanless et al. 1997
	6%	Muzaffar 2000
	8%	Barton 1996
	67%	Eveleigh & Threlfall 1975
Crested Auklet (*Aethia cristatella*)	0%	Engström et al. 2000
	2%	Douglas 2006a
Atlantic Puffin (*Fratercula arctica*)	5%	Barton 1996
	13%	Muzaffar 2000
	18%	Eveleigh & Threlfall 1975

Appendix II- Lice prevalence in Alcids

All available lice prevalence data from the literature for Alcides. Multiple entries from the same resource represent multiple colonies that were independently reported or different species of ticks that were broken down and not reported pooled.

Host	Prevalence	Reference
Common Murre (*Uria aalge)*	7%	Muzaffar 2000
	21%	Muzaffar 2000
	24%	Muzaffar 2000
	72%	Choe & Kim 1987b
	82%	Eveleigh & Threlfall 1976
	100%	Choe & Kim 1987b
Thick-billed Murre (*Uria lomvia*)	10%	Muzaffar 2000
	13%	Choe & Kim 1987b
	17%	Muzaffar 2000
	24%	Muzaffar 2000
	63%	Choe & Kim 1987b
	75%	Choe & Kim 1987b
	85%	Eveleigh & Threlfall 1976
Dovkie (*Alle alle*)	100%	Eveleigh & Threlfall 1976
Razorbill (*Alca torda*)	17%	Muzaffar 2000
	22%	Muzaffar 2000
	28%	Muzaffar 2000
	75%	Eveleigh & Threlfall 1976
Black Guillemot (*Cepphus grille*)	50%	Eveleigh & Threlfall 1976
Crested Auklet (*Aethia cristatella*)	4%	Douglas 2006a
Atlantic Puffin (*Fratercula arctica*)	3%	Muzaffar 2000
	17%	Muzaffar 2000
	33%	Muzaffar 2000
	67%	Eveleigh & Threlfall 1976

Appendix III- Detailed dust ruffling protocol and calculations

HM dust ruffled all birds after measurements were taken. To ensure that tick and flea powder did not contaminate the birds during measurement taking a pair of latex gloves were worn during dust ruffling and removed once birds were released. Gloves were reused but visually inspected between individuals to ensure no cross contamination.

Birds were held over a 1 gallon Ziplock® bag. The premeasured amount of powder (Sergeant's® tick and flea power for dogs, Carbaryl 5.0%, Pyrethrins 0.1%, Piparony Butoxide 1.0%) was thoroughly distributed over the surface of the bird's body within the first 20 seconds. Special care was made around the face to get powder as close to the eyes and mouth without getting any in the birds face. HM massaged powder to the base of the feathers. Each bird was continuously ruffled over the Ziplock® bag for 3 or 5 minutes depending on species. The first minute was used to distribute the powder over the bird, while the next two or four minutes were spent ruffling the powder. It took the same time to distribute the powder for both species.

While birds were being massaged with powder I inspected birds for attached ticks. Areas around the face, legs, and brood patch were visually inspected. Like many seabirds, auklets have dense plumage so the rest of the surface area was palpated for attached ticks.

If a bird defecated in the bag, no attempt was made to remove it on the off-chance that parasites became associated with it.

Crested Auklets have a surface area ratio relative to Least Auklets of 2.1:1 (see calculations below) based on the relationship between mass and surface area by Walsberg & King (1978). To accommodate for this the amount of powder applied to each individual differed based on species. The length of time spent ruffling differed as it would take less time to evenly distribute powder on a smaller bird and massage the powder into the feather.

Calculations for surface area

Equation for surface area
$h=10\ M^{0.667}$ (Walsberg & King 1978)
Symbols in equation
M=mass
h=surface area

Crested Auklets
M=243g (Jones 1993b)

$h=10\ (243)^{2/3}$
$h=390\text{cm}^2$

Least Auklets
M=81.4g (Jones 1993a)

$h=10\ (81.4)^{2/3}$
$h=180\ \text{cm}^2$

Ratio of Crested Auklet surface area to Least Auklet surface area

Ratio=area of Crested Auklet/area of Least Auklet
Ratio=390 cm^2/180 cm^2
Ratio=2.07

Appendix IV

Raw data of all Crested Auklets (*Aethia cristatella)* caught during the breeding season in 2009 and 2010. All louse specimens are mounted and ID by Ricardo Palma of Museum of New Zealand Te Papa Tongarewa. Day= numeric date from 1 January of the respective year; Yr= year; Snt= scent level on a scale of 0-4 (0- no noticeable scent; 1- lightly scented; 2- medium scent; and 3- highly scented); A= adult; S= sub-adult; U= unknown sex; F= female; M= male; Rictal=rictal plate height; Crest= maximum crest length;Web= score of 0-2(0-no holes in either foot web;1- individuals had a single circular hole in either foot web; and 2- had greater than one hole); Tick= number of *Ixodes uriea*; Lice-Q is the number of *Quadraceps aethereus*; L-S= number of *Saemundssonia wumisuzume*; Lice-A= number of *Austromenopon nigropleurum*.

								Auricular plume length								
Day	Yr	Snt	Age	Sex	Mass	Rictal	Crest	Left	Right	Mean	Wing	Web	Tick	Lice-Q	Lice-S	Lice-A
153	09	1	A	U	263	5.5	30.2	28.3	25.4	26.85	141	0	3	0	0	0
183	10	3	A	F	259	.	31.9	24.2	25.5	24.85	135	0	2	0	0	0
195	10	1	A	F	242	0	48.5	28	28	28	143	0	2	0	0	0
167	09	2	A	M	255	6.1	38	28.3	27.5	27.9	137	0	1	6	4	0
161	09	2	A	M	267	3.6	38.1	24.5	29.1	26.8	143	1	1	4	0	0
178	09	1	A	M	279	4.2	50.2	28.7	29.6	29.15	139	0	1	2	1	1
167	09	2	A	F	246	5.2	36.6	24.5	28.5	26.5	138	0	1	1	0	0
201	09	.	A	F	226	3.5	45.6	31	33.5	32.25	145	0	1	0	0	1
164	09	2	A	F	245	5	35.6	26.1	27.5	26.8	137	0	1	0	0	0
178	09	1	A	U	249	4.5	43.7	26.7	28.6	27.65	132	1	1	0	0	0
157	10	2	A	M	266	6.5	39	29.6	30	29.8	149	0	1	0	0	0
167	10	2	A	M	206	5.3	37.4	24.7	19.5	22.1	141	0	1	0	0	0
167	10	3	A	M	283	7.4	40.3	21.4	26.4	23.9	143	0	1	0	0	0

								Auricular plume length								
Day	Yr	Snt	Age	Sex	Mass	Rictal	Crest	Left	Right	Mean	Wing	Web	Tick	Lice-Q	Lice-S	Lice-A
183	10	2	A	F	262	4.7	36	24.6	27.5	26.05	138	0	1	0	0	0
191	10	3	A	F	242	3.9	46.5	29.2	31.6	30.4	142	0	1	0	0	0
195	10	2	A	F	261	3.8	52.6	30	29.4	29.7	141	0	1	0	0	0
195	10	3	A	F	270	2.9	36	23.2	23.4	23.3	144	0	1	0	0	0
161	09	1	A	M	257	5.5	37.6	24	22	23	146	0	0	3	0	0
164	09	2	A	F	274	5	43.1	26	29.9	27.95	143	0	0	3	0	0
167	09	3	A	M	251	6.2	38.5	30.9	31.9	31.4	142	0	0	2	0	1
159	09	2	A	U	260	6.1	28.4	35.2	35.6	35.4	140	1	0	2	0	0
164	09	2	A	U	270	5.6	41.4	27.8	33.7	30.75	146	0	0	2	0	0
174	09	.	A	M	271	5.7	44.6	28.4	30.3	29.35	145	1	0	2	0	0
188	09	1	A	F	231	4.6	32.4	23	27.6	25.3	140	0	0	2	0	0
159	09	2	A	M	269	5.7	36.4	27.6	30	28.8	145	1	0	1	0	0
161	09	2	A	F	247	5.2	32.2	31.6	35	33.3	143	0	0	1	0	0
164	09	3	S	U	246	4.3	24.5	21.5	22.3	21.9	140	0	0	1	0	0
164	09	3	A	U	254	5.8	26.4	30.5	32	31.25	140	0	0	1	0	0
164	09	2	A	U	264	5.6	41.5	32.1	32.5	32.3	147	2	0	1	0	0
164	09	1	S	U	236	4.5	23	24.8	27.2	26	144	0	0	1	0	0
167	09	2	A	M	290	6	26.4	28.4	29.2	28.8	144	0	0	1	0	0
167	09	2	A	F	.	5.7	45.5	27.5	25.2	26.35	141	0	0	1	0	0
170	09	2	A	M	282	4.8	37.6	28.6	28.3	28.45	142	0	0	1	0	0
170	09	2	A	U	265	5	40.9	27.5	31.2	29.35	140	0	0	1	0	0
174	09	.	A	U	238	5	43	26.8	28.1	27.45	143	0	0	1	0	0
174	09	.	A	U	246	4.7	32.4	21.4	23.2	22.3	141	0	0	1	0	0

Day	Yr	Snt	Age	Sex	Mass	Rictal	Crest	Auricular plume length Left	Right	Mean	Wing	Web	Tick	Lice-Q	Lice-S	Lice-A
174	09	.	A	F	223	5.3	43	27.6	28.9	28.25	137	0	0	1	0	0
174	09	.	A	F	245	5.7	42.2	29.9	30.5	30.2	142	1	0	1	0	0
182	09	2	A	M	240	5.4	47.9	22.8	21.2	22	142	0	0	1	0	0
152	10	2	A	M	253	6.1	39.6	26.4	23.8	25.1	142	0	0	1	0	0
157	10	2	A	M	259	5.6	51.4	27.9	29.5	28.7	143	2	0	1	0	0
164	10	2	A	F	265	4	47.9	28.4	31.9	30.15	143	0	0	1	0	0
175	10	3	A	M	266	4	42.1	26.4	28.3	27.35	143	0	0	1	0	0
175	10	2	A	F	264	3.2	41.1	28.1	20.6	24.35	142	0	0	1	0	0
183	10	3	A	F	257	3.6	41.8	23.6	24.8	24.2	141	1	0	1	0	0
188	10	1	A	M	267	5.1	52.8	23.2	26.2	24.7	143	0	0	1	0	0
188	10	3	A	F	249	3.6	37.6	6.9	11.1	9	141	0	0	1	0	0
191	10	1	A	F	253	3.8	41.7	19.4	20.6	20	144	0	0	1	0	0
193	10	1	A	M	237	3.6	40.3	23.7	26.7	25.2	136	0	0	1	0	0
193	10	2	A	M	246	4.7	40.1	23.1	26.1	24.6	141	0	0	1	0	0
195	10	2	A	M	273	6	47.1	35	36.6	35.8	141	0	0	1	0	0
195	10	0	A	M	273	5.8	55	27.9	24	25.95	145	0	0	1	0	0
161	09	2	A	M	229	5.4	33.8	34.5	33.4	33.95	134	0	0	0	1	3
193	10	2	A	F	270	4.6	41.4	31.2	28.7	29.95	142	0	0	0	1	0
159	09	3	A	M	263	5.4	37	27.5	28.2	27.85	143	2	0	0	0	1
161	09	1	A	U	266	4.2	36	26.5	30	28.25	138	2	0	0	0	1
161	09	1	A	M	269	6	32.5	26.4	26.8	26.6	144	0	0	0	0	1
164	09	3	A	M	278	6.4	42.4	34	36.6	35.3	145	0	0	0	0	1
164	09	3	A	M	254	6.2	45.8	32	34	33	144	2	0	0	0	1

								Auricular plume length								
Day	Yr	Snt	Age	Sex	Mass	Rictal	Crest	Left	Right	Mean	Wing	Web	Tick	Lice-Q	Lice-S	Lice-A
157	10	3	A	F	240	5.4	30.4	23.6	25.8	24.7	136	0	0	0	0	1
188	10	1	A	M	234	3.8	40	27.9	32.3	30.1	143	0	0	0	0	1
153	09	.	A	F	252	5.2	35.7	29.2	29.2	29.2	137	1	0	0	0	0
153	09	.	A	F	250	5.6	41.9	29.4	30.8	30.1	144	1	0	0	0	0
153	09	0	A	F	235	5	38.1	29.7	28	28.85	140	0	0	0	0	0
153	09	1	A	M	274	6.8	35	24.1	26.4	25.25	136	0	0	0	0	0
153	09	3	A	M	262	4.4	33.6	30.5	31	30.75	139	0	0	0	0	0
153	09	3	A	M	254	5.5	40.2	22.6	20.6	21.6	137	0	0	0	0	0
153	09	3	A	U	272	5	34.8	27.6	27.6	27.6	144	0	0	0	0	0
153	09	3	A	M	274	6.6	35.6	25	25.1	25.05	142	0	0	0	0	0
156	09	2	A	F	273	4.9	34.9	27.9	27.3	27.6	140	0	0	0	0	0
156	09	2	A	U	260	6	41	26.6	24	25.3	141	0	0	0	0	0
159	09	3	A	U	230	3.2	26.2	23.5	25	24.25	134	0	0	0	0	0
159	09	2	A	F	257	4.7	37.3	27	27.8	27.4	147	1	0	0	0	0
159	09	2	A	F	227	4.4	40.6	29	33	31	136	1	0	0	0	0
161	09	2	A	F	252	4.8	43.9	27.2	28.4	27.8	142	2	0	0	0	0
161	09	2	A	M	255	5.4	46.5	27.8	28.4	28.1	144	1	0	0	0	0
161	09	2	A	M	270	4.9	32.2	22.1	25.6	23.85	142	1	0	0	0	0
161	09	2	A	M	263	5	48.1	31.9	33.2	32.55	145	0	0	0	0	0
161	09	3	A	M	295	5.8	36.1	27.4	27.6	27.5	143	0	0	0	0	0
161	09	1	A	F	261	6.3	50.2	28.5	26	27.25	145	0	0	0	0	0
161	09	2	A	F	257	5.8	34.7	20.7	22.1	21.4	138	0	0	0	0	0
161	09	1	A	M	289	7.6	42	30.9	25.6	28.25	143	0	0	0	0	0

								Auricular plume length								
Day	Yr	Snt	Age	Sex	Mass	Rictal	Crest	Left	Right	Mean	Wing	Web	Tick	Lice-Q	Lice-S	Lice-A
164	09	2	A	F	279	4.6	35.2	24.5	26.9	25.7	141	0	0	0	0	0
164	09	2	A	F	268	5.7	42.3	19.3	18.2	18.75	143	0	0	0	0	0
164	09	3	A	M	251	5	37.4	25.1	26.6	25.85	136	1	0	0	0	0
164	09	1	A	M	250	5.6	40.8	27.4	28.6	28	140	0	0	0	0	0
164	09	3	A	M	263	6.5	9.6	28.8	30.5	29.65	148	0	0	0	0	0
167	09	3	A	M	268	5.3	39.1	29	30.2	29.6	145	0	0	0	0	0
167	09	1	A	F	237	4.6	41.6	24.5	26.4	25.45	140	0	0	0	0	0
167	09	2	A	F	225	5.9	46.7	24.7	23.5	24.1	139	0	0	0	0	0
170	09	0	A	F	229	4.6	34.8	22.4	26.6	24.5	143	0	0	0	0	0
170	09	0	A	U	256	5.2	45.1	26.9	23.9	25.4	144	0	0	0	0	0
170	09	2	A	M	267	6.1	39.6	29.2	28.4	28.8	144	0	0	0	0	0
170	09	2	A	U	279	5.7	37.4	29.2	28.7	28.95	137	0	0	0	0	0
170	09	3	A	U	264	6.9	34.7	27.2	29.3	28.25	142	0	0	0	0	0
174	09	.	A	U	256	3.6	41.1	34.6	34.3	34.45	143	2	0	0	0	0
174	09	.	A	M	263	5	43.7	28.5	26.1	27.3	143	0	0	0	0	0
174	09	.	A	M	258	5.4	44	22.9	24.8	23.85	145	1	0	0	0	0
174	09	.	A	F	243	5.2	47.6	28.5	32.7	30.6	144	0	0	0	0	0
174	09	.	A	M	224	5.4	49.3	22.6	22.3	22.45	136	0	0	0	0	0
174	09	.	A	U	242	4	44.3	27	26.5	26.75	138	0	0	0	0	0
174	09	.	A	M	238	6.1	42.8	32	34.4	33.2	141	0	0	0	0	0
174	09	.	A	U	251	5.1	32.1	27.8	33.1	30.45	146	0	0	0	0	0
178	09	1	A	M	287	0	48.5	25.8	26.7	14.8	148	0	0	0	0	0
178	09	.	A	U	278	.	.	.	.	.	.	.	0	0	0	0

								Auricular plume length								
Day	Yr	Snt	Age	Sex	Mass	Rictal	Crest	Left	Right	Mean	Wing	Web	Tick	Lice-Q	Lice-S	Lice-A
178	09	1	A	U	272	.	.	.	.	.	.	.	0	0	0	0
182	09	2	A	M	256	3.7	41.9	26.9	32.5	29.7	143	1	0	0	0	0
182	09	0	A	U	259	4.3	29.4	23.9	25.3	24.6	142	0	0	0	0	0
182	09	1	A	F	243	2.8	33.1	23.5	29.2	26.35	134	0	0	0	0	0
182	09	1	A	M	246	4.7	47.4	28.1	24.3	26.2	140	0	0	0	0	0
185	09	.	A	U	226	4.9	39	28.8	30.8	29.8	143	0	0	0	0	0
185	09	.	A	F	240	3.1	32.5	28.2	29.4	28.8	136	0	0	0	0	0
185	09	.	A	M	246	4.6	41.2	14.2	19.1	16.65	138	0	0	0	0	0
185	09	.	A	M	257	5	45.8	24.5	26.2	25.35	158	0	0	0	0	0
185	09	.	A	M	246	4.8	34.5	28.6	30.8	29.7	145	0	0	0	0	0
185	09	.	A	M	254	6.5	45.7	22.5	23.6	23.05	143	0	0	0	0	0
185	09	.	A	M	239	3.4	37.9	19.5	19.8	19.65	145	0	0	0	0	0
188	09	3	A	M	234	3.1	33.1	29.9	29.1	29.5	141	0	0	0	0	0
188	09	2	A	M	246	4.9	39.4	29.2	31.1	30.15	144	0	0	0	0	0
188	09	1	A	M	265	4.5	30.7	20.6	25.9	23.25	140	0	0	0	0	0
188	09	1	A	M	255	4	35.9	22.5	23.2	22.85	140	0	0	0	0	0
188	09	1	A	M	272	5.4	40.9	23.7	24	23.85	145	0	0	0	0	0
188	09	1	A	U	338	3.1	48.5	26.8	30.9	28.85	146	0	0	0	0	0
188	09	1	A	F	252	0	34.4	19.6	20	19.8	141	2	0	0	0	0
188	09	2	A	F	251	3.7	43.2	30.5	28.8	29.65	141	0	0	0	0	0
188	09	2	A	F	255	4.3	43.6	27.3	23.2	25.25	143	0	0	0	0	0
188	09	2	A	F	257	3.9	44.9	30.7	25.5	28.1	140	1	0	0	0	0
188	09	1	A	M	256	4.5	39.9	28.5	27.9	28.2	131	0	0	0	0	0

Day	Yr	Snt	Age	Sex	Mass	Rictal	Crest	Auricular plume length Left	Right	Mean	Wing	Web	Tick	Lice-Q	Lice-S	Lice-A
192	09	3	A	U	241	3.6	42.1	21.4	20.9	21.15	145	0	0	0	0	0
192	09	2	S	U	258	3	23.7	25	28.2	26.6	141	0	0	0	0	0
192	09	1	A	M	243	2.9	34.5	21.4	21.9	21.65	141	0	0	0	0	0
197	09	3	A	M	276	4.7	48.7	36.5	37.4	36.95	146	0	0	0	0	0
197	09	2	A	M	250	5.1	39.1	33.1	33.2	33.15	137	1	0	0	0	0
197	09	2	A	U	244	0	36.5	31	28.7	29.85	141	0	0	0	0	0
197	09	3	A	F	238	4.2	41.4	26.4	23.8	25.1	134	0	0	0	0	0
197	09	1	A	M	231	0	31.8	30	27	28.5	138	0	0	0	0	0
197	09	2	A	M	245	0	42.2	30.4	33.1	31.75	142	0	0	0	0	0
197	09	2	A	F	235	0	45.5	14.5	17.5	16	143	0	0	0	0	0
201	09	3	A	U	242	na	45.3	22.2	24.7	23.45	140	0	0	0	0	0
201	09	2	A	U	229	3.1	38.2	24.1	25.7	24.9	142	0	0	0	0	0
201	09	2	A	M	257	3.4	49.6	28.4	29.7	29.05	149	0	0	0	0	0
201	09	3	A	M	212	4.4	46.3	34	38.8	36.4	141	0	0	0	0	0
205	09	3	A	M	243	5.7	40.5	22.5	21.7	22.1	143	1	0	0	0	0
205	09	2	A	M	254	4.4	39.4	33.8	26.3	30.05	143	0	0	0	0	0
152	10	2	A	M	263	5	47.1	30.4	28.6	29.5	141	0	0	0	0	0
152	10	2	A	F	238	5.2	39.1	18.8	15.2	17	142	0	0	0	0	0
152	10	3	A	M	281	6.2	44.5	29.1	27	28.05	145	0	0	0	0	0
152	10	2	A	F	242	5.5	41.6	24.8	28.2	26.5	139	0	0	0	0	0
154	10	3	A	M	289	5.7	42	33	36.7	34.85	145	0	0	0	0	0
154	10	3	A	M	283	5.5	33.9	29.1	28.5	28.8	142	0	0	0	0	0
154	10	2	A	M	289	6.5	39.6	23.6	20.5	22.05	145	1	0	0	0	0

Day	Yr	Snt	Age	Sex	Mass	Rictal	Crest	Auricular plume length Left	Right	Mean	Wing	Web	Tick	Lice-Q	Lice-S	Lice-A
154	10	2	A	M	274	6.8	49.4	23.3	26.9	25.1	144	0	0	0	0	0
157	10	2	A	F	248	6.6	38.4	23.4	23.6	23.5	144	0	0	0	0	0
157	10	2	A	M	283	6.1	36	12	14	13	146	1	0	0	0	0
157	10	2	A	M	251	6	41.1	23.2	22.6	22.9	142	0	0	0	0	0
157	10	3	A	M	278	5.2	47.1	27.5	26.4	26.95	142	0	0	0	0	0
157	10	2	A	M	252	5	49.5	32	29.7	30.85	141	2	0	0	0	0
157	10	3	A	M	280	6.8	44.5	29.6	27.7	28.65	146	0	0	0	0	0
157	10	2	A	M	265	4.5	38.4	32.9	32.7	32.8	140	0	0	0	0	0
157	10	2	A	M	249	6.5	41.5	25	26.7	25.85	142	1	0	0	0	0
157	10	3	A	M	287	6.1	43.4	30.8	32.1	31.45	149	0	0	0	0	0
157	10	1	A	F	243	4.8	42.1	28	26.8	27.4	139	0	0	0	0	0
160	10	2	A	M	234	5.7	52.1	25.2	31.6	28.4	136	0	0	0	0	0
160	10	3	A	M	294	6.4	36.4	31.1	35.1	33.1	149	0	0	0	0	0
160	10	2	A	F	263	5.9	36	28.2	37.5	32.85	140	0	0	0	0	0
160	10	3	A	M	295	6.3	48.7	32.8	36.6	34.7	147	1	0	0	0	0
160	10	2	A	F	256	5.4	31.9	28.5	28.7	28.6	144	0	0	0	0	0
160	10	2	A	M	289	5.6	47.8	23.2	23.4	23.3	147	0	0	0	0	0
160	10	3	A	M	272	4	50	21.7	24	22.85	146	0	0	0	0	0
160	10	1	S	U	243	4	23.7	14.4	20.1	17.25	141	0	0	0	0	0
164	10	2	A	F	274	5.2	30.7	26.8	25.5	26.15	146	0	0	0	0	0
164	10	2	A	F	272	5.6	47	27.6	28.5	28.05	143	3	0	0	0	0
164	10	2	A	M	259	6.7	33.8	18	20.9	19.45	141	0	0	0	0	0
167	10	2	A	F	265	4.6	47	19.6	16.7	18.15	136	0	0	0	0	0

Day	Yr	Snt	Age	Sex	Mass	Rictal	Crest	Auricular plume length Left	Right	Mean	Wing	Web	Tick	Lice-Q	Lice-S	Lice-A
167	10	2	A	F	305	4	43.5	31.1	32.3	31.7	145	0	0	0	0	0
167	10	2	A	F	285	3.8	42.1	25.1	23.8	24.45	143	0	0	0	0	0
167	10	2	A	M	282	6.8	42.9	21.4	25.6	23.5	144	0	0	0	0	0
167	10	3	A	M	257	6.6	42.9	23.6	21.5	22.55	132	0	0	0	0	0
167	10	3	A	F	243	5.6	44.7	29.5	25.4	27.45	142	0	0	0	0	0
167	10	2	A	M	252	5.4	41.4	20.3	19.6	19.95	139	1	0	0	0	0
167	10	2	A	M	253	5.8	42.6	28.2	28.9	28.55	145	0	0	0	0	0
167	10	3	A	M	250	3.7	32.6	25.1	24.6	24.85	142	0	0	0	0	0
173	10	2	A	F	221	4.1	35.6	22.5	28.2	25.35	141	0	0	0	0	0
173	10	2	A	F	249	5.4	43.4	19	21.4	20.2	141	0	0	0	0	0
173	10	2	A	M	263	5.4	41.6	28.9	29.5	29.2	139	0	0	0	0	0
173	10	1	S	U	230	3.4	26.4	21.4	18	19.7	145	0	0	0	0	0
173	10	2	A	F	300	4.1	43.9	24.9	24	24.45	146	1	0	0	0	0
173	10	2	A	M	296	4.1	41.1	28.4	26	27.2	143	1	0	0	0	0
173	10	3	A	M	245	6.8	38.5	29.4	32.5	30.95	147	0	0	0	0	0
173	10	1	A	M	269	6.3	48.7	27.7	28.5	28.1	151	0	0	0	0	0
173	10	1	S	U	236	3.2	27.7	19.4	22.3	20.85	136	0	0	0	0	0
173	10	0	S	U	237	3	15.1	28	28.7	28.35	139	0	0	0	0	0
173	10	2	A	M	305	7.4	41.6	24.6	34.5	29.55	145	0	0	0	0	0
173	10	2	A	M	271	7.5	36.1	21.1	27.7	24.4	148	0	0	0	0	0
173	10	2	S	U	265	3.5	23.1	22	19	20.5	138	0	0	0	0	0
173	10	2	A	M	271	4.6	41.4	25.5	31.5	28.5	146	1	0	0	0	0
173	10	3	A	M	260	6	50.9	32.9	32	32.45	143	2	0	0	0	0

Day	Yr	Snt	Age	Sex	Mass	Rictal	Crest	Auricular plume length Left	Right	Mean	Wing	Web	Tick	Lice-Q	Lice-S	Lice-A
173	10	1	A	F	265	4.6	41.7	28.1	28.6	28.35	131	0	0	0	0	0
173	10	2	A	F	241	4.7	47	26.9	27.7	27.3	143	0	0	0	0	0
175	10	2	A	F	235	4.5	39.2	32.1	31.9	32	128	0	0	0	0	0
175	10	1	A	M	249	6.4	36.8	24.9	28.6	26.75	146	0	0	0	0	0
175	10	2	A	M	277	3.8	45.3	32.4	31	31.7	146	1	0	0	0	0
175	10	1	A	F	253	6.5	46.9	28.4	23	25.7	147	0	0	0	0	0
175	10	2	A	F	304	3.9	42.5	29.6	32.4	31	148	0	0	0	0	0
175	10	2	A	F	237	5	37.4	20.4	23.1	21.75	145	0	0	0	0	0
175	10	2	A	M	258	6.3	43.7	25.3	25	25.15	143	0	0	0	0	0
175	10	1	A	F	251	4.3	40.7	25.1	31.2	28.15	140	0	0	0	0	0
175	10	3	A	M	258	4.9	42.1	34.9	30.1	32.5	144	0	0	0	0	0
175	10	3	A	F	251	4.5	36.2	22	19.2	20.6	134	0	0	0	0	0
175	10	2	A	F	242	5.6	33.4	23.1	22	22.55	143	0	0	0	0	0
175	10	1	A	F	243	5.7	43.7	19.8	20.7	20.25	146	0	0	0	0	0
175	10	2	A	F	284	6.1	44.6	29.1	29	29.05	145	0	0	0	0	0
175	10	3	A	F	256	4.6	41.9	26.8	27.1	26.95	140	0	0	0	0	0
177	10	3	A	M	264	5	39.8	33.9	33.5	33.7	138	0	0	0	0	0
177	10	2	A	F	269	2.5	28.8	29.8	24.6	27.2	145	0	0	0	0	0
177	10	2	A	M	252	6	46.2	19.6	20.6	20.1	143	0	0	0	0	0
177	10	2	A	F	277	6	40.3	28.6	28.1	28.35	147	0	0	0	0	0
177	10	2	A	M	281	6.5	30.4	20.1	28	24.05	146	0	0	0	0	0
177	10	3	A	M	285	4.9	41.5	36	37.2	36.6	146	0	0	0	0	0
177	10	2	A	F	268	6.1	43.7	17.9	21.1	19.5	142	0	0	0	0	0

Day	Yr	Snt	Age	Sex	Mass	Rictal	Crest	Auricular plume length Left	Right	Mean	Wing	Web	Tick	Lice-Q	Lice-S	Lice-A
177	10	2	A	F	263	3.8	57.2	27.1	21.5	24.3	146	0	0	0	0	0
177	10	2	A	M	266	5.3	37.6	25.7	26.6	26.15	145	2	0	0	0	0
177	10	2	A	F	281	5.2	46	26.3	27.9	27.1	140	0	0	0	0	0
177	10	2	A	F	265	3	44.6	30.9	23.1	27	142	0	0	0	0	0
177	10	2	A	F	268	5.4	35	29.2	29.5	29.35	138	0	0	0	0	0
179	10	2	A	F	260	3.1	34.8	19.1	28.6	23.85	141	1	0	0	0	0
179	10	3	A	F	275	4.7	39.1	18.5	20.1	19.3	138	0	0	0	0	0
179	10	1	A	M	284	4	48.7	30.3	26.5	28.4	145	1	0	0	0	0
179	10	3	A	F	253	5.7	43.7	29.6	34.2	31.9	143	0	0	0	0	0
179	10	1	A	M	294	4	42.2	28.7	27.9	28.3	150	0	0	0	0	0
179	10	2	A	F	256	4.5	34	25.8	26	25.9	144	0	0	0	0	0
179	10	2	A	F	270	3.5	39.8	26.9	24.1	25.5	142	0	0	0	0	0
179	10	2	A	M	270	3.4	47.1	28	33.1	30.55	143	0	0	0	0	0
179	10	2	A	M	278	4.8	34.2	31	36.3	33.65	143	0	0	0	0	0
179	10	2	A	F	274	4.4	47.6	28.9	27.1	28	145	0	0	0	0	0
179	10	1	A	M	266	5.2	43.4	23.8	29.6	26.7	143	0	0	0	0	0
179	10	2	A	F	255	4.1	41.4	32.6	31	31.8	143	0	0	0	0	0
179	10	2	A	M	267	4.1	41.4	23.4	18.2	20.8	143	0	0	0	0	0
179	10	2	S	U	229	4.3	35.6	19.9	15.8	17.85	138	0	0	0	0	0
179	10	3	A	M	264	2.4	40.7	23.1	24.6	23.85	142	0	0	0	0	0
179	10	2	A	F	268	4.7	28.7	17.1	13.8	15.45	141	0	0	0	0	0
179	10	2	S	U	251	4.5	25	14.9	16.7	15.8	143	0	0	0	0	0
183	10	2	A	M	308	4.5	40.5	25.5	39.5	32.5	146	2	0	0	0	0

Day	Yr	Snt	Age	Sex	Mass	Rictal	Crest	Auricular plume length Left	Right	Mean	Wing	Web	Tick	Lice-Q	Lice-S	Lice-A
183	10	1	A	F	248	4.1	39.7	24.6	25.4	25	141	0	0	0	0	0
183	10	3	A	F	261	4.1	43.3	10	15.6	12.8	143	2	0	0	0	0
183	10	2	A	F	287	5.3	34.9	28.1	27.1	27.6	148	0	0	0	0	0
183	10	2	A	F	255	4.4	41.3	31	33.6	32.3	143	0	0	0	0	0
183	10	3	A	M	247	3.1	38.9	22.2	24.6	23.4	138	0	0	0	0	0
183	10	2	A	F	232	3.7	38.9	21.4	21.7	21.55	141	0	0	0	0	0
183	10	3	A	M	253	3.4	33.3	29.7	29.6	29.65	138	0	0	0	0	0
183	10	1	A	M	259	6.3	44.6	26.8	26.8	26.8	146	0	0	0	0	0
183	10	1	A	F	246	3.2	20.1	21.6	21.9	21.75	140	0	0	0	0	0
183	10	2	A	F	242	3.6	31.4	24.2	27.1	25.65	140	0	0	0	0	0
186	10	1	A	F	251	3.2	43.2	27.3	23.4	25.35	145	0	0	0	0	0
186	10	3	A	F	243	4.5	38.6	27.8	24	25.9	141	2	0	0	0	0
186	10	0	A	M	264	4.9	41.8	28.5	23.1	25.8	144	1	0	0	0	0
186	10	3	A	M	240	2.5	43.1	27	26.2	26.6	143	1	0	0	0	0
186	10	2	A	M	255	.	39.1	16.9	19.1	18	145	0	0	0	0	0
186	10	1	A	M	289	4.4	35.5	26.2	27	26.6	146	0	0	0	0	0
186	10	1	S	U	242	3.6	30.1	18	20.7	19.35	151	0	0	0	0	0
186	10	2	A	M	244	4.8	41.32	30.5	35	32.75	140	0	0	0	0	0
186	10	1	A	M	273	6.3	41.6	35	36.8	35.9	148	0	0	0	0	0
186	10	2	S	U	244	4.3	13.6	18.9	19.9	19.4	143	0	0	0	0	0
186	10	1	S	U	224	3.1	19.8	27.3	23.5	25.4	136	0	0	0	0	0
186	10	0	A	M	261	2.3	43.2	29.8	25.1	27.45	138	1	0	0	0	0
186	10	1	A	F	263	2	47	22.8	28.6	25.7	145	0	0	0	0	0

								Auricular plume length								
Day	Yr	Snt	Age	Sex	Mass	Rictal	Crest	Left	Right	Mean	Wing	Web	Tick	Lice-Q	Lice-S	Lice-A
188	10	1	A	F	274	3	42.3	26	27.3	26.65	145	0	0	0	0	0
188	10	2	A	M	255	3.5	39.4	24.4	24.5	24.45	146	0	0	0	0	0
188	10	2	A	M	253	5.4	39.1	21.9	22.7	22.3	145	0	0	0	0	0
188	10	3	A	F	273	2.6	42.8	25.9	24.1	25	141	0	0	0	0	0
188	10	2	A	F	243	3.5	37.4	18.1	22.3	20.2	142	0	0	0	0	0
188	10	3	A	M	268	4.2	47.9	26	32.2	29.1	143	0	0	0	0	0
188	10	3	A	M	248	4.9	42.5	28.7	29.2	28.95	144	0	0	0	0	0
188	10	2	A	F	256	3.1	43.4	22.5	29.1	25.8	143	0	0	0	0	0
188	10	2	A	M	247	3.4	36.2	22.5	27.8	25.15	142	2	0	0	0	0
188	10	1	A	F	264	2.9	43.1	22.9	24.4	23.65	143	2	0	0	0	0
188	10	2	A	F	256	4.9	35.3	29.6	30	29.8	138	0	0	0	0	0
188	10	2	A	F	268	4.8	44.5	24	29.1	26.55	143	0	0	0	0	0
188	10	3	A	M	254	3.7	40.3	24.8	26.8	25.8	143	0	0	0	0	0
188	10	3	A	F	238	3.5	42.2	24.7	24	24.35	138	0	0	0	0	0
188	10	3	A	M	278	4.3	46	27.5	26.3	26.9	151	0	0	0	0	0
188	10	2	S	U	225	5.1	22.1	23.3	19.6	21.45	138	0	0	0	0	0
188	10	2	A	M	272	4.2	49.3	26.4	27.5	26.95	145	0	0	0	0	0
191	10	0	A	F	252	2.6	50.4	33	29.3	31.15	143	0	0	0	0	0
191	10	1	A	F	246	3.6	38.6	28.7	29.1	28.9	138	0	0	0	0	0
191	10	2	A	F	260	3.7	31.1	22.9	21.8	22.35	141	1	0	0	0	0
191	10	3	A	M	282	2.6	43.5	25.1	24.9	25	144	2	0	0	0	0
191	10	2	A	M	294	3.7	48.3	29.4	29.6	29.5	150	1	0	0	0	0
191	10	2	A	F	237	5.2	37.4	23.9	22.3	23.1	140	0	0	0	0	0

Day	Yr	Snt	Age	Sex	Mass	Rictal	Crest	Auricular plume length Left	Right	Mean	Wing	Web	Tick	Lice-Q	Lice-S	Lice-A
191	10	3	A	F	235	3.9	41.2	18.1	18.2	18.15	146	0	0	0	0	0
191	10	3	A	M	267	4.9	29.2	26.2	27.1	26.65	147	0	0	0	0	0
191	10	2	A	F	254	0	42.4	17.4	14.4	15.9	143	0	0	0	0	0
191	10	2	A	M	273	2.9	43.5	27.6	29.9	28.75	143	0	0	0	0	0
191	10	2	S	U	219	2.4	29.5	26.4	25.8	26.1	141	0	0	0	0	0
193	10	0	A	F	255	0	45.3	23.8	25.2	24.5	142	1	0	0	0	0
193	10	1	A	M	249	2.9	34.8	28.9	23.1	26	144	0	0	0	0	0
193	10	2	A	M	287	0	39.8	28.9	27	27.95	149	0	0	0	0	0
193	10	0	A	M	253	4.6	38.9	21.3	27.9	24.6	149	0	0	0	0	0
193	10	3	A	F	255	0	25.3	25.5	24.1	24.8	141	0	0	0	0	0
193	10	2	A	F	248	0	36	23.7	20.6	22.15	139	0	0	0	0	0
193	10	1	A	F	250	0	38.3	23	30.1	26.55	142	0	0	0	0	0
193	10	1	A	M	269	0	39	23.9	24.6	24.25	138	0	0	0	0	0
193	10	3	A	M	267	0	47	26.3	30.1	28.2	145	0	0	0	0	0
193	10	0	A	F	252	3.9	43.8	28.4	32.3	30.35	138	0	0	0	0	0
193	10	2	A	M	271	4.6	46.3	22.4	23.1	22.75	146	0	0	0	0	0
193	10	2	A	M	255	5	41.6	28.4	23.4	25.9	148	0	0	0	0	0
193	10	2	A	M	255	6.7	43.1	34.2	30.1	32.15	146	0	0	0	0	0
195	10	2	A	F	234	0	44.4	29.2	29.3	29.25	140	1	0	0	0	0
195	10	1	A	F	226	0	40.7	25	25.6	25.3	144	0	0	0	0	0
195	10	2	A	M	268	3.9	45.6	19.8	23.8	21.8	143	0	0	0	0	0
195	10	0	A	F	256	0	38.9	24.9	29.5	27.2	145	0	0	0	0	0
195	10	3	A	F	242	0	44.6	25.3	27.3	26.3	138	1	0	0	0	0

								Auricular plume length								
Day	Yr	Snt	Age	Sex	Mass	Rictal	Crest	Left	Right	Mean	Wing	Web	Tick	Lice-Q	Lice-S	Lice-A
195	10	1	A	M	274	0	44.7	27	23.9	25.45	147	0	0	0	0	0
195	10	3	A	M	260	5.2	36.8	18.1	25.8	21.95	143	0	0	0	0	0
195	10	3	A	F	234	0	42.2	29.9	19.1	24.5	138	0	0	0	0	0
195	10	2	A	M	265	0	43.9	31	30	30.5	145	0	0	0	0	0
195	10	1	A	F	273	0	38.1	26.3	27	26.65	142	0	0	0	0	0
195	10	0	A	M	265	0	42.8	17.8	21.6	19.7	144	0	0	0	0	0
195	10	0	A	U	249	0	0	28	24.6	26.3	141	1	0	0	0	0
195	10	0	A	M	270	2.3	39	22.1	16.1	19.1	141	0	0	0	0	0
199	10	3	A	M	281	3.9	40.3	27.6	20.8	24.2	146	0	0	0	0	0
199	10	0	A	M	249	0	43.7	19.9	21.9	20.9	143	2	0	0	0	0
199	10	2	A	M	292	0	34.9	16.8	21.3	19.05	146	0	0	0	0	0
199	10	0	A	F	241	0	38.9	23	21.3	22.15	147	0	0	0	0	0
199	10	1	A	F	241	0	40.4	28	25	26.5	141	1	0	0	0	0

Appendix V

Raw data of all Least Auklets (*Aethia pusilla*) caught during the breeding season in 2009 and 2010. All louse specimens are mounted and ID by Ricardo Palma of Museum of New Zealand Te Papa Tongarewa. Day= numeric date from 1 January of the respective year; Yr= year; A= adult; S= sub-adult; Knob= height of bill knob; Plumage= plumage colouration (the degree of blackness in the breast plumage on a scale of 0 – 4;Jones 1990); Web= score of 0-2(0-no holes in either foot web;1- individuals had a single circular hole in either foot web; and 2- had greater than one hole); Tick= number of *Ixodes uriea*; Lice= number of *Quadraceps aethereus*.

						Auricular plume length						
Day	Yr	Age	Mass	Knob	Plumage	Left	Right	Mean	Wing	Web	Tick	Lice
160	10	A	81	1	2	14.1	12	13.05	91	0	12	0
178	09	A	81	.	.	.	.	.	.	.	6	0
153	09	A	82	1	2	12.2	14	13.1	99	1	3	0
167	09	A	83	1.3	2	12.4	11.6	12	97	0	1	2
161	09	S	78	1.6	2	11	10	10.5	96	0	1	1
167	09	A	82	0.9	3	11.6	8.8	10.2	95	1	1	1
182	09	S	79	0.8	2	10.3	8.7	9.5	96	0	1	1
152	10	A	79	1	2	11.9	13.4	12.65	98	0	1	1
152	10	S	81	1.4	3	14.1	15.2	14.65	96	0	1	1
153	09	A	82	1	3	13.1	12.3	12.7	95	1	1	0
156	09	A	85	1.4	2	11.8	12	11.9	98	0	1	0
161	09	A	80	1.5	3	8.5	8.9	8.7	98	0	1	0
161	09	A	80	1.4	2	12.6	12.1	12.35	98	0	1	0
170	09	A	89	0.8	2	16	19.3	17.65	95	1	1	0

Day	Yr	Age	Mass	Knob	Plumage	Auricular plume length Left	Right	Mean	Wing	Web	Tick	Lice
178	09	A	81	.	.	.	.	.	.	.	1	0
182	09	A	75	0.8	2	11	11	11	96	0	1	0
185	09	S	79	0.8	3	11.3	10.9	11.1	97	0	1	0
192	09	A	84	1	2	18.9	16.5	17.7	97	0	1	0
192	09	A	81	0.4	2	19.2	16.4	17.8	101	2	1	0
192	09	A	84	0.4	2	9.7	10.3	10	97	2	1	0
197	09	A	75	0.2	2	15.8	16.7	16.25	104	0	1	0
152	10	A	85	2.8	3	17.4	13.2	15.3	95	0	1	0
164	10	A	95	0.9	2	16.6	12.9	14.75	95	0	1	0
191	10	A	97	0.8	2	11.8	11.5	11.65	97	0	1	0
167	09	A	75	0.9	2	8.2	5.7	6.95	94	0	0	3
154	10	S	93	1	2	16.9	15	15.95	96	0	0	3
180	10	A	84	1.5	2	12.4	11.3	11.85	91	0	0	3
161	09	A	89	2.2	2	15.2	13.1	14.15	95	1	0	2
153	09	S	76	1	3	16.9	15	15.95	92	1	0	1
159	09	A	85	2.6	3	12	13	12.5	96	0	0	1
167	09	A	88	1.6	3	14.1	15.5	14.8	94	2	0	1
167	09	A	84	.	.	.	.	.	.	.	0	1
167	09	A	79	1.7	2	9.1	8.5	8.8	96	0	0	1
167	09	S	79	1	3	12.4	11.2	11.8	97	1	0	1
167	09	A	85	0.7	2	14.1	14.6	14.35	96	0	0	1
182	09	A	75	1.1	2	13.6	16.9	15.25	97	1	0	1
185	09	A	81	0.5	1	16.7	15.7	16.2	95	0	0	1

						Auricular plume length						
Day	Yr	Age	Mass	Knob	Plumage	Left	Right	Mean	Wing	Web	Tick	Lice
197	09	A	76	1.8	2	12.9	9.2	11.05	97	1	0	1
157	10	A	72	1.2	3	13.1	13.3	13.2	96	0	0	1
173	10	S	79	1.1	3	10.2	8.7	9.45	96	0	0	1
177	10	S	76	0.7	3	14.4	13.4	13.9	96	0	0	1
191	10	A	83	0.6	1	11.1	11.8	11.45	97	2	0	1
153	09	A	90	0.9	2	18.4	16.2	17.3	98	0	0	0
153	09	A	90	1.7	3	14.1	12.5	13.3	99	0	0	0
153	09	A	83	1.5	2	15.4	15.1	15.25	112	0	0	0
153	09	A	82	1.8	3	12.6	13.4	13	96	1	0	0
153	09	A	78	1.4	2	10.4	10.2	10.3	98	0	0	0
153	09	S	76	0.3	2	11.6	11.8	11.7	97	0	0	0
153	09	A	81	1.5	2	5.4	4.9	5.15	95	1	0	0
153	09	A	79	2.1	2	17.9	17	17.45	98	0	0	0
153	09	A	76	1.1	3	12.3	13.6	12.95	91	0	0	0
153	09	A	82	1.4	2	12.8	11.8	12.3	95	1	0	0
153	09	A	73	0.9	2	13	12.7	12.85	96	0	0	0
153	09	A	76	0.7	2	10.8	10.7	10.75	97	1	0	0
153	09	A	86	2.2	2	10.1	11.8	10.95	98	0	0	0
153	09	A	81	1.8	2	10.9	11.3	11.1	99	1	0	0
153	09	A	78	0.5	3	15.5	13	14.25	90	2	0	0
153	09	A	81	1.7	3	17.9	12	14.95	94	0	0	0
153	09	S	76	0.8	3	8.8	9.3	9.05	96	1	0	0
156	09	S	75	1.4	2	10.9	8.5	9.7	93	1	0	0

Day	Yr	Age	Mass	Knob	Plumage	Auricular plume length Left	Right	Mean	Wing	Web	Tick	Lice
156	09	S	74	1.8	2	11.6	11.8	11.7	96	0	0	0
156	09	A	.	0.6	2	17.7	13.5	15.6	90	1	0	0
156	09	A	86	1.2	2	15.1	12.6	13.85	97	0	0	0
156	09	A	90	1.3	2	12.7	13.1	12.9	98	0	0	0
156	09	S	76	1.2	3	13.4	16	14.7	96	0	0	0
156	09	A	74	1.9	2	13.1	13.4	13.25	95	1	0	0
156	09	A	74	1.7	2	12.4	13.9	13.15	94	0	0	0
156	09	A	86	1.2	3	15.5	16.2	15.85	96	1	0	0
156	09	S	74	0.6	3	9.6	11.9	10.75	93	2	0	0
159	09	A	77	1.1	2	12.1	11.1	11.6	94	1	0	0
159	09	S	77	0.6	2	11.8	10.5	11.15	95	0	0	0
159	09	A	78	0.7	2	17.8	17.1	17.45	93	0	0	0
159	09	A	81	0.9	2	10	10.2	10.1	99	1	0	0
159	09	S	78	0.9	3	14.7	16	15.35	100	0	0	0
161	09	A	79	1.6	3	11.6	8.2	9.9	95	0	0	0
161	09	A	91	1.3	2	14.7	8.5	11.6	94	0	0	0
161	09	A	86	.	.	.	.	.	.	.	0	0
161	09	A	94	1.8	2	12.8	13	12.9	100	1	0	0
161	09	A	87	.	.	.	.	.	.	.	0	0
161	09	A	85	1	2	11.5	11.6	11.55	97	0	0	0
161	09	S	72	1.6	3	10.1	12.2	11.15	97	0	0	0
161	09	A	94	.	.	.	.	.	.	.	0	0
161	09	A	88	.	.	.	.	.	.	.	0	0

						Auricular plume length						
Day	Yr	Age	Mass	Knob	Plumage	Left	Right	Mean	Wing	Web	Tick	Lice
161	09	A	83	1.6	2	11	12.6	11.8	98	1	0	0
161	09	A	90	1.2	2	13.8	15	14.4	97	0	0	0
161	09	A	79	1.8	2	15.2	13	14.1	97	1	0	0
164	09	A	79	.	.	.	.	.	.	.	0	0
164	09	S	83	0.2	3	15	13.1	14.05	101	0	0	0
164	09	A	78	.	.	.	.	.	.	.	0	0
167	09	A	.	.	.	.	.	.	.	.	0	0
167	09	S	81	0.3	3	5	6.9	5.95	95	1	0	0
167	09	S	80	0.9	2	11.8	10.1	10.95	97	0	0	0
167	09	A	94	.	.	.	.	.	.	.	0	0
167	09	S	77	1.3	1	10.6	10.3	10.45	98	0	0	0
167	09	A	76	1.5	3	16.8	16.4	16.6	96	0	0	0
167	09	A	85	.	.	.	.	.	.	.	0	0
167	09	A	77	1.4	2	10.6	11.2	10.9	92	0	0	0
167	09	A	79	1.3	3	13.4	10.1	11.75	92	0	0	0
167	09	S	75	1.9	2	15.2	13.5	14.35	96	1	0	0
167	09	S	.	1.4	2	17.2	15.1	16.15	97	0	0	0
170	09	A	81	3.3	2	13	12.6	12.8	98	0	0	0
170	09	A	82	0.5	2	15.9	13.1	14.5	94	0	0	0
170	09	A	79	2.1	2	8.9	7.1	8	93	0	0	0
170	09	S	91	1.9	2	11.1	14	12.55	99	0	0	0
170	09	A	79	2.3	2	15.8	12.1	13.95	101	0	0	0
170	09	A	81	0.4	2	16.5	12.4	14.45	97	0	0	0

						Auricular plume length						
Day	Yr	Age	Mass	Knob	Plumage	Left	Right	Mean	Wing	Web	Tick	Lice
170	09	S	78	0.8	2	17.5	16.6	17.05	101	1	0	0
170	09	A	84	2.6	1	12.5	11.1	11.8	97	0	0	0
170	09	S	83	0.9	3	10	6.4	8.2	94	0	0	0
170	09	A	76	1	2	8.2	8.7	8.45	91	0	0	0
170	09	A	79	1	2	15	14.3	14.65	95	0	0	0
170	09	S	75	0.4	2	13.7	15.4	14.55	94	0	0	0
170	09	S	79	1.1	2	9.4	11.8	10.6	95	0	0	0
170	09	A	88	1.3	2	16.7	17.5	17.1	97	0	0	0
174	09	S	74	0.7	2	18.2	11	14.6	96	0	0	0
174	09	A	82	.	.	.	.	.	.	.	0	0
174	09	A	83	0.9	2	16.7	15.7	16.2	97	0	0	0
174	09	A	80	1.4	3	7.5	6.4	6.95	97	0	0	0
174	09	A	83	1.1	2	14.6	14.1	14.35	94	0	0	0
174	09	S	84	1.1	3	8	7.1	7.55	96	1	0	0
178	09	S	79	1.8	3	8	9.9	8.95	95	0	0	0
178	09	A	85	1.5	3	15.7	14.6	15.15	98	1	0	0
178	09	A	97	.	0	.	.	.	.	.	0	0
178	09	A	86	.	.	.	.	.	.	.	0	0
178	09	A	82	1.2	2	8.1	9.2	8.65	94	0	0	0
178	09	A	75	0.8	2	10.3	13.6	11.95	96	0	0	0
178	09	A	.	.	.	.	.	.	.	.	0	0
182	09	A	79	.	.	.	.	.	.	.	0	0
182	09	A	83	.	.	.	.	.	.	.	0	0

						Auricular plume length						
Day	Yr	Age	Mass	Knob	Plumage	Left	Right	Mean	Wing	Web	Tick	Lice
182	09	A	78	0.5	2	11.4	12	11.7	99	0	0	0
182	09	S	80	0.9	3	15	17.4	16.2	93	0	0	0
182	09	A	82	1.5	2	12.1	9.2	10.65	99	1	0	0
182	09	A	82	0.1	2	14.4	15	14.7	95	1	0	0
182	09	A	82	1.8	3	14.7	13.1	13.9	97	1	0	0
182	09	A	75	0.1	1	14.9	15.2	15.05	97	0	0	0
185	09	A	77	1.3	2	13.5	15.1	14.3	97	0	0	0
185	09	A	82	.	.	.	.	.	.	.	0	0
185	09	A	81	0.3	2	11.3	8.8	10.05	94	0	0	0
185	09	A	80	0.5	2	10.1	10.5	10.3	97	2	0	0
185	09	A	82	0.6	2	14.8	11.7	13.25	100	0	0	0
185	09	A	85	0.6	2	10.4	8	9.2	102	0	0	0
185	09	A	76	.	.	.	.	.	.	.	0	0
185	09	S	77	1	2	8.4	7.8	8.1	97	0	0	0
185	09	A	79	0.5	1	9	10.2	9.6	94	0	0	0
185	09	A	78	1.6	2	17.4	19.9	18.65	94	1	0	0
185	09	A	73	1.3	2	14.5	13.1	13.8	97	0	0	0
185	09	A	75	1	3	12.3	13	12.65	96	0	0	0
185	09	A	83	1.6	2	13.5	17	15.25	96	0	0	0
185	09	A	77	0.5	2	16	13.2	14.6	97	0	0	0
192	09	A	83	0.5	2	11.8	14.1	12.95	101	0	0	0
192	09	A	75	1.4	2	8.9	10	9.45	95	0	0	0
192	09	A	86	0.4	2	18.1	16.8	17.45	99	0	0	0

Day	Yr	Age	Mass	Knob	Plumage	Auricular plume length			Wing	Web	Tick	Lice
						Left	Right	Mean				
192	09	A	89	0.8	2	18.4	20.2	19.3	.	0	0	0
192	09	A	77	0.1	2	11.4	9.6	10.5	98	1	0	0
192	09	A	86	0.4	2	17.5	20.7	19.1	102	1	0	0
197	09	A	88	0.2	2	11.2	15.1	13.15	96	0	0	0
197	09	A	79	0.8	2	10.7	9.2	9.95	100	2	0	0
197	09	A	82	0.4	2	13.9	10	11.95	94	0	0	0
197	09	A	74	1.2	2	11.6	8.7	10.15	97	0	0	0
197	09	A	78	0.3	2	12.7	13.5	13.1	92	1	0	0
198	09	A	85	0.5	2	17.3	13.1	15.2	92	0	0	0
198	09	A	95	1.2	2	18.7	18.9	18.8	103	0	0	0
201	09	A	77	0.8	2	12.3	14.1	13.2	96	0	0	0
201	09	A	84	0.1	2	10.9	13.9	12.4	102	1	0	0
201	09	A	85	0.4	2	10.1	12.2	11.15	96	0	0	0
201	09	A	80	1.2	2	13.5	13.8	13.65	94	0	0	0
152	10	A	78	0.2	2	15.3	18.6	16.95	92	0	0	0
152	10	A	78	1.9	2	11.5	11.4	11.45	97	0	0	0
152	10	A	82	1.2	2	12.1	11.3	11.7	96	1	0	0
152	10	A	84	1.5	3	15.8	15.4	15.6	96	0	0	0
152	10	A	86	2.2	2	11.5	14.6	13.05	98	0	0	0
152	10	A	73	1.8	2	13.7	13.8	13.75	95	0	0	0
152	10	A	80	1.8	3	14	13.2	13.6	95	1	0	0
152	10	A	80	1.1	2	13.3	13.3	13.3	95	0	0	0
152	10	A	93	1.1	3	11.6	14.1	12.85	104	0	0	0

						Auricular plume length						
Day	Yr	Age	Mass	Knob	Plumage	Left	Right	Mean	Wing	Web	Tick	Lice
152	10	A	81	1	2	16	16.9	16.45	97	0	0	0
152	10	A	75	1.3	3	14.5	10.6	12.55	98	0	0	0
152	10	S	83	1.2	.	10.3	11.3	10.8	99	0	0	0
152	10	A	78	1.4	3	9.9	12	10.95	96	0	0	0
152	10	A	81	1.7	3	9.6	13.1	11.35	102	0	0	0
154	10	A	82	1.6	3	13.8	11.5	12.65	97	2	0	0
154	10	S	75	2	2	11.1	10.5	10.8	94	0	0	0
154	10	S	73	1.6	2	14.7	14.5	14.6	97	0	0	0
154	10	S	80	1.5	2	8.4	9.1	8.75	91	0	0	0
154	10	S	83	1.9	4	10.1	12.9	11.5	96	0	0	0
154	10	A	79	0.9	2	16.8	5.7	11.25	97	0	0	0
154	10	A	79	1.5	3	9	8.6	8.8	97	0	0	0
154	10	A	80	0.9	2	7.2	7.4	7.3	96	0	0	0
154	10	S	70	1.3	2	12.8	12.4	12.6	93	1	0	0
154	10	S	84	1.6	2	11.7	13.5	12.6	104	0	0	0
154	10	A	81	2.2	3	12.3	15.1	13.7	96	0	0	0
154	10	A	87	2.1	3	15.5	13.8	14.65	97	1	0	0
154	10	S	86	1.5	3	11.1	14.1	12.6	99	0	0	0
154	10	A	80	1.6	3	8.6	7	7.8	98	2	0	0
154	10	S	75	1	3	9.3	10.4	9.85	98	0	0	0
154	10	A	84	1.9	2	18.5	19	18.75	96	0	0	0
157	10	A	84	1.4	3	14.3	15.8	15.05	94	0	0	0
157	10	S	80	1.1	3	13.7	12.4	13.05	96	1	0	0

Day	Yr	Age	Mass	Knob	Plumage	Auricular plume length			Wing	Web	Tick	Lice
						Left	Right	Mean				
157	10	A	90	1.4	3	18.1	18.6	18.35	99	0	0	0
157	10	A	83	2.8	2	14.7	12.4	13.55	96	0	0	0
157	10	A	82	1.1	3	11.3	11.9	11.6	94	0	0	0
157	10	A	78	1.4	2	9.4	11.6	10.5	99	0	0	0
157	10	A	79	1.1	2	8.7	8.3	8.5	96	0	0	0
157	10	A	77	0.8	2	8.7	10.1	9.4	97	0	0	0
157	10	A	79	1.2	2	15.2	13	14.1	96	1	0	0
157	10	A	78	2.1	3	13.9	13.1	13.5	97	0	0	0
157	10	A	75	1.9	3	18.2	19.2	18.7	98	0	0	0
157	10	A	84	1.2	1	12.1	13.5	12.8	93	0	0	0
157	10	A	78	1.3	3	15	12.4	13.7	98	0	0	0
160	10	A	88	1.2	3	16.1	16.6	16.35	96	0	0	0
160	10	S	81	1.2	3	9.4	10.6	10	97	0	0	0
160	10	A	85	1.6	2	8.7	9.4	9.05	105	0	0	0
160	10	A	81	1.1	3	14.1	16.5	15.3	98	0	0	0
160	10	S	86	0.5	3	14.6	14.4	14.5	95	0	0	0
160	10	A	77	0.8	3	13.3	10.2	11.75	91	0	0	0
160	10	S	79	1	2	9	9.2	9.1	91	0	0	0
164	10	A	82	2.4	2	11.3	7.5	9.4	95	1	0	0
164	10	A	97	0.4	2	17.5	15.1	16.3	96	0	0	0
164	10	S	77	0.9	3	13.4	13.9	13.65	95	0	0	0
164	10	A	87	1.5	2	14.1	13.4	13.75	98	0	0	0
164	10	A	87	1.6	2	10.4	9.5	9.95	99	1	0	0

						Auricular plume length						
Day	Yr	Age	Mass	Knob	Plumage	Left	Right	Mean	Wing	Web	Tick	Lice
164	10	A	83	1.1	3	11	11.3	11.15	96	0	0	0
164	10	S	77	0.8	2	13.6	12.2	12.9	94	0	0	0
164	10	S	82	0.5	3	11.5	11.9	11.7	96	0	0	0
164	10	S	82	1	2	12	13.5	12.75	98	0	0	0
164	10	S	80	1.1	3	8.4	7.3	7.85	93	1	0	0
167	10	A	78	1.9	2	13.1	12.8	12.95	90	0	0	0
167	10	A	78	1	2	12.6	12.5	12.55	94	0	0	0
167	10	A	115	1.1	2	11.7	11	11.35	98	3	0	0
167	10	A	93	1.1	2	11	12	11.5	93	1	0	0
167	10	S	85	0.7	3	12.6	13.2	12.9	100	0	0	0
167	10	S	71	0.5	3	11	8.7	9.85	94	0	0	0
167	10	A	84	1.7	3	16.6	12.9	14.75	94	0	0	0
173	10	A	81	0.8	2	14.8	11.5	13.15	95	0	0	0
173	10	A	87	1.7	2	10.4	12.6	11.5	98	0	0	0
173	10	S	70	0.9	3	13.2	12.3	12.75	97	1	0	0
173	10	A	81	0.6	2	12	12.9	12.45	96	0	0	0
173	10	A	75	1.6	2	9.8	8.8	9.3	96	0	0	0
175	10	A	77	0.8	1	14.9	14	14.45	96	0	0	0
175	10	A	82	1.5	2	10.4	12.1	11.25	94	0	0	0
175	10	S	74	1	3	12.9	11.5	12.2	97	0	0	0
175	10	A	86	0.9	2	14.1	13.2	13.65	96	0	0	0
175	10	A	76	0.5	1	13.4	14.8	14.1	96	0	0	0
175	10	A	84	1.7	3	14.8	14.5	14.65	101	0	0	0

Day	Yr	Age	Mass	Knob	Plumage	Auricular plume length			Wing	Web	Tick	Lice
						Left	Right	Mean				
177	10	A	92	1.5	2	9	10.9	9.95	98	0	0	0
179	10	A	85	0.5	2	14.3	13.5	13.9	99	0	0	0
179	10	A	85	0.4	2	12.8	12	12.4	98	0	0	0
179	10	A	86	1.3	2	12.3	7.4	9.85	95	0	0	0
179	10	S	87	1.1	2	13.3	16.4	14.85	101	0	0	0
179	10	A	87	0.2	3	17	17.1	17.05	102	0	0	0
179	10	A	85	0.9	3	17.6	14.7	16.15	95	0	0	0
179	10	S	83	1.1	3	12.9	10.8	11.85	99	2	0	0
179	10	A	86	1.4	2	11.6	10.2	10.9	98	0	0	0
179	10	A	84	1.7	3	13.8	13	13.4	95	1	0	0
180	10	A	94	1.2	2	9.5	9.5	9.5	98	0	0	0
180	10	A	85	1.1	2	15.4	15.4	15.4	97	0	0	0
183	10	A	86	1	1	14.6	14.7	14.65	99	0	0	0
183	10	S	79	0.9	3	11.6	10.9	11.25	97	0	0	0
183	10	S	74	1.6	2	13.3	13.6	13.45	97	0	0	0
183	10	A	83	0.4	2	16	15	15.5	98	0	0	0
183	10	A	83	1.6	2	12.6	11	11.8	98	0	0	0
186	10	A	86	1.3	2	14.4	13.1	13.75	97	0	0	0
186	10	A	80	0.4	2	12.1	10.3	11.2	100	0	0	0
186	10	S	81	0.8	3	8.6	8.7	8.65	96	1	0	0
186	10	A	93	1.3	2	8.6	10.1	9.35	100	0	0	0
186	10	S	71	1.3	1	11.7	11.3	11.5	93	0	0	0
188	10	A	84	1.2	3	12.3	11	11.65	98	0	0	0

						Auricular plume length						
Day	Yr	Age	Mass	Knob	Plumage	Left	Right	Mean	Wing	Web	Tick	Lice
191	10	A	84	0.5	2	12.1	9.3	10.7	100	0	0	0
195	10	A	100	1.1	1	13.1	10.6	11.85	96	0	0	0
199	10	A	79	0.8	1	15	25.9	20.45	99	0	0	0

THE ROLE OF SCENT AND ECTOPARASITES IN THE ECOLOGY OF THE CRESTED AUKLET (AETHIA CRISTATELLA)

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THE ROLE OF SCENT AND ECTOPARASITES IN THE ECOLOGY OF THE CRESTED AUKLET (*AETHIA CRISTATELLA*)

by

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Abstract

Ectoparasites are ubiquitous, and can have negative effects on their hosts. The prevalence and intensity of ectoparasites are important in determining their effects. Prevalence can vary greatly, from near absence to all host individuals in a population being parasitized. Intensity can also vary greatly. Negative impacts of parasitizes can create the pressure required for a natural defence mechanism to evolve in hosts. Crested Auklets (*Aethia cristella*, Alcidae; Aethiini) are colonial seabirds that produce a unique tangerine-like scent. There are two hypotheses proposed for this scent's function: 1) as a pheromone; and 2) to reduce ectoparasite levels by repelling ticks and lice. My study is broken into three sections: 1) measuring the prevalence and intensity of ticks on *Aethia* auklets and determining the relationship of body condition and ornamentation to tick parasitism; 2) measuring the prevalence and intensity of lice on Least (*Aethia pusilla*) and Crested Auklets and the determining relationship of body condition and ornament expression to lice parasitism; and 3) the relationship of Crested Auklet scent to ectoparasite intensity and tick deterrence. I determined that prevalence and intensity of ticks and lice had no relationship with body condition or ornament expression on any hosts species. Lice or tick intensity were not related to naturally occurring scent levels but ticks were less likely to attach to scented objects. My study suggests that when parasitism is low in Crested and Least Auklets the need for a parasite defence is reduced and will obsure any relationship among quality and parasite load.

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Chapter 1

Introduction to Crested Auklets, their scent, and their ectoparasites

Until recently it was thought that olfaction is not a very important sense in birds. With the realization of its importance there has been growing interest in documenting avian odours and investigating their functions (Hagelin & Jones 2007). Crested Auklets (*Aethia cristatella*) produce a strong citrus-like odour with an unknown function. A number of adaptive functions have been proposed but the two that have received the most attention are intraspecific communication and chemical defence (Clayton et al. 2010; Hagelin & Jones 2007). Experimental studies (Jones et al. 2004) provided evidence that this scent plays a social role, whereas Douglas et al. (2004) suggested it could also act to repel ectoparasites. These two hypotheses are not necessarily mutually exclusive. The scent could be acting to deter ectoparasites and therefore be an honest indicator of quality that is used in mate choice. A solid description of the diversity, prevalence, intensity and ecology of ectoparasites (both for Crested Auklet and related species) is a prerequisite to understanding the function of Crested Auklet odour – this is the knowledge gap I aimed to address with my thesis.

1.1 Crested Auklets and their close relatives

Crested Auklets (Alcidae) are small, locally abundant, colonial, planktivorous seabirds occurring only in the Bering and Okhotsk Seas and adjacent parts of the North Pacific (Gaston & Jones 1998). Least Auklets (*A. pusilla*) are the smallest and most abundant of auklets that are closely related to Crested Auklets. Least Auklets forage close to their breeding colonies during summer and disperses widely at sea in winter (Jones 1993b). Crested Auklets coexist with Least Auklets at nine Alaskan breeding colonies as well as at sea during the summer and throughout the winter (Jones 1993a). Compared with other auklets, Whiskered Auklets (*A. pygmaea*, mean mass 118 g) occupy a slightly different ecological niche. They forage close to land in active tide rips, are known to roost on land during the non-breeding season, and likely remain near their breeding colonies in the Bering Sea year round (Byrd & Williams 1993; Hunter et al. 2002; Williams, Byrd, & Konyukhov 2003; Zubakin & Konyukhov 1999). In Alaska, Whiskered Auklets are rarely observed on the surface of colonies with the exception of Buldir Island where they can join aggregations of Least and Crested Auklets by day (Hunter et al. 2002). At breeding colonies (May-July) auklets congregate densely with birds in direct contact with one another on the surface and underground in their nest burrows on rocky talus slopes and lava flows. These high densities provide an ideal environment for ticks to breed and find hosts.

1.2 Crested Auklets and their scent

Crested Auklets have large crests on their forehead that are favoured by both males and females in mating selection (Jones & Hunter 1993, 1999). Both sexes also have white auricular plumes and an orange bill with accessory plates that are present during breeding but become greatly reduced after breeding (Jones 1993c).

Crested Auklets produce a citrus-like scent during the breeding season that is strongest around the bill, nape, and neck (Humphrey 1958; Jones & Hunter 1999). This strong scent is especially noticeable at nesting colonies (Kenyon & Brooks 1960). The scent was strong enough that out on the water downwind of c.10000 auklets the odour was clearly noticeable to Kenyon & Brooks (1960). Sealy (2006) reported that this scent is not present in the week before the breeding season when birds are at sea.

Using solvent extraction from three specimens the scent was found to be composed of N-hexanal, N-octanal, N-decanal, Z-4-decenal, hexanoic acid, octanoic acid, N-octanal, hexanal and a 12-carbon unsaturated aldehyde, later characterized as Z-4-dodecenal and Z-6-dodecenal (Douglas et al. 2001a; Douglas et al. 2004). In a separate study using a different scent collection method based on quantification of volatile chemicals the scent was composed of Z-4-decenal, hexanoic acid, N-octanal, octanoic acid, and decanal, as well as octanal, undecanal, tridecanal, and heptanal (Hagelin et al. 2003). Based on scent collection focusing on volatile chemical being released over a set period of time the average chemical emission for Crested Auklets was 5.7 μl octanal/50 min ±0.42 (57 individuals) with the highest levels at 19.9 μl/50 min and the lowest at 2.8 μl/50 min (Douglas 2006a) or solvent extraction, which measures chemicals found in a set mass of feathers, was 2.98 μg octanal/g of feather (Hagelin et al.

2003). There is no difference in scent chemical levels in between males and females (Douglas 2006a; Hagelin et al. 2003). The concentrations of the chemicals that make up the scent are stronger in the plumage around the crown and nape than in the mantle feathers (Douglas 2008b).

The exact origin of the scent is unknown but wick-like feathers from 25 individuals found in the interscapular region of birds had high concentrations of some of the scent's chemical constituents (Douglas 2008b), suggesting that they may be involved in scent production. The scent is not likely produced by the skin as no chemical constituents of the scent are found on the skin once feathers are removed (Douglas 2008b). The production of the scent is correlated with progesterone in males during the early chick rearing period, suggesting that hormone levels and scent production are closely linked (Douglas 2008b). Interestingly, captive birds in a zoo did not produce the odour (Douglas 2008b).

The two proposed functions of this scent are that it plays a role in social behaviour (Hagelin et al. 2003) or acts to repel ectoparasites (Clayton et al. 2010; Douglas 2006b), are not mutually exclusive. For example, scent could also have social importance if is primary role is as defence against ectoparasites. It is possible that scent could be acting to deter ectoparasites and so individuals use it as an honest indicator of quality.

1.2.1 Social Function

It has been suggested that the scent plays a social role, indicating status, condition, or being used as a measure of quality in mate choice. The ruff-sniff display (Jones and Hunter 1993) has been suggested to be a form of allopreening, and could transfer scent between individuals (Douglas 2008b). Within a t-maze adults preferentially moved towards a 1:1 mixture of octanal and Z-4-decenal but not towards feathers of Crested Auklets (Hagelin et al. 2003). Auklets in captivity are more likely to approach models with a strong Crested Auklet odour (Douglas 2008b). In a social setting with wild auklets, both male and female auklets showed attraction to scented models; birds were more likely to approach models and spent longer periods of time around them (Jones et al. 2004). Interestingly, Jones et al. (2004) did not see an increase in sexual displays towards the scented models, as had been found for models with increased feather ornament size (Jones and Hunter 1993, 1999). However, individuals can smell the primary components of the scent and are attracted towards them. Within a captive population, concentrations of Z-4 decenal and facial crest length are significant predictors of male social status and are positively correlated with rank (Hagelin 2007b). These results within wild and captive populations suggest that there is a social role for the scent, but the role may not be in mate choice.

1.2.2 Ectoparasite Defence

It has been suggested that the scent produced by Crested Auklets acts to deter ectoparasites (Clayton et al. 2010; Douglas et al. 2001a, 2001b, 2005a, 2005b; Douglas 2006b, 2008a). Studies have focused on ticks and lice the two main ectoparasites of auklets as well as mosquitoes. Studies have been conducted using both natural scent from Crested Auklets and using a mixture of synthetic chemicals that are known to be components of the scent.

Ticks are negatively affected by the chemical components of the Crested Auklet scent. Nymphs of both *Amblyomma americanum* and *Ixodes uriae* had a shorter period of attachment and moved slower when exposed to octanal and varying concentrations of a mixture of the main scent's chemical components (Douglas et al. 2004; Douglas 2008a). *I. uriae* nymphs and adults exposed to octanol had increased morbidity (Douglas et al. 2004). When exposed to fresh feathers of Crested Auklets and unscented feather *I. uriae* did not show any signs of deterrence (Hagelin 2007a). In a past study (Douglas 2006a) only two Crested Auklets of 96 had attached ticks, one of which had the lowest chemical emission rate measured in the study (Douglas 2006a).

Lice are also negatively affected by the chemical components of Crested Auklet scent. *Austromenopon* sp. had increased morbidity when exposed to the scent's chemical components (Douglas et al. 2004). The lice *Columbicola columbae* and *Campanulotes bidentatus* exposed to feather or carcasses of Crested Auklet, Least Auklet, and Rock Pigeon (*Columba livia*) did not differ in survival (Douglas et al. 2005b). Crested Auklets had a higher louse load of *Quadraceps* sp. and *Saemundssonia* sp. than Least Auklets even when body size of host was controlled for (Douglas et al. 2005b). Lice did not show any signs of detterance when exposed to feathers of Crested Auklets, Least Auklets or Parakeet Auklets (*A. psittacula*: Hagelin 2007a).

Mosquitoes do not naturally occur in most Crested Auklet colonies. *Aedes aegypti*, a commonly used mosquito in lab repellence, experiments were more likely to land on a hand with filter paper treated with just ethanol than on paper treated with a mixture of the scent's chemical components at vary concentrations (Douglas et al. 2005a). This study demonstrates that the chemical constituents of the scent of Crested Auklets acts to deter mosquitoes. The significance of these findings is not clear since wild auklets are never exposed to mosquitoes.

1.3 Ectoparasites of Auklets

Ticks (Ixodida) are a large, diverse, cosmopolitan group. They are obligate, non-permanent parasites with four life stages; egg, larva, nymph, and adult. When not attached to hosts, they live in the soil and crawl on to vertebrate hosts for blood meals. Ticks usually require a blood meal during every stage with the exeption of eggs and usually adult males (Oliver 1989). Ixodida is divided into two main families; Argasidae, the soft ticks with ~200 species in 5 genera; and Ixodidae, the hard ticks with ~700 species in 13 genera (Nava et al. 2009). Ticks can have both direct effects, such as tick paralysis and exsanguinations (Oliver 1989); and indirect effects through the transportation of disease (Nuttall 1984).

Lice (Phthiraptera) are obligate, continuous ectoparasites. They infest all orders of birds and most orders of mammals. They are highly specialized for life on their hosts with short legs and dorsal-ventrally flattened to reduce risk of detachment from preening. The two suborders that infest birds are Ischnocera and Amblycera. Ischnocera feed exclusively on feather and the debris found on the feathers. Amblycera are more agile and occur on both skin and feather, and feed on blood and feathers. Both suborders only leave their host to infest other individuals when direct contact occurs (Marshall 1981).

1.4 Purpose

In recent years there has been a debate regarding the function of the citrus-like odour produced by Crested Auklets as described above. I determined the prevalence and intensity of ticks and lice on Crested and Least Auklet. Prevalence is the number of individual birds with one or more parasite, and mean intensity is the mean number of parasites on individuals that are have at least one parasite (Bush et al. 1997; Rózsa et al. 2000). I determined whether naturally occurring levels of ectoparasites are related to body condition or ornament expression in those species, and important question to address before looking defence mechanisms. With the closely related, Least Auklet living along side Crested Auklets it is possible to examine patterns in these two species and view the unscented Least Auklet almost like a “control” next to the scented Crested Auklet. If ectoparasites are causing negative effects I would expect that Least Auklets to have higher intensities and prevalence of tick and lice, as well as more negative impacts from parasitism then the Crested Auklets. I determined the relationship between lice and tick levels and the scent in Crested Auklets in the natural environment. This is important as all work has focused on experiments, with no study examining as many individual as I have from a wild population.

Chapter 2

Tick (*Ixodes uriae*) prevalence in *Aethia* auklets on Buldir Island, Aleutian Islands, Alaska during 2009 and 2010

Abstract

Ticks (Ixodoida) are terrestrial, obligate, non-permanent ectoparasites that affect birds. Direct feeding on individual adult birds and nestlings can result in paralysis or excessive blood loss. I documented the prevalence and intensity of the tick *Ixodes uriae* on Least (*Aethia pusilla*, n=184) and Crested (*A. cristatella*, n=280) Auklets on Buldir Island, Aleutian Islands, Alaska in 2009 and 2010. I also investigated the relationship of tick intensity to body condition and ornament expression, and the relationship of tick-inflicted damage to toe webbing to body condition and ornament expression in several auklet species. Tick prevalence was low (Least Auklets, 9.2%; Crested Auklets, 5.2%) as was intensity (1.12 and 1, respectively) in parasitized individuals. I found no statistically significant relationships between ticks and body condition or ornamental traits in either Crested or Least Auklets. I also found no evidence for a relationship between web damage and body condition or ornamental traits. These results suggest that ticks had no measurable impact on body condition or ornament expression and may not play a role in auklet ecology in this colony at this time.

2.1 Introduction

Avian ectoparasites are ubiquitous and infest most bird species (Marshall 1981). The impact of these parasites can be diverse depending on type of parasite and site of infestation. Their presence can result in reduced body mass (Rózsa 1997), slower nestling growth rates (Huber 2008), or reduced breeding success (Hoodless et al. 2003). The reduction in adult health often leads to reduced fitness because of lower nestling survival (Dudaniec et al. 2006), poorer mating success (Clayton 1990), or reduced long-term survival (Hoodless et al. 2003). Though ticks have been documented on auks (Muzaffar & Jones 2004; Appendix I) the studies that have found negative impacts are limited to those focusing on condition in chicks (Mangin et al. 2003).

A common species on seabirds is *Ixodes uriae,* which parasitizes more than 50 species of seabirds (Mangin et al. 2003; McCoy et al. 1999; Muzaffar & Jones 2004). All four life stages live underground in soil and only those individuals seeking a blood meal will crawl onto a passing bird, leading to attachment and feeding lasting for 2-7 days (Finney et al. 1999). The feeding of ticks can transfer neurotoxins from their salivary glands which can result in paralysis, and occasionally excessive blood loss from the site of the bite (Oliver 1989). Indirect effects include the transmission of diseases such as Lyme disease, *Borellia* sp. (Nuttall 1984; Gylfe et al. 1999; Muzaffar et al. in press).

The impact of ticks on seabirds has been documented for a number of species (Dietrich et al. 2010; Gauthier-Clerc et al. 1998; Mangin et al. 2003;

Proctor & Owens 2000; Wanless et al. 1997). Infestation of ticks in nestlings is related to reduced feather growth rates and later chicks fledging and with shorter wings in Cassin's Auklets (*Ptychoramphus aleuticus*; Morbey 1996). High tick prevalence has been linked to reduced immune response in nestling Black-legged Kittiwakes (*Rissa tridactyla*; McCoy & Tirard 2002). Mangin et al. (2003) reported that adult King Penguins (*Aptenodytes patagonicus*) with ticks have lower success in raising chicks to one year of age. Infestation of ticks in nestlings may also have population level impacts within Black-legged Kittiwakes (Boulinier and Danchin 2008).

Ticks are commonly abundant within North Pacific seabird colonies making mixed colonies of Least (*Aethia pusilla*), Crested (*A. cristatella*), and Whiskered Auklets (*A. pygmaea*) an excellent location to document prevalence and relationships with body condition and ornament expression. Auklets (Alcidae: Aethiini) are small, locally abundant, colonial, planktivorous seabirds that occur only in the Bering and Okhotsk Seas and adjacent parts of the North Pacific (Gaston & Jones 1998). Whiskered Auklets are normally nocturnal in relation to colony surface activity but on Buldir Island some Whiskered Auklets join aggregations of Least and Crested Auklets during the day (Hunter et al. 2002). At breeding colonies (May-July) Least and Crested Auklets congregate densely (with birds often touching one another) on the surface and underground on rocky talus slopes and lava flows. These high densities appear to provide an ideal environment for questing ticks. However, auklets spend only their breeding season on land limiting the amount of time that they are exposed to ticks as they cannot pick up ticks during the winter season. These seasonal patterns allow my study to focus on the impacts of tick parasitism without having to consider tick parasitism that may occur outside of the breeding season when seabirds are difficult to study.

Douglas (2004) has suggested that chemical emissions from the feathers of Crested Auklets function to deter ectoparasites including ticks, based on the assumption that ticks have negative effects on auklet condition and ornamentation. I was also interested in testing whether Least Auklets, which lack a pungent plumage odour, have different levels of tick infestation from Crested Auklets.

The objectives of my study were to: 1) quantify prevalence of *Ixodes uriae* on Least and Crested Auklets at Buldir Island in order to establish a baseline; and 2) investigate the relationships between tick prevalence and intensity as well as foot web damage (an inferred measure of tick parasitism on nestlings) and body condition index and ornament expression in Least, Crested, and Whiskered Auklets. I focused on *I. uriae* because they are abundant in some years at Buldir Island, have been shown to affect breeding success in other seabird species (Danchin 1992; Morbey 1996) and are easily quantified.

2.2 Methods

2.2.1 Study location

I studied auklets at a colony of more than 100,000 Crested, Least, and Whiskered Auklets at Main Talus, Buldir Island, Aleutian Islands, Alaska (52°2'N 175°5'E; Byrd & Day, 1986) during early June to mid August of 2009 and 2010. Data on Whiskered Auklets were collected between 1992 and 2006 by ILJ as part of a long-term monitoring project at a smaller colony, located just west of Main Talus, also on Buldir Island.

2.2.2 Quantification of ticks

Adult Least and Crested Auklets were captured during the morning activity period 900-1300HADT (Hawaiian Aleutian daylight-savings Time: GMT-9:00) using noose carpets set on the colony surface. Birds were placed in a freshly washed cloth bag to reduce stress on birds and parasite contamination of previously caught birds. Birds were processed in the order of capture. An individual that displayed any apparent distress (hot feet, open bill breathing) was immediately released. Each captured auklet was given a numbered US FWS stainless steel leg band, and was assigned a unique combination of three Darvik plastic colour bands.

Birds were visually inspected and palpated for attached and non-attached ticks from head to toe (Clayton & Walther 1997). Crested Auklets were inspected for 5 minutes and Least Auklets for 3 minutes to account for differences in body size. The feet and area around the eyes were visually inspected. The life stage (larval, nymph, and female adult) and location of each tick was noted.

2.2.3 Condition and body ornamentation

I weighed birds to the nearest 1 g using an Ohaus electronic balance. I measured wing length (flattened and straightened on the right wing; from the wrist to the time of the longest primary, P10), and auricular plume length (from the exposed proximal end of the plumes just below the eye to the end of the longest plume: Jones et al. 2000) to the nearest 0.1 mm using calipers. Sub-adults were excluded from this study as tick prevalence found on both Least and Crested Auklets were quite low and not enough sub-adults were caught to perform a meaningful analysis.

For Crested Auklets, I measured crest length (length of the longest straightened crest feather shaft: Jones et al. 2000) and right auricular plume length. For Least Auklets, I measured bill depth (measured twice, once from the angle of the gonys to the uppermost tip of the bill knob, and a second time from the angle of the gonys to the point where the bill meets the ridge of the culmen) and mean auricular plume length.

Whiskered Auklets, were captured using mistnets as they returned to their colony at dusk (2300-0100 HADT). ILJ banded, weighed, and measured crest length from 1992 to 2006. All measurements were taken by a single observer, and followed the same protocols applied in 2009 and 2010 for Least and Crested Auklets, except some bird bags were reused before washing.

2.2.4 Foot web damage

Damage to the webbing between the toes was scored for each bird, with a scale of 0-2: 0- both feet undamaged; 1- one small hole in either foot, 2- multiple holes or tears in the webbing. These were old healed injuries that are acquired at the nestling stage when ticks attach to the chick's soft webbing (Hoberg & Wehle 1982; Morbey 1996).

2.2.5 Statistical techniques

Statistics were conducted in SPSS (version 19) or Quantitative Parasitology (Reiczigel & Rózsa 2005). Prevalence and mean intensity of tick infestation are reported with 95% confidence limits. Prevalence is the number of individual birds with one or more parasite, and mean intensity is the mean number of parasites on individuals that are have at least one parasite (Bush et al. 1997; Rózsa et al. 2000). I calculated day as the day number from January 1 of the respective year. Web damage was used as a score of impact of tick infestation that occurred as a nestling. I compared the number of ticks and foot web damage observed in Least and Crested Auklets using MANOVA. Web damage and number of ticks on an individual were the dependent variables with species, year, and day being the independent variables. All non-significant interaction terms were removed. I analyzed Least, Crested, and Whiskered Auklet data separately from this point forward as ornament measures and size differ between species.

In both species body condition index was defined as the residual mass from a linear regression of body mass against body size (with wing length as a body size proxy) expressed as the percentage of the predicted value (Janicke et al. 2008). In Crested Auklets I used body condition index, wing length, crest length, and right auricular plume length as my measures of condition and degree of ornamentation. Crest length and right auricular plume length were not correlated (Pearson correlation, $r=0.10$, $p=0.10$, $n=280$). In Least Auklets I used body condition index, wing length, bill knob height and mean auricular plume length as measures of condition and degree of ornamentation. Bill knob was not correlated with mean auricular plume length (Pearson correlation, $r=-0.10$, $p=0.19$, $n=184$) and wing length was not correlated with body condition index (Pearson correlation, $r=0.01$, $p=0.97$, $n=184$). These measures were related to number of ticks found and foot web damage with day and year of capture as covariates using MANOVA.

Tick prevalence data were available only for a small number of individuals for Whiskered Auklets so analysis focused only on web damage. Mass and crest length were related to web damage score, year of sample, and day date of sample using a MANOVA.

2.3 Results

The prevalence (95% confidence interval) of ticks on Crested Auklets 5.2% (2.9-8.7%; n=251) and on Least Auklets was 9.2% (5.6-14.3%; n=184; Figure 2.1). The mean intensity (95% confidence interval) was 1 (1-1) and 1.12 (1-1.35) for Crested and Least Auklets, respectively. In Least, Crested, and Whiskered Auklets most individuals had no visible damage to their feet (Table 2.1; Figure 2.2).

Least or Crested Auklets did not differ in number of ticks (MANOVA, F=0.99, p=0.32) or the web damage (MANOVA, F=0.217, p=0.64) when accounting for year and date of capture.

In Crested Auklets, the number of ticks and foot web score were not correlated with body condition index, wing length, crest length, or length of the right auricular plume. Body condition index was related to day of collection in the season, and year (Table 2.2: Figure 2.3). Individuals that were caught in 2010 were in better condition and had longer wings than those caught in 2009 (Figure 2.4). Body condition index decreased throughout the season (Figure 2.5).

In Least Auklets, the number of ticks found on individuals or level of damage on foot webs was not correlated with body condition index, wing length, knob height, or mean auricular plume length (Figure 2.6). Body condition varied by year (greater in 2010; Figure 2.7) and bill knob height was related to date of measurement (Table 2.2; Figure 2.8). The size of bill knobs decreased over the season (Figure 2.8).

In Whiskered Auklets, foot web score was not correlated with mass or crest length (Table 2.3; Figure 2.9). Body mass was not related to year or day of capture, but crest length varied between years (Table 2.3; Figure 2.10).

2.4 Discussion

2.4.1 Tick Prevalence and intensity

For both Least and Crested Auklets, the prevalence of ticks and mean intensity were low on Buldir Island in 2009 and 2010. There was no difference in intensity of ticks found between Least or Crested Auklets. In other studies, prevalence of ticks in alcids has ranged widely by species, locality, and year of sampling (Muzaffar and Jones 2004, Appendix I). For example, Common Murres (*Uria aalge*) have been reported to have tick prevalence range from 1% (Barton 1996) to as high as 97% of individuals (Choe & Kim 1987a). Within Crested Auklets, Engström et al. (2000) found no ticks on 131 Crested Auklets at Talan Island in the 1997 breeding season. On Buldir Island some years nearly 100% of auklet individuals have at least one tick – indicating that inter-year and inter-colony variability in prevalence are high (I.L. Jones pers. comm.).

2.4.2 Impact of ticks on body condition and ornament expression

Tick prevalence was not related to body condition or ornament expression in either species. The impact of ticks on condition may be difficult to detect when tick intensity is low, because they attach for brief period (7.7 days; Finney et al. 1999), which reduces both the chances of finding the few ticks that an individual bird attracts, and also the physiological effect of parasitism.

Ticks are known of a wide range of diseases and arboviruses (Nuttall 1984) that can cause infection at the site of attachment. These infections may have greater impacts than the impacts of direct feeding and would require monitoring of over long periods of time to examine survival and other factors throughout individuals lifetimes. Web damage was measured to address long-term negative impacts of ticks, as this damage arises when tick(s) attach to the toe webbing of seabird chicks (Hoberg & Wehle 1982; Morbey 1996). These holes are thought to be caused by infection at site of attachment. Primarily small holes in the web between toes are observed. Occasionally damage as non circular holes and loss of web is seen and could be caused by other factors. My findings are important because this measure was not be related to body condition and ornament expression later in life, perhaps because individuals that survived tick parasitism were strong fitter.

Assessing the question of tick impacts on auklet health was difficult due to the low intensity of the parasite and small number of affected birds (17 and 13 individuals ticks out of 184 and 251 Least and Crested Auklets examined respectively). These low levels require large samples sizes to achieve adequate statistical power and body condition and ornament expression are related to various other environmental factors simply adding noise to the analysis. Confounding this, many factors influence tick densities (Oliver 1989), and the impacts that ticks will have (Whiteman & Parker 2004). To address the complexity of this system a study must be carried out over numerous seasons to remove noise and quantify the impact of as many additional variables as possible.

2.5 Summary

1. Prevalence and intensity of ticks in both Least and Crested Auklets were low on Buldir in 2009 and 2010. In Crested Auklets, prevalence (95% confidence interval) was 5.2% (2.9-8.7%) in 251 individuals and in Least Auklets was 9.2% (5.6-14.3%) in 184 individuals. The mean intensity (95% confidence interval) was 1 (1-1) and 1.12 (1-1.35) Crested and Least Auklets respectively.
2. The number of ticks did not differ between Least or Crested Auklets, or on the web damage between the two species.
3. Prevalence of ticks was not related to condition or ornament expression in Crested Auklets or Least Auklets measured at Buldir Island during 2009 and 2010.
4. Foot web damage score, an indication of earlier tick parasitism at the nestling stage, was not related to condition or ornament expression in Crested or Least Auklets at Buldir.

5. Foot web damage score in Whiskered Auklets was not related to body mass or ornament expression.

Table 2.1. Most Least (*Aethia pusilla*), Crested (*A. cristatella*) and Whiskered Auklets (*A. pygmaea*) captured on Buldir Island, Alaska do not have any web damage. Individuals with scores of 0 had no holes in either foot web; 1- individuals had a single circular hole in either foot web; and 2- had greater than one hole with non-circular holes and tears in their foot webs rarely observed.

	Incidence (%)		
Foot web score	**Least Auklet N=184**	**Crested Auklet N=251**	**Whiskered Auklet N=256**
0	75%	81%	86%
1	19%	13%	13%
2	6%	6%	1%

Table 2.2. Within 184 Least Auklets (*Aethia pusilla*) and 251 Crested Auklets (*A. cristatella*) captured on Buldir Island in 2009 and 2010 there was no relationship among tick intensity, web damage, body condition, and ornament expression. The year and day of capture was included as dependent variables in MANOVA to address variation in body condition and ornament expression between and within breeding seasons.

		Overall		Body condition index		Wing length		Mean auricular plume length		Bill knob height	
	Wilks's λ	F	P	F	P	F	P	F	P	F	P
Least Auklet											
Ticks	1.0	0.8	ns	0.9	ns	0.9	ns	0.2	ns	1.0	ns
Web	1.0	0.5	ns	0.5	ns	0.1	ns	0.6	ns	0.9	ns
Year	0.9	2.3	ns	8.4	<0.01	0.6	ns	0.1	ns	0.1	ns
Day	0.8	13	<0.01	1.5	ns	2.9	ns	0.6	ns	44	<0.01
Crested Auklet								**Crest length**		**Length of right plume**	
Ticks	1.0	0.6	ns	0.1	ns	1.6	ns	0.1	ns	0.3	ns
Web	1.0	0.6	ns	0.3	ns	0.1	ns	1.8	ns	0.1	ns
Year	0.9	6.9	<0.01	11	<0.01	6.1	0.01	3.8	ns	3.4	ns
Day	0.9	5.4	<0.01	19	<0.01	0.4	ns	1.2	ns	2.5	ns

Table 2.3. Within 256 Whiskered Auklets (*Aethia pygmaea*) captured at Buldir Island, Alaska from 1992 to 2007 there was no relationship among web damage, body condition, and ornament expression. The year and day of capture was included as dependent variables in MANOVA to address variation in mass and ornament expression between and within breeding seasons.

				Mass		Crest	
	Wilks's λ	**F**	**P**	**F**	**P**	**F**	**P**
Web	1.0	1.6	ns	2.8	ns	0.1	ns
Year	0.8	2.7	<0.01	1.2	ns	4.4	<0.01
Day	1.0	0.1	ns	0.2	ns	1.0	ns

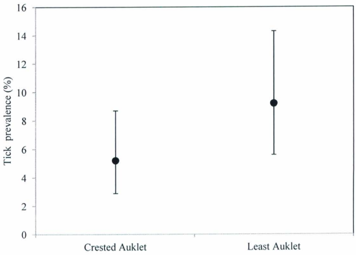

Figure 2.1 Prevalence of ticks in Least (*Aethia pusilla*) and Crested Auklets (*A. cristatella*) on Buldir Island during 2009 and 2010. Error bars represent 95% confidence limits.

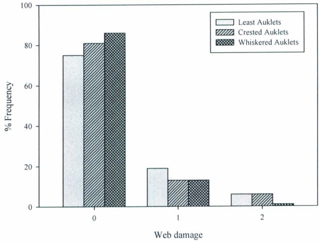

Figure 2.2 Percent frequency of web damage in Least (*Aethia pusilla*), Crested (*A. cristatella*), and Whiskered Auklets (*A. pygmaea*) caught on Buldir Island.

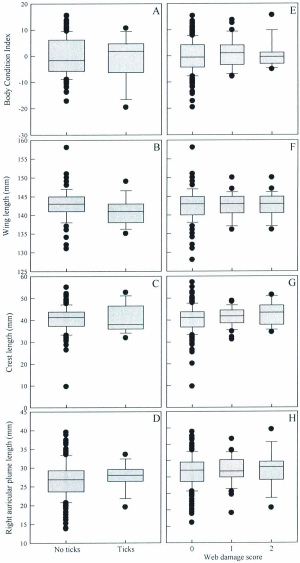

Figure 2.3 In Crested Auklets (*Aethia cristatella*; n=251), body condition index (A,E), wing length (B,F), crest length (C,G), and right auricular plume length (D,H) was not related to the intensity of ticks (A-D) or web damage score (E-H) on Buldir Island during 2009 and 2010.

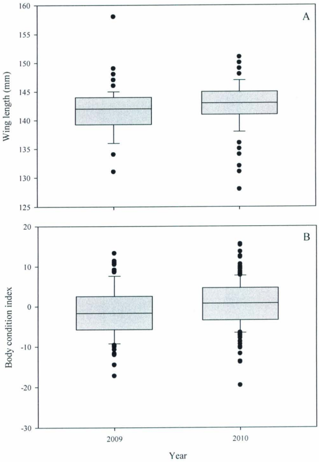

Figure 2.4 Crested Auklets (*Aethia cristatella*; 251) caught on Buldir Island in 2009 had shorter wings and lower body condition index scores than those caught during 2010.

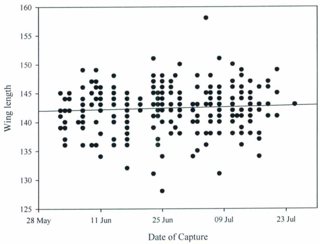

Figure 2.5 Crested Auklets (*Aethia cristatella* ; n=251) caught later in the season in both 2009 and 2010 on Buldir Island have longer wing lengths.

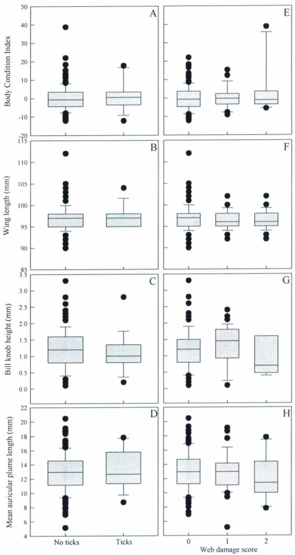

Figure 2.6 In Least Auklets (*Aethia pusilla*; n=184), body condition index (A,E), wing length (B,F), bill knob height (C,G), and mean auricular plume length (D,H) was not related to the intensity of ticks (A-D) or web damage score (E-H) on Buldir Island during 2009 and 2010.

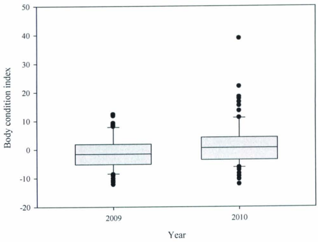

Figure 2.7 Least Auklets (*Aethia pusilla*; n=184) caught on Buldir Island in 2009 had a lower body condition index than those caught during 2010.

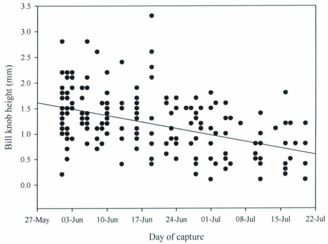

Figure 2.8 Least Auklets (*Aethia pusilla*; n=184) caught on Buldir Island had a smaller bill knobs later in the season than those caught earlier in the season in both 2009 and 2010.

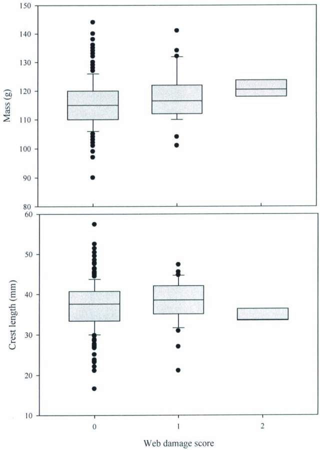

Figure 2.9 Web damage score in Whiskered Auklets (*Aethia pygmaea*, n=256) caught from 1992 to 2006 was not related to mass or crest length.

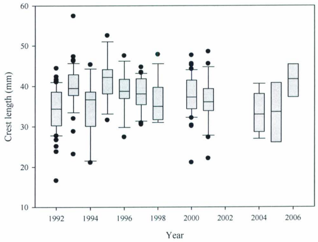

Figure 2.10 Crest length in 256 Whiskered Auklets (*Aethia pygmaea*) auklets caught from 1992 to 2006 varied significantly between years.

Chapter 3

Louse (Phthiraptera) prevalence on adult Least (*Aethia pusilla*) and Crested Auklets (*A. cristatella*) at Buldir Island, Aleutians Islands, Alaska during 2009 and 2010

Abstract

Lice are a common ectoparasites on many seabirds. The prevalence of lice can range from below 10% to as high as 100% in alcids. Lice prevalence is important to quantify before considering the negative impacts that lice may have on hosts. I caught Least and Crested Auklets on Buldir Island during the 2009 and 2010 breeding seasons, determined louse prevalence and mean intensity. Birds were caught during the breeding season and lice collected by dust ruffling with an insecticide. Louse prevalence was low (7.1%-12.9%) in Least and Crested Auklets respectively with mean intensity similarly being low at 1.20 in Least Auklets and 1.22 in Crested Auklets. In addition I investigated the relationships of prevalence to body condition and ornament expression. In both Least and Crested Auklets I found no relationship between the number of lice found on individual auklets and their body condition or ornament expression. My results provide baseline information on louse prevalence and intensity on these two seabird species which is integral to understand the impacts that lice have on their hosts.

3.1 Introduction

Bird lice are ubiquitous and infest most bird species in all habitats and regions of the world (Price et al. 2003). These parasites can have detrimental impacts when prevalence is high, e.g. reduced body mass (Booth et al. 1993), reduced body condition (Blanco et al. 2001; Calvete et al. 2003; Whiteman and Parker 2004), and reduced breeding success (Clayton 1990). Nevertheless, although lice sometimes occur in very large numbers on auks (Choe & Kim 1987), there is no published evidence that they have any negative impact in that group of seabirds (Muzaffar and Jones 2004).

In the Galápagos Hawk (*Buteo galapagoensis*), Whiteman and Parker (2004) found a negative relationship between lice abundance and body condition (Whiteman and Parker 2004). In Rock Pigeons (*Columba livia*), birds infested with high levels of lice had lower body mass and basal metabolic rate (Booth et al. 1993). Reduced body mass was thought to be the result of feather damage as those same individuals had lighter feathers, which resulted in lower minimal whole-body thermal conductance (Booth et al. 1993). A reduction in body mass, and increased energy output can result in reduced nutritional condition, e.g. in Red-legged Partridge (*Alectoris rufa*, Calvete et al. 2003) and European Magpie (*Pica pica,* Blanco et al. 2001).

Auk (Alcidae) lice have been studied in general (Muzaffar and Jones 2004), but little is known about lice of auklets (Aethiini). Lice on auklets on Buldir Island have been documented(Table 3.1) but prevalence has been reported only for Crested Auklets (*Aethia cristatella*, 4.0% at Big Koniuji Island; Douglas 2006). Prevalence and intensity of lice are variable so it is useful to document these parameters at more than one colony and across species.

Auklets are small, locally abundant, colonial, planktivorous seabirds that occur only in the Bering and Okhotsk Seas and adjacent parts of the North Pacific (Gaston and Jones 1998). The smallest and most abundant species, Least Auklet (*Aethia pusilla*, mean mass 85 g) forages close to its breeding colonies during summer and disperses widely at sea in winter (Jones 1993). Crested Auklets (mean mass 260 g) coexist at most Alaskan colony sites and at sea with Least Auklets in summer and in winter form dense concentrations near Aleutian passes (Jones 1993; Jones and Hunter 1993). Least and Crested Auklets breed at only nine colony sites in the Aleutian Islands (Williams et al. 2003). At breeding colonies (May-July) auklets congregate densely (with birds in direct contact with one another) on the surface and underground on rocky talus slopes and lava flows.

Douglas (2004) has suggested that chemical emissions from the feathers of Crested Auklets function to deter ectoparasites including lice, based on the assumption that lice have negative effects on auklet condition and ornamentation. I was also interested in testing whether Least Auklets, which lack a pungent plumage odour, have different levels of louse infestation from Crested Auklets.

In summary, the objectives of my study were: 1) to quantify the prevalence and intensity of lice on adult Least and Crested Auklets on Buldir

Island during the 2009 and 2010 breeding seasons; 2) to compare between the two auklet species; and 3) to test for relationships between louse prevalence and intensity and body condition and ornamentation.

3.2 Methods

3.2.1 Location

Fieldwork was carried out at a colony of more than 100,000 Crested, Least and other auklets at Main Talus, Buldir Island, Aleutian Islands, Alaska (52°2'N 175°5'E; (Byrd and day 1986) from early June to late August of 2009 and 2010.

3.2.2 Capture and measurement of auklets

Adult Least and Crested Auklets were captured during the morning activity period 900-1300HADT (Hawaiian Aleutian daylight-savings Time: GMT-9:00) using noose carpets set on the colony surface. Birds were placed in a washed cloth bag to reduce stress and contamination of previously caught birds. Birds were processed in the order of capture. An individual that displayed any apparent distress (hot feet, open bill breathing) was immediately released. Each captured auklet was given a numbered US FWS stainless steel leg band, and was assigned a unique combination of three Darvik plastic colour bands.

I weighed birds to the nearest 1 g using an Ohaus electronic balance. I measured wing length (flattened and straightened on the right wing; from the wrist to the time of the longest primary, P10), and auricular plume length (from the exposed proximal end of the plumes just below the eye to the end of the longest plume: Jones et al. 2000) to the nearest 0.1 mm using callipers. Sub-adults were excluded from this study as louse prevalence found on both Least and Crested Auklets were quite low and not enough sub-adults were caught to perform a meaningful analysis.

For Crested Auklets, I measured crest length (length of the longest straightened crest feather shaft: Jones et al. 2000) and the rictal plate height (on the right side, from its mid-point along the cutting edge of the bill near the gape to its highest point). For Least Auklets, I measured mean auricular plume length and quantified underpart plumage colouration (i.e., the degree of blackness in the breast plumage) on a scale of 0 – 4 (Jones 1990).

3.2.3 Louse collection and quantification

After they were banded and measured birds were dust-ruffled (Walther and Clayton 1997) using dog flea powder (Sergeant's® tick and flea power for dogs, Carbaryl 5.0%, Pyrethrins 0.1%, Piperonyl Butoxide 1.0%) to collect lice. In order to apply an equal amount of insecticide per unit area of skin surface of each species, a ratio of 1 (Least Auklet) : 2.1 (Crested Auklets) was applied (based on calculations of the relative surface area of the two species; Appendix III). Birds were held over a clear plastic Ziplock® bag with powder applied evenly across the body following the procedure described by Walther and Clayton (1997). Powder was massaged into the feathers to ensure that the insecticide reached the bird's skin. Least Auklets were ruffled for three minutes and Crested Auklets for five minutes, again to account for differences in body size. The first minute was used to distribute the powder over the bird, while the next two or four minutes were spent ruffling the powder. It took the same time to distribute the powder for both species. The Ziplock® with powder and lice were visually inspected in the lab using a dissecting microscope so that all lice could be removed and placed in 70% ethanol for later identification. Lice have previously been collected from Buldir Island and identified to species (Table 3.1). Based on these previous identifications I refer to louse taxa by genus since each auklet species had only one louse species from each of the three genera.

3.2.4 Statistical techniques

All statistics were conducted in SPSS (version 19) and Quantitative Parasitology (Reiczigel & Rózsa 2005). Prevalence and mean intensity of lice infestation are reported with 95% confidence limits. Prevalence is the number of individual birds with one or more parasite, and mean intensity is the mean number of parasites on individuals that are have at least one parasite (Bush et al. 1997; Rózsa et al. 2000). I calculated day as the day number from January 1 of the respective year. To determine if the intensity of lice on the two species of auklets differed, a generalized linear model with was used to compare individual intensities of lice. A negative binomial distribution was assumed and a log link function applied. Number of lice was the dependent variable and species the independent with day and year included to control for variation between and within season. The interactions between species and year or day were excluded as they were not significant. It was assumed that number of lice found on an individual could be directly compared as differences in body size were controlled for in sampling technique. All future analyses examined Least and Crested Auklet data separately.

In both species body condition index was defined as the residual mass from a linear regression of body mass against body size (with flatened wing length as a proxy) expressed as the percentage of the predicted value (Janicke et al. 2008). In Least Auklets I used body condition index, wing length, breast plumage score (correlated with age and social dominance; Jones 1990) and mean auricular plume length (favoured by mating preferences) as my measures of condition, body size and degree of ornamentation. Breast plumage score was not correlated with mean auricular plume length (Pearson correlation, $r=0.02$, $p=0.79$, $n=140$) and wing length was not correlated with body condition index (Pearson correlation, $r=0.01$, $p=0.99$, $n=140$). All non-significant two-way interactions were removed. In Crested Auklets I used body condition index (Janicke et al. 2008), wing length, crest length (favoured by mating preferences; Jones and Hunter 1993, 1999), and bill rictal plate height as measures of condition, body size and degree of ornamentation. Crest length and rictal plate height were not correlated (Pearson correlation, $r=0.09$, $p=0.18$, $n=209$). Using a MANOVA these measures were related to number of lice found on an individual with day and year of capture as covariates. All non-significant two-way interactions were removed.

3.3 Results

Austromenopon, *Quadraceps*, and *Saemundssonia* were collected from Least and Crested Auklets. Prevalence of each species was low (Table 3.2) so data were pooled (i.e. I used a total count of all lice of all genera present to quantify each individual's ectoparasite loads). In Crested Auklets 12.9% (8.2-18.0%, 95%CL) in 210 individuals and in Least Auklets the prevalence of lice was 7.1% (3.8-12.7%, 95%CL) in 140 individuals. The mean intensity was 1.22 (1.04-1.47, 95%CL) and 1.20 (1-1.6, 95%CL) and Crested and Least Auklets respectively.

Abundance of lice on individual Least Auklets did not differ significantly from the abundance on individual Crested Auklets (GlzLM, χ^2=1.36, p=0.24; Figure 3.1). With intensity of lice being low on both species, the analysis included both parasitized and non parasitized individual thus addressing abundance instead of intensity, which is a metric that accounts for both prevalence and intensity.

In Least and Crested Auklets the intensity of lice was not correlated with body condition index, wing length, plumage colour or ornament expression (Table 3.3; Figure 3.2-3.3). There were however some statistically significant relationships with day in the breeding season and year of sampling in each species.

3.4 Discussion

Least and Crested Auklets had low prevalence and low mean intensity of lice in my study area at Buldir Island during the breeding seasons in 2009 and 2010. Alcids can have variable levels of lice (Muzaffar and Jones 2004; Appendix II) with reported levels as low as 3% in Atlantic Puffins (*Fratercula arctica,* Muzaffar 2000) and as high as 100% in Dovekies (*Alle alle*; Eveleigh & Threlfall 1976). A previous study of Crested Auklets found prevalence to be 4% (Douglas 2006). This result underscores the high inter-year and inter-colony variation in ectoparasitism rates that have been previously reported (Muzaffar and Jones 2004).

I found no difference between the number of lice found on Least versus Crested Auklets. Differences in body size between the two species should not have influenced the results since I accounted for this by sampling Crested Auklets with more tick and flea powder and for a longer length of time based on calculations of body size (Appendix III). With such low prevalence's and intensities in both species it is likely that any differences would be very subtle and require large samples sizes to detect. Douglas (2005) suggested that chemical emissions from the feathers of Crested Auklets function to deter ectoparasites. If this were the case there might be a difference in prevalence or intensity between species, especially at a mixed-species colony such as Buldir Island. My results do not show this; however it is possible that plumage odour of Crested Auklets plays a role but relationship is subtle and difficult to detect. It is possible that the plumage odour of Crested Auklets reduces the pressures of parasitism to levels seen in Least Auklets and so that is why no difference was observed. One way to address the possibility of Crested Auklet scent acting to reduce lice levels would be to determine louse prevalence and intensity on unscented Crested Auklets compared to Least Auklets. Unscented Crested Auklets have not been recorded in nature, though the captive population in the Cincinnati Zoo does not produce the distinctive odour (Douglas 2008b).

The low prevalence and intensity of lice on Crested and Least Auklets observed in this study were not high enough to cause any measurable impact on body condition or ornament expression. The low prevalence and low intensity makes correlations difficult to address and likely is responsible for the lack of relationship between prevalence and condition in these two species via a sampling effect (i.e., I was unable to measure enough infested birds to provide a comparative sample for an analysis capable of detecting differences between infested and non-infested individuals). Alternatively, because the lice identified are scavengers that live principally off feather debris, it is possible that they have no effect on auklet health or viability, which is consistent with some previous suggestions about this group (Muzaffar and Jones 2004). However, my results do not exclude the possibility of a deleterious effect of these louse taxa at high levels of infestation (i.e., heavily infested birds would not have been included in my sample of healthy birds caught at a breeding colony). If at low levels parasites cause dramatic negative impacts, high levels of parasitism will rarely be observed in wild populations, as individual that become infested will quickly be lost from the population, so only these that are unparasitized, or with extremely low levels of parasitism and are healthy will be observed. It is difficult to distinguish between these two mechanisms without experimental manipulation of the system.

It is likely that my observed number of infested birds was not large enough to disentangle the multitude of factors that influence condition and ornament expression in Least and Crested Auklets. Multiple years of data, with many hundreds of birds would have to be caught in order to control for such factors. My study found variation between years and levels were higher than those reported in another colony (4%, Big Koniuji Island; Douglas 2006) suggesting that there may be considerable inter-annual and inter-colony variability in intensity and prevalence. Mean intensity and prevalence of lice infestation on both Least and Crested Auklets may have been so low enough that it did not affect body condition or ornament size. In addition, lice populations tend to be highly variable in many seabird species and the low prevalence found in these species of seabirds requires that extraordinarily large numbers of individuals be sampled over a number of breeding seasons.

The complex nature of host parasite relationships make it difficult to measure any impacts on host fitness, especially when prevalence is low and infested individuals have few parasites. The low prevalence and intensity of *Austromenopon*, *Quadraceps*, and *Saemundssonia* lice on the two alcid species, Least and Crested Auklets with high degrees of annual and seasonal variability in condition emphasize the subtleties of impact of these parasites and the need for large scale, long-term data sets as well as experimental studies to address the vital ecological questions of the impacts of parasites on their host species.

3.5 Summary

1. Lice prevalence and intensity was low in both species with Crested Auklets 12.9% (8.2-18.0%) in 210 individuals and in Least Auklets the prevalence was only 7.1% (3.8-12.7%) in 140 individuals. The mean intensity was only 1.22 (1.04-1.47) and 1.20 (1-1.6) Crested and Least Auklets respectively.
2. Intensity of lice found on individual Crested Auklets did not differ significantly from the intensity found on Least Auklets when sampling methods to control for body size were applied.
3. I was unable to detect a relationship between louse infestation and either body condition or ornament expression in Crested or Least Auklets, but the low prevalence of lice in my large sample of dust-ruffled birds may have affected my ability to detect such relationships.

Table 3.1. Summary of lice collected from Crested and Least Auklets on Buldir Island and housed at the Museum of New Zealand Te Papa Tongarewa. Specimens collected in the breeding season of 1997-1998 by Fiona Hunter on Buldir Island. The number of specimens and corresponding registration numbers (Reg. Num.) are included. Number of specimens in the collection is broken down into nymphs (N), adult males (M), and adult females (F). Lice were identified to species by Ricardo L. Palma or Roger D. Price.

		No. of specimens			Reg. Num.
Host Species	**Louse Species**	**N**	**M**	**F**	**AI.-**
Crested Auklet *Aethia cristatella*	*Austromenopon nigropleurum* (Denny, 1842)		14	12	015651 015652 015653
	Quadraceps aethereus (Giebel, 1874)		1	22	017867 017868
	Saemundssonia wumisuzume (Uchida, 1949)	5	1	7	018935
Least Auklet *Aethia pusilla*	*Austromenopon nigropleurum* (Denny, 1842)		7	22	015648 015649 015650
	Quadraceps aethereus (Giebel, 1874)	2	20	18	017863 017864
	Saemundssonia boschi (Price *et al.*, 2003)	4	12	18	018741 018742

Table 3.2. Least (*Aethia pusilla*) and Crested Auklets (*A. cristatella*) dust-ruffled at Buldir Island Alaska during 2009 -2010 had *Quadraceps aethereus* while Crested Auklets also were infested with *Austromenopon nigropleurum* and *Saemundssonia wumisuzume*. Prevalence(P) and mean intensity (MI) are reported with 95% confidence limits.

	Louse species					
	Quadraceps aethereus		***Austromenopon nigropleurum***		***Saemundssonia wumisuzume***	
Host Species	**P**	**MI**	**P**	**MI**	**P**	**MI**
Least Auklet						
2009 (N=80)	10.7% (4.8-22.1%)	1.00 (1-1)	0	-	0	-
2010 (N=116)	4.8% (1.7-11.7%)	1.5 (1-2)	0	-	0	-
Total	**7.1% (3.8-12.7%)**	**1.20 (1-1.6)**	**0**	**-**	**0**	**-**
Crested Auklet						
2009 (N=66)	15.2% (8.1-25.6%)	1.3 (1-1.5)	3% (0.5-10.38%)	1.00 (1-1)	1.5% (0.08-8.07%)	1.00 (1-1)
2010 (N=206)	6.3% (3.5-10.6%)	1.00 (1-1)	1.0% (0.18-3.5%)	1.00 (1-1)	0.5% (0.03-2.79%)	1.00 (1-1)
Total	**11.0% (7.3-15.9%)**	**1.13 (1-1.3)**	**1.6% (0.6-4.1%)**	**1.00 (1-1)**	**0.8% (13.6%)**	**1.00 (1-1)**

Table 3.3. Within 140 Least Auklets (*Aethia pusilla*) and 210 Crested Auklets (*A. cristatella*) captured on Buldir Island in 2009 and 2010 there was no relationship among louse intensity, body condition, and ornament expression. The year and day of capture was included as dependent variables in MANOVA to address variation in body condition and ornament expression between and among breeding seasons.

				Body Condition Index		**Wing Length**		**Mean Auricular Plume Length**		**Breast Plumage Score**	
	Wilks's λ	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**
Least Auklet											
Lice	0.92	1.47	ns	1.3	ns	2.9	ns	0.1	ns	1.4	ns
Year	0.81	7.62	<0.01	7.4	<0.01	5.1	0.03	0.1	ns	17	<0.01
Day	0.89	4.22	0.01	15	<0.01	1.4	ns	0.2	ns	0.1	ns
Crested Auklet								**Crest Length**		**Rictal Plate Height**	
Lice	0.97	0.7	ns	0.1	ns	0.8	ns	1.34	ns	0.2	ns
Year	0.91	5.1	<0.01	13	>0.01	3.0	ns	0.01	ns	2.4	ns
Day	0.71	20	<0.01	4.3	0.04	0.2	ns	0.13	ns	72	>0.01

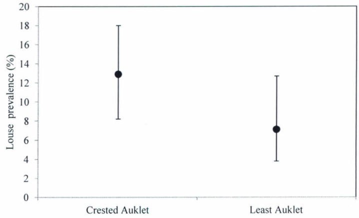

Figure 3.1 Prevalence of lice in 210 Crested Auklets (*Aethia cristatella*)and 140 Least Auklets (*A. pusilla*) captured on Buldir Island during 2009 and 2010. Error bars represent 95% confidence limits around the mean prevalence for each species.

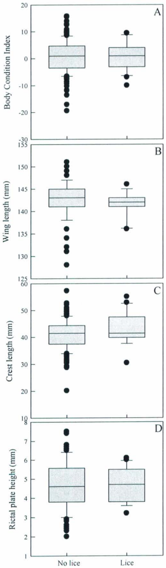

Figure 3.2 In Crested Auklets (*Aethia cristatella*; n=210), body condition index (A), wing length (B), crest length (C), and rictal plate height (D) was not related to the intensity of ticks (A-D) on Buldir Island during 2009 and 2010.

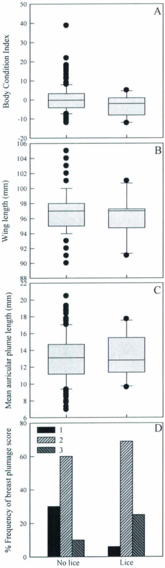

Figure 3.3 In Least Auklets (*Aethia pusilla*; n=140), body condition index (A), wing length (B), mean auricular plume length (C), and breast plumage score (D) was not related to the intensity of lice (A-D) on Buldir Island during 2009 and 2010.

Chapter 4

An experimental study of anti-parasite function for Crested Auklet (*Aethia cristatella*) feather odour

Abstract

The function of the unique tangerine-like scent produced by Crested Auklets (*Aethia cristatella*) provides an interesting Darwinian puzzle. Experimental evidence suggests a social role for the odour, but evidence that it functions to repel ectoparasites is equivocal. These two functions are not mutually exclusive. To test the ectoparasite hypothesis, at Buldir Island, Aleutian Islands, Alaska in 2009 and 2010 I investigated the relationship between tangerine odour to ectoparasite prevalence in wild caught individual Crested Auklets. I experimentally tested whether cloth treated with the two major components of the scent (Z-4-decenal and octanal), with an emission level duplicating that seen in nature, deterred questing adult ticks (*Ixodes uriae*) from attaching, compared to a scent-free control. More ticks (2.73x) were collected on unscented sheets. To examine the relationship of odour to ectoparasitism, I quantified individual birds' scent through a standard observer measure and quantified ectoparasite prevalence via collection by dust-ruffling with an insecticide. I found no relationship between odour and levels of parasitism.

4.1 Introduction

It has been traditionally assumed that olfaction plays a minor role in birds compared with other senses, so the study of avian odours and their functions has been neglected (Hagelin & Jones 2007). However, since the realization that most birds have a fully functional olfactory system there has been growing interest in birds' use of smell, avian odours, and odour functions (Balthazart & Taziaux 2009; Bonadonna & Nevitt 2004; Mínguez 1997).

Crested Auklets (*Aethia cristatella*) have a strong citrus-like odour during the breeding season (Douglas et al. 2001a; Hagelin et al. 2003; Humphrey 1958; Hunter & Jones 1999; Jones 1993a; Jones et al. 2000). Two functions have been proposed for this smell: intra-specific communication and chemical defence against ectoparasites (Clatyon et al. 2010; Hagelin & Jones 2007). Experimental evidence suggests a social role, because birds are attracted to the tangerine smell (Douglas et al. 2001a; Hagelin et al. 2003; Jones et al. 2004). Evidence for the ectoparasite repulsion hypothesis has been mixed (Douglas 2006a; Hagelin 2007; Hagelin and Jones 2007; Table 4.1). Due to the difficulty of reproducing realistic presentations of the odour to naturally occurring auklet ectoparasites in controlled experiments in the birds' remote and harsh environment. A dual function for the odour is possible, so a research priority is for more tests of the anti-parasite hypothesis.

Crested Auklets are small, locally abundant, colonial, planktivorous seabirds that occur only in the Bering and Okhotsk Seas and adjacent parts of the North Pacific (Jones 1993a). Crested Auklets coexist at most Alaskan colony sites and at sea with Least Auklets in summer and in winter form dense concentrations near Aleutian passes (Jones 1993a). They are known to only breed in nine colony sites in the Aleutian Islands (Williams et al. 2003). At breeding colonies (May-July) auklets congregate densely (with birds in direct contact with one another) on the surface and underground on rocky talus slopes and lava flows. These high densities provide an ideal environment for parasite transfer, tick attachment, and social interactions. However, auklets spend only their breeding season on land, limiting the amount of time that they are exposed to ticks. Crested Auklets have large crests on their forehead that are favoured by both males and females in mating selection (Jones & Hunter 1993, 1998). Both sexes also have white auricular plumes, and an orange bill with accessory plates that are displayed during breeding but become highly reduced after breeding (Jones 1993c; Jones & Hunter 1993). Their scent is composed of primarily short-chained, highly volatile aldehydes, alcohols and acids: N-hexanal, N-octanal, N-decanal, Z-4-decenal, hexanoic acid, octanoic acid, N-octanal, Z-4-dodecenal and Z-6-dodecenal as well as octanol, undecanal, tridecanal, and heptanal (Douglas et al. 2001a; Douglas et al. 2004; Hagelin et al. 2003). Emission rates differ depending on the measurement technique; solvent extraction: 5.7 μl octanal/50 min ±0.42 with a range of 19.9 μl/50 min to 2.8 μl/50 min (Douglas 2006a); head space analysis: 2.98 μg octanal/g of feather (Hagelin et al. 2003).The citrus-like scent is strongest during the breeding season and greatly reduced during the winter (Hagelin et al. 2003), and individuals vary in strength of the scent (IL Jones pers. com.; Douglas 2006a). The scent appears to be stronger in the plumage around the crown and nape than in the mantle feathers (IL Jones pers. comm.; Douglas 2006a). The anatomical source of the scent is unknown but Douglas (2008b) speculated that wick-like feathers in the interscapular region might be involved as some of the chemical constituents found in the scent were associated with this area (Douglas 2008b). The scent is not likely produced by the skin as no chemical constituents of the scent are found on the skin once feathers are removed (Douglas 2008b). Finally, captive birds at the Cincinnati Zoo do not produce the odour at all (Douglas 2008b), suggesting that some factors present in natural habitat are required for scent production.

Scent may play a social role, indicating status, condition, or being used in mate choice (Douglas 2006b; Jones et al. 2004). The ruff-sniff display (Jones and Hunter 1993) has been suggested to be a form of allopreening (Douglas 2008b), and transfers of scent between individuals. Douglas (2001b) speculated that the scent of the Crested Auklets acts to deter ectoparasites. Subsequent studies focusing on this role of the scent (Table 4.1) can be separated into those that used natural source Crested Auklet feather odour, and those that used a mixture of synthetic chemicals (available from commercial suppliers). These laboratory studies have focused on the two primary ectoparasites of auklets (ticks; lice) and have equivocal results (Table 4.1). Studies with natural presentation of scent did not reveal deterrence, but when synthetic chemicals were used (some with concentrations above natural levels), some results were consistent with the function of the scent as an ectoparasite repellent. Accordingly, I set out to perform more tests of the ectoparasite deterrence hypothesis with field experiments. I will: 1) test for a relationship between naturally occurring scent levels and ectoparasite prevalence on free-living Crested Auklets as predicted by the anti-parasite hypothesis; and 2) determine if a simulated odour treatment with the main components of Crested Auklet scent deterred questing ticks *(Ixodes uriae)*.

4.2 Methods

4.2.1 Study Location

Fieldwork was carried out at a colony of more than 100,000 Crested, Least other auklets at Main Talus, Buldir Island, Aleutian Islands, Alaska (52°2'N 175°5'E; Byrd & Day, 1986) during early June to late August of 2009 and 2010.

4.2.2 Capture and measurement of adults

Adult Crested Auklets were captured during the morning activity period 900-1300HADT (Hawaiian Aleutian daylight-savings Time: GMT-9:00) using noose carpets set on the colony surface. Birds were placed in a washed cloth bag to reduce stress and contamination of previously caught birds. Birds were processed in the order of capture. An individual that displayed any apparent distress (hot feet, open bill breathing) was immediately released. Each captured auklet was given a numbered US FWS stainless steel leg band, and was assigned a unique combination of three Darvik plastic colour bands.

Damage to the webbing between the toes was scored for each bird, with a scale of 0-2: 0- both feet undamaged; 1- one small hole in either foot, 2- multiple holes or tears in the webbing). These were old healed injuries that are acquired at the nestling stage when ticks attach to the chick's soft webbing (Hoberg & Wehle 1982; Morbey 1996).

Before bird were measured or sampled for parasites, I assessed their odour by smelling the nape for 5 seconds (Brattoli et al. 2011; Craven et al. 1996; Peris & Escuder-Gilabert 2009). Scent was quantified on a discrete scale of 0 to 3 (0 being unscented and 3 being highly scented).

4.2.3 Quantification of ectoparasite prevalence and intensity

Birds were visually inspected and palpated for attached and non-attached ticks from head to toe for 5 minutes (Clayton & Walther 1997). The feet and area around the eyes were visually inspected. The life stage (larval, nymph, and female adult), location of each tick was noted.

Birds were dust-ruffled (Walther and Clayton 1997) using dog flea powder (Sergeant's® tick and flea power for dogs, Carbaryl 5.0%, Pyrethrins 0.1%, Piperonyl Butoxide 1.0%) to collect lice. Birds were held over a clear plastic Ziplock® bag with powder applied evenly across the body following the procedure described by Walther and Clayton (1997). Powder was massaged into the feathers to ensure that the insecticide reached the bird's skin for five minutes. The first minute was used to distribute the powder over the bird, while the four minutes were spent ruffling the powder. The Ziplock® with powder and lice were visually inspected in the lab using a dissecting microscope so that all lice could be removed and placed in 70% ethanol for later identification. Lice have previously been collected from Buldir Island and identified to species (Table 3.1). For the purpose of this study, the level of louse prevalence was a measure by the count of individuals detected, regardless of species. Previous work indicates the taxa of lice present on Crested Auklets at Buldir are *Austromenopon nigropleurum*, *Quadraceps aethereus*, and *Saemundssonia wumisuzume* (Chapter 3).

4.2.4 Odour and tick questing experiment

To test whether questing ticks are deterred by chemicals I deployed a modification of a standard 'flagging technique' (Falco & Fish 1992), commonly used to collect ticks from the surrounding environment. I used two 1 m^2 (1.2m x 0.83m) cotton sheets, with a 1.5 cm diameter hardwood dowel supporting one side and weights applied to the opposite side to sample questing ticks. The sheets were placed on rocks throughout the colony and flipped over every minute for 30 minutes. Ticks were removed from the sheet with forceps, placed in 70% ethanol and later identified. Ticks were quantified as ticks per hour caught. Two treatments were used 1) control, the sheet was stored in a sealed container and so could not pick up the scent of auklets from any source and 2) experimental, sheet was stored in a container that had volatizing synthetic Crested Auklet scent. I restricted my experiment to a single treatment and a single control because I anticipated that few days would be suitable for sheet presentations due to the frequency of precipitation and water-soaked ground at Buldir. The scent treatment consisted of the two major components of the scent Z-4-decenal and octanal in a 1:3 ratio, the same chemicals used by Hagelin et al. (2003; presented 1:1) and Jones et al. (2004; presented 1:2) but in a ratio dominated more by octanal to replicate natural conditions as closely as possible (Douglas et al. 2004; Hagelin et al. 2003). To dose the sheet with an odour concentration similar to that emitted by wild birds I placed one drop of mixture onto a cotton ball housed inside the container 3-5 days before flagging. The container had a total volume of 2.5 L allowing the scent to reach the entire sheet. One drop contained 50 μl of mixture. Based on the density of octanal at 0.84 g/mL, sheets were exposed to 31.6 μg of octanal. An average Crested Auklet has a total feather mass of 11.9 g (Hagelin 2007a) and past estimates indicated that feathers of living wild birds have a mean of 2.98 μg of octanal per gram of feather mass (Hagelin et al. 2003). Based on these measurements an auklet would emit about 35.6 μg of octanal for its entire mass which is similar to the levels used in my experiment. At the same time two people each with one sheet walked through the colony placing a sheet on rocks and low vegetation. Sheets were never pulled through vegetation when it was raining or when the ground was water-soaked.

4.2.5 Analysis

All statistics were conducted in SPSS (version 19) and Quantitative Parasitology (Reiczigel & Rózsa 2005). Prevalence and mean intensity of tick infestation are reported with 95% confidence limits. Prevalence is the number of individual birds with one or more parasite, and mean intensity is the mean number of parasites on individuals that are have at least one parasite (Bush et al. 1997; Rózsa et al. 2000). Mean scent level is reported with 95% confidence limits. I used prevalence of lice, ticks and foot web damage as my scores of ectoparasites on individuals. I calculated day as the day number from January 1 of the respective year. These measures were related to the smell score with day and year of capture as covariates using a MANOVA. For the experiment, the number of ticks found on each sheet was related to treatment, and date of trial using a generalized linear model with a loglinear link function and a Poisson error structure.

4.3 Results

4.3.1 Tick and louse prevalence and their relation to odour

I captured individual Crested Auklets during the periods 3 June – 27 July 2009 and 2 June - 19 July 2010. Odour varied greatly across individuals, with scent score 2 individuals being the most frequent and large numbers of individuals scoring in all other categories (Table 4.2). The prevalence of ticks was 4.7% (2.4-8.2%, 95%CL) and prevalence of lice was 10.6% (7.1-15.2%, 95%CL). The mean intensity on birds that had at least one ectoparasite was 1.18 (1.00-1.36, 95%CL) and 1.20 (1.00-1.68, 95%CL) for ticks and lice, respectively. Neither the count of ticks nor count of lice found related to scent level (Table 4.3). All biologically relevant interaction terms were included, but removed from subsequent analysis when effect was not significant. Sex was removed from the analysis as there was not effect or interaction with scent and all previous studies have not reported a difference (Douglas 2006a; Hagelin et al. 2003).

4.3.2 Odour and tick questing experiment

I presented the scented and control sheets on 7 days (c. 3.5 hours of presentations) during the period 12 June – 28 July 2010. In the dragging experiment 2.73x more ticks were collected on (i.e., attached to) the unscented sheet than the scented sheet (scented=9.3±5.3, unscented=25.3±16.7, one standard deviation; χ^2=47.709, df=1, 11, p<0.001). The number of ticks collected was not related to date of season (χ^2=0.029, df=1, 11, p=0.864).

4.4 Discussion

I found no relationship between ectoparasite levels and natural scent levels on Crested Auklets. Conversely when scent levels were manipulated ticks were less likely to climb on to scented flagging cloths than unscented cloths suggesting a link between scent and tick behaviour. These results follow the pattern observed in many of the past studies (e.g., Douglas et al. 2001b; Hagelin et al. 2003; Douglas 2008), suggesting that variation at natural levels are too low to see the effect but with experimental manipulations there is an effect. It is important in scent presentation experiments is the concentration of odour presented to ectoparasites – if the odour concentration is higher than that expressed in nature on wild Crested Auklets, then any inference of repellency function is questionable. I believe my odour presentation was realistic because the sheet was dragged across Crested Auklet display rocks at a colony site during the breeding season when birds were present, and the dosed sheets emitted similar levels of chemical emissions to those found in wild Crested Auklets.

Tick and louse prevalence on Crested Auklet individuals were low, with only 4-10% of individuals having at least one ectoparasite individual detected (Chapter 2 and 3). Crested Auklets are known to have variable infestations of ectoparasites with some past studies failing to find any attached ticks (Engström et al. 2000), while in some years at Buldir, nearly every individual captured had ticks (IL Jones pers. comm.). Low ectoparasite prevalence could be attributed to the scent produced by this species, but closely related species at the same colony site including Least Auklets had similarly low levels during the same breeding seasons (Chapter 2 and 3). Low parasite levels require a large sample size to attain enough statistical power for a robust analysis and disentangle the other factors that are known to influence parasite levels including but not limited to interannual variability (T. Boulinier pers. comm.; Chapters 2 and 3) and climatic factors (Oorebeek & Kleindorfer 2008), limiting my ability to make strong inferences in this study.

Another issue concerns whether lice found on auklets are deleterious to the birds (i.e., whether they are in fact parasites as opposed to mere commensals). In a review of ectoparasites of the Alcidae, Muzaffar and Jones (2004) found no published evidence that lice (*Austromenopon* sp., *Quadraceps* sp., or *Saemundssonia* sp.) cause harmful effects. Because they feed on dead skin and feather particles, lice may perform a beneficial function, in which case it would not be expected that Crested Auklets would have chemical emissions adapted to repel them. In contrast, deleterious effects of *Ixodes* ticks on auks (both adults and nestlings) are widely known. Further research is required concerning health effects of bird lice on auklets and other seabird species to clarify this issue.

My method of scent quantification (Brattoli et al. 2011; Craven M.A. et al. 1996; Peris & Escuder-Gilabert 2009) was basic and allowed large numbers of individuals to be quickly assessed, but did not quantify the chemical components analytically using laboratory instruments. Scent is complicated, with each observer experiencing it differently, but my approach allowed all chemical components to be addressed. The disadvantage of chemical analyses previously used (Douglas et al. 2001a; Douglas 2006a; Hagelin et al. 2003) is that one is limited to quantifying a small subset of chemical components due to logistical constraints. I was able to qualify the scent addressing more components than measuring a single chemical component, e.g. octanal (Brattoli et al. 2011; Craven M.A. et al. 1996; Peris & Escuder-Gilabert 2009). This approach is limited in that year-to-year variation in criteria cannot be tested for, and it was unfortunate that I did not have the resources to compare my technique to a chemical analysis. As a result I used a 4-category scale to reduce the influences of these constraints. I do believe that this technique was robust, as human observers are commonly used in scent analyses (Brattoli et al. 2011; Craven et al. 1996; Peris & Escuder-Gilabert 2009).

The chemical components did reduce the number of questing tick collected on the experimental flagging sheets. This supports past results that the two primary chemical components do act as a defence against ticks (Douglas et al. 2001b; Douglas 2008b, 2006a). Though compelling these results are difficult to compare to natural circumstances with absolute certainty. Odours are not necessarily the sum of their parts, with the entire scent having to be considered – therefore I recommend that further attempts be made in future studies of wild birds. The most crucial further research on relationships between Crested Auklet ectoparasites and the tangerine odour would ideally take place at a colony site and in a year with high numbers of *Ixodes* ticks present. Ticks were relatively rare at Main Talus, Buldir Island in 2009 and 2010 (IL Jones pers. comm.), hampering my ability to make inferences.

4.4.1 Conclusion

Past studies have failed to find relationships between parasites and scent at natural levels acting as a defence mechanism (Douglas et al. 2005b; Hagelin et al. 2003; Hagelin 2007a). My results support the patterns found in past studies that at naturally occurring levels, with parasites at low levels, the scent produced by Crested Auklets does not act as a defence against ectoparasites. It also fits with past results that when scent is experimentally manipulated parasite levels are reduced, activity reduced, and morbidity increased. It is important to look at scent levels at natural occurring levels, with realistic environmental conditions (humidity, temperatures, wind, etc.) and understanding naturally occurring parasite levels. It will be necessary to establish natural relationships in conjunction with experimental manipulations before any conclusions can be made about whether Crested Auklet scent does act to deter parasites, or most specifically ticks.

4.5 Summary

1. Number of ticks, lice, or foot web damage was not related to the strength of scent on Crested Auklets.
2. More ticks were collected on unscented sheets than sheets with the two major components of the Crested Auklet scent, Z-4-decenal and Octanal in a dragging experiment in the breeding colony.

Table 4.1. Summary of published experimental and observational laboratory studies examining the function of Crested Auklet scent as an ectoparasite repellent. Studies are organized by parasite taxon studied, how the scent was presented, and if the study replicated natural odour emission intensity. N=natural; S=synthetic; O=observational study; E=experimental study; Yes=effect; No=no effect.

Ref.	Parasite species	Scent	Study	Results
1	_Ixodes uriae_	N	O	No. Small sample size
2	_I. uriae_	N	E	No.
3	_Amblyomma americanum_*	S**	E	Yes. Tick mobility reduced
4	_A. americanum_*	S**	E	Yes. Reduced time of attachment to artificial host
4	_I. uriae_	S**	E	Yes. Reduced time of attachment to artificial host
4	_I. uriae_	S**	E	Yes. Increased nymph and adult mortality
5	_Quadraceps aethereus_	N	O	Yes. More lice on Crested Auklets
5	_Saemundssonia wumisuzume, S. boschi, Austromenopon nigropleurum_	N	O	No. Louse prevalence similar within genus between Least and Crested Auklets
5	_Columbicola columbae_*, _Campanulotes bidentatus_*	N	E	No.
5	_Co.columbae_*, _Ca.bidentatus_*	N	E	No.
4	_Q. aethereus, Au.nigropleurum_	S**	E	Yes. Increased nymph and adult mortality
6	_Aedes aegypti_*	S	E	Yes. Reduced chances of landing on host

*Species not found within the range/habitat of Crested Auklets
**Odour concentration likely higher than that found naturally on Crested Auklet feathers

1-Douglas 2006a; 2-Hagelin 2007a; 3-Douglas 2008b; 4-Douglas et al. 2004; 5-Douglas et al. 2005b;6- Douglas et al. 2005a

Table 4.2. Most Crested Auklets (*Aethia cristatella*) caught on Buldir Island in 2009 and 2010 during the breeding season had no ticks or lice. Frequency of individuals with a scent (0- no noticeable scent; 1- lightly scented; 2- medium scent; and 3- highly scented) and parasite status (no parasites, just lice, just ticks, and both lice and ticks).

Scent level	Parasite status				
	No parasites	Lice	Ticks	Lice and ticks	**Total**
0	7	0	0	0	**7**
1	15	2	1	1	**19**
2	43	5	2	0	**50**
3	20	2	2	0	**24**
Total	**85**	**9**	**5**	**1**	**100**

Table 4.3 Within 236 Crested Auklets (*Aethia cristatella*) captured on Buldir Island in 2009 and 2010 there was no relationship among intensity of ticks, foot web damage, intensity of lice and the scent. The year and day of capture was included as dependent variables in MANOVA to address variation in body condition and ornament expression between and among breeding seasons.

				Ticks		Web damage		Lice	
	Wilks's λ	F	p	F	p	F	p	F	P
Scent	0.97	0.75	ns	0.96	ns	0.64	ns	0.87	ns
Year	0.97	2.12	ns	0.15	ns	0.39	ns	5.62	0.02
Day	0.99	0.25	ns	0.12	ns	0.01	ns	0.57	ns

Chapter 5

General Discussion

In recent years there has been a debate regarding the function of the citrus-like odour produced by Crested Auklets (*Aethia cristatella*). A number of adaptive functions have been proposed but the two that have received the most attention are intraspecific communication and chemical defence (Hagelin and Jones 2007). Jones et al. (2004) has provided evidence that this scent plays a social role, whereas Douglas et al. (2004) suggest that it acts to repel ectoparasites. These two hypotheses are not necessarily mutually exclusive.

I addressed the question: does this odour act as a chemical defence against ectoparasites and what effect do these parasites have on the birds? Before directly addressing the hypothesis it is important look at the relationship between ectoparasites and Crested Auklets. There must be negative impacts from ectoparasites for this likely energetically expensive scent to be worth producing if it simply protects these birds. In addition relationships between the intensity and body condition or ornament expression, which are related to quality can highlight the biological importance of these parasites.

I have demonstrated several points:

a) Within both Least and Crested Auklets the prevalence and mean intensity of tick were low. These intensities were not related to body condition or ornament expression in either species suggesting that they may not be biologically important to quality low levels.

b) In Whiskered, Least, and Crested Auklets there was no relationship between foot web damage and body condition or ornament expression. This further suggests that the levels of tick parasitism as a chick may not be related to adult health.

c) Louse prevalence in Least and Crested Auklets was low and mean intensity was also low. The intensity observed was not related to body condition or ornament expression suggesting that lice intensities observed in 2009 and 2010 on Buldir Island.

d) There was no relationship between ectoparasite levels and natural scent levels, but ticks are less likely to climb on to scented objects than unscented. The lack of naturally occurring relationship suggests that despite the fact that ticks may be repelled by the chemical components of the Crested Auklet scent, it may not be biologically important when ticks are in low abundance.

Literature examining the impacts of ectoparasites on the condition of individuals is quickly growing. Due to the fascinating nature of ectoparasites and interesting ecology of both host and parasite it is often difficult to determine when a relationship exists between their population level on a host and measures of condition. My findings add to the wealth of knowledge, demonstrating low levels of parasitism had no apparent negative effects on adult Least, Crested, and Whiskered Auklets.

Past studies have failed to find relationships between parasites and scent acting as a defence mechanism (Douglas et al. 2005b; Hagelin et al. 2003; Hagelin 2007a), and I believe that my results support the trend that at naturally occurring levels, with parasites at low levels, the scent produced by Crested Auklets does not act as a defence against ectoparasites. It is important that we have natural relationships in conjunction with experimental manipulations before any conclusions can be made about whether Crested Auklet scent does act to deter parasites, or most specifically ticks.

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Appendix I- Tick Prevalence in Alcids

Review of all available tick prevalence data from the literature for Alcids. Multiple entries from the same resource represent multiple colonies that were independently reported within source.

Host	Prevalence	Reference
Common Murre (*Uria aalge)*	1%	Barton 1996
	14%	Muzaffar 2000
	28%	Choe & Kim 1987a
	29%	Wanless et al. 1997
	54%	Eveleigh & Threlfall 1975
	97%	Choe & Kim 1987a
Thick-billed Murre (*Uria lomvia*)	2%	Coulson et al. 2009
	21%	Muzaffar 2000
	50%	Choe & Kim 1987a
	97%	Choe & Kim 1987a
Razorbill (*Alca torda*)	0%	Wanless et al. 1997
	6%	Muzaffar 2000
	8%	Barton 1996
	67%	Eveleigh & Threlfall 1975
Crested Auklet (*Aethia cristatella*)	0%	Engström et al. 2000
	2%	Douglas 2006a
Atlantic Puffin (*Fratercula arctica*)	5%	Barton 1996
	13%	Muzaffar 2000
	18%	Eveleigh & Threlfall 1975

Appendix II- Lice prevalence in Alcids

All available lice prevalence data from the literature for Alcides. Multiple entries from the same resource represent multiple colonies that were independently reported or different species of ticks that were broken down and not reported pooled.

Host	Prevalence	Reference
Common Murre (*Uria aalge)*	7%	Muzaffar 2000
	21%	Muzaffar 2000
	24%	Muzaffar 2000
	72%	Choe & Kim 1987b
	82%	Eveleigh & Threlfall 1976
	100%	Choe & Kim 1987b
Thick-billed Murre (*Uria lomvia*)	10%	Muzaffar 2000
	13%	Choe & Kim 1987b
	17%	Muzaffar 2000
	24%	Muzaffar 2000
	63%	Choe & Kim 1987b
	75%	Choe & Kim 1987b
	85%	Eveleigh & Threlfall 1976
Dovkie (*Alle alle*)	100%	Eveleigh & Threlfall 1976
Razorbill (*Alca torda*)	17%	Muzaffar 2000
	22%	Muzaffar 2000
	28%	Muzaffar 2000
	75%	Eveleigh & Threlfall 1976
Black Guillemot (*Cepphus grille*)	50%	Eveleigh & Threlfall 1976
Crested Auklet (*Aethia cristatella*)	4%	Douglas 2006a
Atlantic Puffin (*Fratercula arctica*)	3%	Muzaffar 2000
	17%	Muzaffar 2000
	33%	Muzaffar 2000
	67%	Eveleigh & Threlfall 1976

Appendix III- Detailed dust ruffling protocol and calculations

HM dust ruffled all birds after measurements were taken. To ensure that tick and flea powder did not contaminate the birds during measurement taking a pair of latex gloves were worn during dust ruffling and removed once birds were released. Gloves were reused but visually inspected between individuals to ensure no cross contamination.

Birds were held over a 1 gallon Ziplock® bag. The premeasured amount of powder (Sergeant's® tick and flea power for dogs, Carbaryl 5.0%, Pyrethrins 0.1%, Piparony Butoxide 1.0%) was thoroughly distributed over the surface of the bird's body within the first 20 seconds. Special care was made around the face to get powder as close to the eyes and mouth without getting any in the birds face. HM massaged powder to the base of the feathers. Each bird was continuously ruffled over the Ziplock® bag for 3 or 5 minutes depending on species. The first minute was used to distribute the powder over the bird, while the next two or four minutes were spent ruffling the powder. It took the same time to distribute the powder for both species.

While birds were being massaged with powder I inspected birds for attached ticks. Areas around the face, legs, and brood patch were visually inspected. Like many seabirds, auklets have dense plumage so the rest of the surface area was palpated for attached ticks.

If a bird defecated in the bag, no attempt was made to remove it on the off-chance that parasites became associated with it.

Crested Auklets have a surface area ratio relative to Least Auklets of 2.1:1 (see calculations below) based on the relationship between mass and surface area by Walsberg & King (1978). To accommodate for this the amount of powder applied to each individual differed based on species. The length of time spent ruffling differed as it would take less time to evenly distribute powder on a smaller bird and massage the powder into the feather.

Calculations for surface area

Equation for surface area
$h=10\ M^{0.667}$ (Walsberg & King 1978)
Symbols in equation
M=mass
h=surface area

Crested Auklets
M=243g (Jones 1993b)

$h=10\ (243)^{2/3}$
$h=390cm^2$

Least Auklets
M=81.4g (Jones 1993a)

$h=10\ (81.4)^{2/3}$
$h=180\ cm^2$

Ratio of Crested Auklet surface area to Least Auklet surface area

Ratio=area of Crested Auklet/area of Least Auklet
Ratio=$390\ cm^2/180\ cm^2$
Ratio=2.07

Appendix IV

Raw data of all Crested Auklets (*Aethia cristatella)* caught during the breeding season in 2009 and 2010. All louse specimens are mounted and ID by Ricardo Palma of Museum of New Zealand Te Papa Tongarewa. Day= numeric date from 1 January of the respective year; Yr= year; Snt= scent level on a scale of 0-4 (0- no noticeable scent; 1- lightly scented; 2- medium scent; and 3- highly scented); A= adult; S= sub-adult; U= unknown sex; F= female; M= male; Rictal=rictal plate height; Crest= maximum crest length;Web= score of 0-2(0-no holes in either foot web;1- individuals had a single circular hole in either foot web; and 2- had greater than one hole); Tick= number of *Ixodes uriea*; Lice-Q is the number of *Quadraceps aethereus*; L-S= number of *Saemundssonia wumisuzume*; Lice-A= number of *Austromenopon nigropleurum*.

								Auricular plume length								
Day	Yr	Snt	Age	Sex	Mass	Rictal	Crest	Left	Right	Mean	Wing	Web	Tick	Lice-Q	Lice-S	Lice-A
153	09	1	A	U	263	5.5	30.2	28.3	25.4	26.85	141	0	3	0	0	0
183	10	3	A	F	259	.	31.9	24.2	25.5	24.85	135	0	2	0	0	0
195	10	1	A	F	242	0	48.5	28	28	28	143	0	2	0	0	0
167	09	2	A	M	255	6.1	38	28.3	27.5	27.9	137	0	1	6	4	0
161	09	2	A	M	267	3.6	38.1	24.5	29.1	26.8	143	1	1	4	0	0
178	09	1	A	M	279	4.2	50.2	28.7	29.6	29.15	139	0	1	2	1	1
167	09	2	A	F	246	5.2	36.6	24.5	28.5	26.5	138	0	1	1	0	0
201	09	.	A	F	226	3.5	45.6	31	33.5	32.25	145	0	1	0	0	1
164	09	2	A	F	245	5	35.6	26.1	27.5	26.8	137	0	1	0	0	0
178	09	1	A	U	249	4.5	43.7	26.7	28.6	27.65	132	1	1	0	0	0
157	10	2	A	M	266	6.5	39	29.6	30	29.8	149	0	1	0	0	0
167	10	2	A	M	206	5.3	37.4	24.7	19.5	22.1	141	0	1	0	0	0
167	10	3	A	M	283	7.4	40.3	21.4	26.4	23.9	143	0	1	0	0	0

								Auricular plume length								
Day	Yr	Snt	Age	Sex	Mass	Rictal	Crest	Left	Right	Mean	Wing	Web	Tick	Lice-Q	Lice-S	Lice-A
183	10	2	A	F	262	4.7	36	24.6	27.5	26.05	138	0	1	0	0	0
191	10	3	A	F	242	3.9	46.5	29.2	31.6	30.4	142	0	1	0	0	0
195	10	2	A	F	261	3.8	52.6	30	29.4	29.7	141	0	1	0	0	0
195	10	3	A	F	270	2.9	36	23.2	23.4	23.3	144	0	1	0	0	0
161	09	1	A	M	257	5.5	37.6	24	22	23	146	0	0	3	0	0
164	09	2	A	F	274	5	43.1	26	29.9	27.95	143	0	0	3	0	0
167	09	3	A	M	251	6.2	38.5	30.9	31.9	31.4	142	0	0	2	0	1
159	09	2	A	U	260	6.1	28.4	35.2	35.6	35.4	140	1	0	2	0	0
164	09	2	A	U	270	5.6	41.4	27.8	33.7	30.75	146	0	0	2	0	0
174	09	.	A	M	271	5.7	44.6	28.4	30.3	29.35	145	1	0	2	0	0
188	09	1	A	F	231	4.6	32.4	23	27.6	25.3	140	0	0	2	0	0
159	09	2	A	M	269	5.7	36.4	27.6	30	28.8	145	1	0	1	0	0
161	09	2	A	F	247	5.2	32.2	31.6	35	33.3	143	0	0	1	0	0
164	09	3	S	U	246	4.3	24.5	21.5	22.3	21.9	140	0	0	1	0	0
164	09	3	A	U	254	5.8	26.4	30.5	32	31.25	140	0	0	1	0	0
164	09	2	A	U	264	5.6	41.5	32.1	32.5	32.3	147	2	0	1	0	0
164	09	1	S	U	236	4.5	23	24.8	27.2	26	144	0	0	1	0	0
167	09	2	A	M	290	6	26.4	28.4	29.2	28.8	144	0	0	1	0	0
167	09	2	A	F	.	5.7	45.5	27.5	25.2	26.35	141	0	0	1	0	0
170	09	2	A	M	282	4.8	37.6	28.6	28.3	28.45	142	0	0	1	0	0
170	09	2	A	U	265	5	40.9	27.5	31.2	29.35	140	0	0	1	0	0
174	09	.	A	U	238	5	43	26.8	28.1	27.45	143	0	0	1	0	0
174	09	.	A	U	246	4.7	32.4	21.4	23.2	22.3	141	0	0	1	0	0

								Auricular plume length								
Day	Yr	Snt	Age	Sex	Mass	Rictal	Crest	Left	Right	Mean	Wing	Web	Tick	Lice-Q	Lice-S	Lice-A
174	09	.	A	F	223	5.3	43	27.6	28.9	28.25	137	0	0	1	0	0
174	09	.	A	F	245	5.7	42.2	29.9	30.5	30.2	142	1	0	1	0	0
182	09	2	A	M	240	5.4	47.9	22.8	21.2	22	142	0	0	1	0	0
152	10	2	A	M	253	6.1	39.6	26.4	23.8	25.1	142	0	0	1	0	0
157	10	2	A	M	259	5.6	51.4	27.9	29.5	28.7	143	2	0	1	0	0
164	10	2	A	F	265	4	47.9	28.4	31.9	30.15	143	0	0	1	0	0
175	10	3	A	M	266	4	42.1	26.4	28.3	27.35	143	0	0	1	0	0
175	10	2	A	F	264	3.2	41.1	28.1	20.6	24.35	142	0	0	1	0	0
183	10	3	A	F	257	3.6	41.8	23.6	24.8	24.2	141	1	0	1	0	0
188	10	1	A	M	267	5.1	52.8	23.2	26.2	24.7	143	0	0	1	0	0
188	10	3	A	F	249	3.6	37.6	6.9	11.1	9	141	0	0	1	0	0
191	10	1	A	F	253	3.8	41.7	19.4	20.6	20	144	0	0	1	0	0
193	10	1	A	M	237	3.6	40.3	23.7	26.7	25.2	136	0	0	1	0	0
193	10	2	A	M	246	4.7	40.1	23.1	26.1	24.6	141	0	0	1	0	0
195	10	2	A	M	273	6	47.1	35	36.6	35.8	141	0	0	1	0	0
195	10	0	A	M	273	5.8	55	27.9	24	25.95	145	0	0	1	0	0
161	09	2	A	M	229	5.4	33.8	34.5	33.4	33.95	134	0	0	0	1	3
193	10	2	A	F	270	4.6	41.4	31.2	28.7	29.95	142	0	0	0	1	0
159	09	3	A	M	263	5.4	37	27.5	28.2	27.85	143	2	0	0	0	1
161	09	1	A	U	266	4.2	36	26.5	30	28.25	138	2	0	0	0	1
161	09	1	A	M	269	6	32.5	26.4	26.8	26.6	144	0	0	0	0	1
164	09	3	A	M	278	6.4	42.4	34	36.6	35.3	145	0	0	0	0	1
164	09	3	A	M	254	6.2	45.8	32	34	33	144	2	0	0	0	1

								Auricular plume length								
Day	Yr	Snt	Age	Sex	Mass	Rictal	Crest	Left	Right	Mean	Wing	Web	Tick	Lice-Q	Lice-S	Lice-A
157	10	3	A	F	240	5.4	30.4	23.6	25.8	24.7	136	0	0	0	0	1
188	10	1	A	M	234	3.8	40	27.9	32.3	30.1	143	0	0	0	0	1
153	09	.	A	F	252	5.2	35.7	29.2	29.2	29.2	137	1	0	0	0	0
153	09	.	A	F	250	5.6	41.9	29.4	30.8	30.1	144	1	0	0	0	0
153	09	0	A	F	235	5	38.1	29.7	28	28.85	140	0	0	0	0	0
153	09	1	A	M	274	6.8	35	24.1	26.4	25.25	136	0	0	0	0	0
153	09	3	A	M	262	4.4	33.6	30.5	31	30.75	139	0	0	0	0	0
153	09	3	A	M	254	5.5	40.2	22.6	20.6	21.6	137	0	0	0	0	0
153	09	3	A	U	272	5	34.8	27.6	27.6	27.6	144	0	0	0	0	0
153	09	3	A	M	274	6.6	35.6	25	25.1	25.05	142	0	0	0	0	0
156	09	2	A	F	273	4.9	34.9	27.9	27.3	27.6	140	0	0	0	0	0
156	09	2	A	U	260	6	41	26.6	24	25.3	141	0	0	0	0	0
159	09	3	A	U	230	3.2	26.2	23.5	25	24.25	134	0	0	0	0	0
159	09	2	A	F	257	4.7	37.3	27	27.8	27.4	147	1	0	0	0	0
159	09	2	A	F	227	4.4	40.6	29	33	31	136	1	0	0	0	0
161	09	2	A	F	252	4.8	43.9	27.2	28.4	27.8	142	2	0	0	0	0
161	09	2	A	M	255	5.4	46.5	27.8	28.4	28.1	144	1	0	0	0	0
161	09	2	A	M	270	4.9	32.2	22.1	25.6	23.85	142	1	0	0	0	0
161	09	2	A	M	263	5	48.1	31.9	33.2	32.55	145	0	0	0	0	0
161	09	3	A	M	295	5.8	36.1	27.4	27.6	27.5	143	0	0	0	0	0
161	09	1	A	F	261	6.3	50.2	28.5	26	27.25	145	0	0	0	0	0
161	09	2	A	F	257	5.8	34.7	20.7	22.1	21.4	138	0	0	0	0	0
161	09	1	A	M	289	7.6	42	30.9	25.6	28.25	143	0	0	0	0	0

								Auricular plume length								
Day	Yr	Snt	Age	Sex	Mass	Rictal	Crest	Left	Right	Mean	Wing	Web	Tick	Lice-Q	Lice-S	Lice-A
164	09	2	A	F	279	4.6	35.2	24.5	26.9	25.7	141	0	0	0	0	0
164	09	2	A	F	268	5.7	42.3	19.3	18.2	18.75	143	0	0	0	0	0
164	09	3	A	M	251	5	37.4	25.1	26.6	25.85	136	1	0	0	0	0
164	09	1	A	M	250	5.6	40.8	27.4	28.6	28	140	0	0	0	0	0
164	09	3	A	M	263	6.5	9.6	28.8	30.5	29.65	148	0	0	0	0	0
167	09	3	A	M	268	5.3	39.1	29	30.2	29.6	145	0	0	0	0	0
167	09	1	A	F	237	4.6	41.6	24.5	26.4	25.45	140	0	0	0	0	0
167	09	2	A	F	225	5.9	46.7	24.7	23.5	24.1	139	0	0	0	0	0
170	09	0	A	F	229	4.6	34.8	22.4	26.6	24.5	143	0	0	0	0	0
170	09	0	A	U	256	5.2	45.1	26.9	23.9	25.4	144	0	0	0	0	0
170	09	2	A	M	267	6.1	39.6	29.2	28.4	28.8	144	0	0	0	0	0
170	09	2	A	U	279	5.7	37.4	29.2	28.7	28.95	137	0	0	0	0	0
170	09	3	A	U	264	6.9	34.7	27.2	29.3	28.25	142	0	0	0	0	0
174	09	.	A	U	256	3.6	41.1	34.6	34.3	34.45	143	2	0	0	0	0
174	09	.	A	M	263	5	43.7	28.5	26.1	27.3	143	0	0	0	0	0
174	09	.	A	M	258	5.4	44	22.9	24.8	23.85	145	1	0	0	0	0
174	09	.	A	F	243	5.2	47.6	28.5	32.7	30.6	144	0	0	0	0	0
174	09	.	A	M	224	5.4	49.3	22.6	22.3	22.45	136	0	0	0	0	0
174	09	.	A	U	242	4	44.3	27	26.5	26.75	138	0	0	0	0	0
174	09	.	A	M	238	6.1	42.8	32	34.4	33.2	141	0	0	0	0	0
174	09	.	A	U	251	5.1	32.1	27.8	33.1	30.45	146	0	0	0	0	0
178	09	1	A	M	287	0	48.5	25.8	26.7	14.8	148	0	0	0	0	0
178	09	.	A	U	278	.	.	.	.	.	.	.	0	0	0	0

Day	Yr	Snt	Age	Sex	Mass	Rictal	Crest	Auricular plume length Left	Right	Mean	Wing	Web	Tick	Lice-Q	Lice-S	Lice-A
178	09	1	A	U	272	.	.	.	.	.	.	.	0	0	0	0
182	09	2	A	M	256	3.7	41.9	26.9	32.5	29.7	143	1	0	0	0	0
182	09	0	A	U	259	4.3	29.4	23.9	25.3	24.6	142	0	0	0	0	0
182	09	1	A	F	243	2.8	33.1	23.5	29.2	26.35	134	0	0	0	0	0
182	09	1	A	M	246	4.7	47.4	28.1	24.3	26.2	140	0	0	0	0	0
185	09	.	A	U	226	4.9	39	28.8	30.8	29.8	143	0	0	0	0	0
185	09	.	A	F	240	3.1	32.5	28.2	29.4	28.8	136	0	0	0	0	0
185	09	.	A	M	246	4.6	41.2	14.2	19.1	16.65	138	0	0	0	0	0
185	09	.	A	M	257	5	45.8	24.5	26.2	25.35	158	0	0	0	0	0
185	09	.	A	M	246	4.8	34.5	28.6	30.8	29.7	145	0	0	0	0	0
185	09	.	A	M	254	6.5	45.7	22.5	23.6	23.05	143	0	0	0	0	0
185	09	.	A	M	239	3.4	37.9	19.5	19.8	19.65	145	0	0	0	0	0
188	09	3	A	M	234	3.1	33.1	29.9	29.1	29.5	141	0	0	0	0	0
188	09	2	A	M	246	4.9	39.4	29.2	31.1	30.15	144	0	0	0	0	0
188	09	1	A	M	265	4.5	30.7	20.6	25.9	23.25	140	0	0	0	0	0
188	09	1	A	M	255	4	35.9	22.5	23.2	22.85	140	0	0	0	0	0
188	09	1	A	M	272	5.4	40.9	23.7	24	23.85	145	0	0	0	0	0
188	09	1	A	U	338	3.1	48.5	26.8	30.9	28.85	146	0	0	0	0	0
188	09	1	A	F	252	0	34.4	19.6	20	19.8	141	2	0	0	0	0
188	09	2	A	F	251	3.7	43.2	30.5	28.8	29.65	141	0	0	0	0	0
188	09	2	A	F	255	4.3	43.6	27.3	23.2	25.25	143	0	0	0	0	0
188	09	2	A	F	257	3.9	44.9	30.7	25.5	28.1	140	1	0	0	0	0
188	09	1	A	M	256	4.5	39.9	28.5	27.9	28.2	131	0	0	0	0	0

Day	Yr	Snt	Age	Sex	Mass	Rictal	Crest	Auricular plume length Left	Right	Mean	Wing	Web	Tick	Lice-Q	Lice-S	Lice-A
192	09	3	A	U	241	3.6	42.1	21.4	20.9	21.15	145	0	0	0	0	0
192	09	2	S	U	258	3	23.7	25	28.2	26.6	141	0	0	0	0	0
192	09	1	A	M	243	2.9	34.5	21.4	21.9	21.65	141	0	0	0	0	0
197	09	3	A	M	276	4.7	48.7	36.5	37.4	36.95	146	0	0	0	0	0
197	09	2	A	M	250	5.1	39.1	33.1	33.2	33.15	137	1	0	0	0	0
197	09	2	A	U	244	0	36.5	31	28.7	29.85	141	0	0	0	0	0
197	09	3	A	F	238	4.2	41.4	26.4	23.8	25.1	134	0	0	0	0	0
197	09	1	A	M	231	0	31.8	30	27	28.5	138	0	0	0	0	0
197	09	2	A	M	245	0	42.2	30.4	33.1	31.75	142	0	0	0	0	0
197	09	2	A	F	235	0	45.5	14.5	17.5	16	143	0	0	0	0	0
201	09	3	A	U	242	na	45.3	22.2	24.7	23.45	140	0	0	0	0	0
201	09	2	A	U	229	3.1	38.2	24.1	25.7	24.9	142	0	0	0	0	0
201	09	2	A	M	257	3.4	49.6	28.4	29.7	29.05	149	0	0	0	0	0
201	09	3	A	M	212	4.4	46.3	34	38.8	36.4	141	0	0	0	0	0
205	09	3	A	M	243	5.7	40.5	22.5	21.7	22.1	143	1	0	0	0	0
205	09	2	A	M	254	4.4	39.4	33.8	26.3	30.05	143	0	0	0	0	0
152	10	2	A	M	263	5	47.1	30.4	28.6	29.5	141	0	0	0	0	0
152	10	2	A	F	238	5.2	39.1	18.8	15.2	17	142	0	0	0	0	0
152	10	3	A	M	281	6.2	44.5	29.1	27	28.05	145	0	0	0	0	0
152	10	2	A	F	242	5.5	41.6	24.8	28.2	26.5	139	0	0	0	0	0
154	10	3	A	M	289	5.7	42	33	36.7	34.85	145	0	0	0	0	0
154	10	3	A	M	283	5.5	33.9	29.1	28.5	28.8	142	0	0	0	0	0
154	10	2	A	M	289	6.5	39.6	23.6	20.5	22.05	145	1	0	0	0	0

								Auricular plume length								
Day	Yr	Snt	Age	Sex	Mass	Rictal	Crest	Left	Right	Mean	Wing	Web	Tick	Lice-Q	Lice-S	Lice-A
154	10	2	A	M	274	6.8	49.4	23.3	26.9	25.1	144	0	0	0	0	0
157	10	2	A	F	248	6.6	38.4	23.4	23.6	23.5	144	0	0	0	0	0
157	10	2	A	M	283	6.1	36	12	14	13	146	1	0	0	0	0
157	10	2	A	M	251	6	41.1	23.2	22.6	22.9	142	0	0	0	0	0
157	10	3	A	M	278	5.2	47.1	27.5	26.4	26.95	142	0	0	0	0	0
157	10	2	A	M	252	5	49.5	32	29.7	30.85	141	2	0	0	0	0
157	10	3	A	M	280	6.8	44.5	29.6	27.7	28.65	146	0	0	0	0	0
157	10	2	A	M	265	4.5	38.4	32.9	32.7	32.8	140	0	0	0	0	0
157	10	2	A	M	249	6.5	41.5	25	26.7	25.85	142	1	0	0	0	0
157	10	3	A	M	287	6.1	43.4	30.8	32.1	31.45	149	0	0	0	0	0
157	10	1	A	F	243	4.8	42.1	28	26.8	27.4	139	0	0	0	0	0
160	10	2	A	M	234	5.7	52.1	25.2	31.6	28.4	136	0	0	0	0	0
160	10	3	A	M	294	6.4	36.4	31.1	35.1	33.1	149	0	0	0	0	0
160	10	2	A	F	263	5.9	36	28.2	37.5	32.85	140	0	0	0	0	0
160	10	3	A	M	295	6.3	48.7	32.8	36.6	34.7	147	1	0	0	0	0
160	10	2	A	F	256	5.4	31.9	28.5	28.7	28.6	144	0	0	0	0	0
160	10	2	A	M	289	5.6	47.8	23.2	23.4	23.3	147	0	0	0	0	0
160	10	3	A	M	272	4	50	21.7	24	22.85	146	0	0	0	0	0
160	10	1	S	U	243	4	23.7	14.4	20.1	17.25	141	0	0	0	0	0
164	10	2	A	F	274	5.2	30.7	26.8	25.5	26.15	146	0	0	0	0	0
164	10	2	A	F	272	5.6	47	27.6	28.5	28.05	143	3	0	0	0	0
164	10	2	A	M	259	6.7	33.8	18	20.9	19.45	141	0	0	0	0	0
167	10	2	A	F	265	4.6	47	19.6	16.7	18.15	136	0	0	0	0	0

								Auricular plume length								
Day	Yr	Snt	Age	Sex	Mass	Rictal	Crest	Left	Right	Mean	Wing	Web	Tick	Lice-Q	Lice-S	Lice-A
167	10	2	A	F	305	4	43.5	31.1	32.3	31.7	145	0	0	0	0	0
167	10	2	A	F	285	3.8	42.1	25.1	23.8	24.45	143	0	0	0	0	0
167	10	2	A	M	282	6.8	42.9	21.4	25.6	23.5	144	0	0	0	0	0
167	10	3	A	M	257	6.6	42.9	23.6	21.5	22.55	132	0	0	0	0	0
167	10	3	A	F	243	5.6	44.7	29.5	25.4	27.45	142	0	0	0	0	0
167	10	2	A	M	252	5.4	41.4	20.3	19.6	19.95	139	1	0	0	0	0
167	10	2	A	M	253	5.8	42.6	28.2	28.9	28.55	145	0	0	0	0	0
167	10	3	A	M	250	3.7	32.6	25.1	24.6	24.85	142	0	0	0	0	0
173	10	2	A	F	221	4.1	35.6	22.5	28.2	25.35	141	0	0	0	0	0
173	10	2	A	F	249	5.4	43.4	19	21.4	20.2	141	0	0	0	0	0
173	10	2	A	M	263	5.4	41.6	28.9	29.5	29.2	139	0	0	0	0	0
173	10	1	S	U	230	3.4	26.4	21.4	18	19.7	145	0	0	0	0	0
173	10	2	A	F	300	4.1	43.9	24.9	24	24.45	146	1	0	0	0	0
173	10	2	A	M	296	4.1	41.1	28.4	26	27.2	143	1	0	0	0	0
173	10	3	A	M	245	6.8	38.5	29.4	32.5	30.95	147	0	0	0	0	0
173	10	1	A	M	269	6.3	48.7	27.7	28.5	28.1	151	0	0	0	0	0
173	10	1	S	U	236	3.2	27.7	19.4	22.3	20.85	136	0	0	0	0	0
173	10	0	S	U	237	3	15.1	28	28.7	28.35	139	0	0	0	0	0
173	10	2	A	M	305	7.4	41.6	24.6	34.5	29.55	145	0	0	0	0	0
173	10	2	A	M	271	7.5	36.1	21.1	27.7	24.4	148	0	0	0	0	0
173	10	2	S	U	265	3.5	23.1	22	19	20.5	138	0	0	0	0	0
173	10	2	A	M	271	4.6	41.4	25.5	31.5	28.5	146	1	0	0	0	0
173	10	3	A	M	260	6	50.9	32.9	32	32.45	143	2	0	0	0	0

								Auricular plume length								
Day	Yr	Snt	Age	Sex	Mass	Rictal	Crest	Left	Right	Mean	Wing	Web	Tick	Lice-Q	Lice-S	Lice-A
173	10	1	A	F	265	4.6	41.7	28.1	28.6	28.35	131	0	0	0	0	0
173	10	2	A	F	241	4.7	47	26.9	27.7	27.3	143	0	0	0	0	0
175	10	2	A	F	235	4.5	39.2	32.1	31.9	32	128	0	0	0	0	0
175	10	1	A	M	249	6.4	36.8	24.9	28.6	26.75	146	0	0	0	0	0
175	10	2	A	M	277	3.8	45.3	32.4	31	31.7	146	1	0	0	0	0
175	10	1	A	F	253	6.5	46.9	28.4	23	25.7	147	0	0	0	0	0
175	10	2	A	F	304	3.9	42.5	29.6	32.4	31	148	0	0	0	0	0
175	10	2	A	F	237	5	37.4	20.4	23.1	21.75	145	0	0	0	0	0
175	10	2	A	M	258	6.3	43.7	25.3	25	25.15	143	0	0	0	0	0
175	10	1	A	F	251	4.3	40.7	25.1	31.2	28.15	140	0	0	0	0	0
175	10	3	A	M	258	4.9	42.1	34.9	30.1	32.5	144	0	0	0	0	0
175	10	3	A	F	251	4.5	36.2	22	19.2	20.6	134	0	0	0	0	0
175	10	2	A	F	242	5.6	33.4	23.1	22	22.55	143	0	0	0	0	0
175	10	1	A	F	243	5.7	43.7	19.8	20.7	20.25	146	0	0	0	0	0
175	10	2	A	F	284	6.1	44.6	29.1	29	29.05	145	0	0	0	0	0
175	10	3	A	F	256	4.6	41.9	26.8	27.1	26.95	140	0	0	0	0	0
177	10	3	A	M	264	5	39.8	33.9	33.5	33.7	138	0	0	0	0	0
177	10	2	A	F	269	2.5	28.8	29.8	24.6	27.2	145	0	0	0	0	0
177	10	2	A	M	252	6	46.2	19.6	20.6	20.1	143	0	0	0	0	0
177	10	2	A	F	277	6	40.3	28.6	28.1	28.35	147	0	0	0	0	0
177	10	2	A	M	281	6.5	30.4	20.1	28	24.05	146	0	0	0	0	0
177	10	3	A	M	285	4.9	41.5	36	37.2	36.6	146	0	0	0	0	0
177	10	2	A	F	268	6.1	43.7	17.9	21.1	19.5	142	0	0	0	0	0

								Auricular plume length								
Day	Yr	Snt	Age	Sex	Mass	Rictal	Crest	Left	Right	Mean	Wing	Web	Tick	Lice-Q	Lice-S	Lice-A
177	10	2	A	F	263	3.8	57.2	27.1	21.5	24.3	146	0	0	0	0	0
177	10	2	A	M	266	5.3	37.6	25.7	26.6	26.15	145	2	0	0	0	0
177	10	2	A	F	281	5.2	46	26.3	27.9	27.1	140	0	0	0	0	0
177	10	2	A	F	265	3	44.6	30.9	23.1	27	142	0	0	0	0	0
177	10	2	A	F	268	5.4	35	29.2	29.5	29.35	138	0	0	0	0	0
179	10	2	A	F	260	3.1	34.8	19.1	28.6	23.85	141	1	0	0	0	0
179	10	3	A	F	275	4.7	39.1	18.5	20.1	19.3	138	0	0	0	0	0
179	10	1	A	M	284	4	48.7	30.3	26.5	28.4	145	1	0	0	0	0
179	10	3	A	F	253	5.7	43.7	29.6	34.2	31.9	143	0	0	0	0	0
179	10	1	A	M	294	4	42.2	28.7	27.9	28.3	150	0	0	0	0	0
179	10	2	A	F	256	4.5	34	25.8	26	25.9	144	0	0	0	0	0
179	10	2	A	F	270	3.5	39.8	26.9	24.1	25.5	142	0	0	0	0	0
179	10	2	A	M	270	3.4	47.1	28	33.1	30.55	143	0	0	0	0	0
179	10	2	A	M	278	4.8	34.2	31	36.3	33.65	143	0	0	0	0	0
179	10	2	A	F	274	4.4	47.6	28.9	27.1	28	145	0	0	0	0	0
179	10	1	A	M	266	5.2	43.4	23.8	29.6	26.7	143	0	0	0	0	0
179	10	2	A	F	255	4.1	41.4	32.6	31	31.8	143	0	0	0	0	0
179	10	2	A	M	267	4.1	41.4	23.4	18.2	20.8	143	0	0	0	0	0
179	10	2	S	U	229	4.3	35.6	19.9	15.8	17.85	138	0	0	0	0	0
179	10	3	A	M	264	2.4	40.7	23.1	24.6	23.85	142	0	0	0	0	0
179	10	2	A	F	268	4.7	28.7	17.1	13.8	15.45	141	0	0	0	0	0
179	10	2	S	U	251	4.5	25	14.9	16.7	15.8	143	0	0	0	0	0
183	10	2	A	M	308	4.5	40.5	25.5	39.5	32.5	146	2	0	0	0	0

								Auricular plume length								
Day	Yr	Snt	Age	Sex	Mass	Rictal	Crest	Left	Right	Mean	Wing	Web	Tick	Lice-Q	Lice-S	Lice-A
183	10	1	A	F	248	4.1	39.7	24.6	25.4	25	141	0	0	0	0	0
183	10	3	A	F	261	4.1	43.3	10	15.6	12.8	143	2	0	0	0	0
183	10	2	A	F	287	5.3	34.9	28.1	27.1	27.6	148	0	0	0	0	0
183	10	2	A	F	255	4.4	41.3	31	33.6	32.3	143	0	0	0	0	0
183	10	3	A	M	247	3.1	38.9	22.2	24.6	23.4	138	0	0	0	0	0
183	10	2	A	F	232	3.7	38.9	21.4	21.7	21.55	141	0	0	0	0	0
183	10	3	A	M	253	3.4	33.3	29.7	29.6	29.65	138	0	0	0	0	0
183	10	1	A	M	259	6.3	44.6	26.8	26.8	26.8	146	0	0	0	0	0
183	10	1	A	F	246	3.2	20.1	21.6	21.9	21.75	140	0	0	0	0	0
183	10	2	A	F	242	3.6	31.4	24.2	27.1	25.65	140	0	0	0	0	0
186	10	1	A	F	251	3.2	43.2	27.3	23.4	25.35	145	0	0	0	0	0
186	10	3	A	F	243	4.5	38.6	27.8	24	25.9	141	2	0	0	0	0
186	10	0	A	M	264	4.9	41.8	28.5	23.1	25.8	144	1	0	0	0	0
186	10	3	A	M	240	2.5	43.1	27	26.2	26.6	143	1	0	0	0	0
186	10	2	A	M	255	.	39.1	16.9	19.1	18	145	0	0	0	0	0
186	10	1	A	M	289	4.4	35.5	26.2	27	26.6	146	0	0	0	0	0
186	10	1	S	U	242	3.6	30.1	18	20.7	19.35	151	0	0	0	0	0
186	10	2	A	M	244	4.8	41.32	30.5	35	32.75	140	0	0	0	0	0
186	10	1	A	M	273	6.3	41.6	35	36.8	35.9	148	0	0	0	0	0
186	10	2	S	U	244	4.3	13.6	18.9	19.9	19.4	143	0	0	0	0	0
186	10	1	S	U	224	3.1	19.8	27.3	23.5	25.4	136	0	0	0	0	0
186	10	0	A	M	261	2.3	43.2	29.8	25.1	27.45	138	1	0	0	0	0
186	10	1	A	F	263	2	47	22.8	28.6	25.7	145	0	0	0	0	0

Day	Yr	Snt	Age	Sex	Mass	Rictal	Crest	Auricular plume length			Wing	Web	Tick	Lice-Q	Lice-S	Lice-A
								Left	Right	Mean						
188	10	1	A	F	274	3	42.3	26	27.3	26.65	145	0	0	0	0	0
188	10	2	A	M	255	3.5	39.4	24.4	24.5	24.45	146	0	0	0	0	0
188	10	2	A	M	253	5.4	39.1	21.9	22.7	22.3	145	0	0	0	0	0
188	10	3	A	F	273	2.6	42.8	25.9	24.1	25	141	0	0	0	0	0
188	10	2	A	F	243	3.5	37.4	18.1	22.3	20.2	142	0	0	0	0	0
188	10	3	A	M	268	4.2	47.9	26	32.2	29.1	143	0	0	0	0	0
188	10	3	A	M	248	4.9	42.5	28.7	29.2	28.95	144	0	0	0	0	0
188	10	2	A	F	256	3.1	43.4	22.5	29.1	25.8	143	0	0	0	0	0
188	10	2	A	M	247	3.4	36.2	22.5	27.8	25.15	142	2	0	0	0	0
188	10	1	A	F	264	2.9	43.1	22.9	24.4	23.65	143	2	0	0	0	0
188	10	2	A	F	256	4.9	35.3	29.6	30	29.8	138	0	0	0	0	0
188	10	2	A	F	268	4.8	44.5	24	29.1	26.55	143	0	0	0	0	0
188	10	3	A	M	254	3.7	40.3	24.8	26.8	25.8	143	0	0	0	0	0
188	10	3	A	F	238	3.5	42.2	24.7	24	24.35	138	0	0	0	0	0
188	10	3	A	M	278	4.3	46	27.5	26.3	26.9	151	0	0	0	0	0
188	10	2	S	U	225	5.1	22.1	23.3	19.6	21.45	138	0	0	0	0	0
188	10	2	A	M	272	4.2	49.3	26.4	27.5	26.95	145	0	0	0	0	0
191	10	0	A	F	252	2.6	50.4	33	29.3	31.15	143	0	0	0	0	0
191	10	1	A	F	246	3.6	38.6	28.7	29.1	28.9	138	0	0	0	0	0
191	10	2	A	F	260	3.7	31.1	22.9	21.8	22.35	141	1	0	0	0	0
191	10	3	A	M	282	2.6	43.5	25.1	24.9	25	144	2	0	0	0	0
191	10	2	A	M	294	3.7	48.3	29.4	29.6	29.5	150	1	0	0	0	0
191	10	2	A	F	237	5.2	37.4	23.9	22.3	23.1	140	0	0	0	0	0

								Auricular plume length								
Day	Yr	Snt	Age	Sex	Mass	Rictal	Crest	Left	Right	Mean	Wing	Web	Tick	Lice-Q	Lice-S	Lice-A
191	10	3	A	F	235	3.9	41.2	18.1	18.2	18.15	146	0	0	0	0	0
191	10	3	A	M	267	4.9	29.2	26.2	27.1	26.65	147	0	0	0	0	0
191	10	2	A	F	254	0	42.4	17.4	14.4	15.9	143	0	0	0	0	0
191	10	2	A	M	273	2.9	43.5	27.6	29.9	28.75	143	0	0	0	0	0
191	10	2	S	U	219	2.4	29.5	26.4	25.8	26.1	141	0	0	0	0	0
193	10	0	A	F	255	0	45.3	23.8	25.2	24.5	142	1	0	0	0	0
193	10	1	A	M	249	2.9	34.8	28.9	23.1	26	144	0	0	0	0	0
193	10	2	A	M	287	0	39.8	28.9	27	27.95	149	0	0	0	0	0
193	10	0	A	M	253	4.6	38.9	21.3	27.9	24.6	149	0	0	0	0	0
193	10	3	A	F	255	0	25.3	25.5	24.1	24.8	141	0	0	0	0	0
193	10	2	A	F	248	0	36	23.7	20.6	22.15	139	0	0	0	0	0
193	10	1	A	F	250	0	38.3	23	30.1	26.55	142	0	0	0	0	0
193	10	1	A	M	269	0	39	23.9	24.6	24.25	138	0	0	0	0	0
193	10	3	A	M	267	0	47	26.3	30.1	28.2	145	0	0	0	0	0
193	10	0	A	F	252	3.9	43.8	28.4	32.3	30.35	138	0	0	0	0	0
193	10	2	A	M	271	4.6	46.3	22.4	23.1	22.75	146	0	0	0	0	0
193	10	2	A	M	255	5	41.6	28.4	23.4	25.9	148	0	0	0	0	0
193	10	2	A	M	255	6.7	43.1	34.2	30.1	32.15	146	0	0	0	0	0
195	10	2	A	F	234	0	44.4	29.2	29.3	29.25	140	1	0	0	0	0
195	10	1	A	F	226	0	40.7	25	25.6	25.3	144	0	0	0	0	0
195	10	2	A	M	268	3.9	45.6	19.8	23.8	21.8	143	0	0	0	0	0
195	10	0	A	F	256	0	38.9	24.9	29.5	27.2	145	0	0	0	0	0
195	10	3	A	F	242	0	44.6	25.3	27.3	26.3	138	1	0	0	0	0

								Auricular plume length								
Day	Yr	Snt	Age	Sex	Mass	Rictal	Crest	Left	Right	Mean	Wing	Web	Tick	Lice-Q	Lice-S	Lice-A
195	10	1	A	M	274	0	44.7	27	23.9	25.45	147	0	0	0	0	0
195	10	3	A	M	260	5.2	36.8	18.1	25.8	21.95	143	0	0	0	0	0
195	10	3	A	F	234	0	42.2	29.9	19.1	24.5	138	0	0	0	0	0
195	10	2	A	M	265	0	43.9	31	30	30.5	145	0	0	0	0	0
195	10	1	A	F	273	0	38.1	26.3	27	26.65	142	0	0	0	0	0
195	10	0	A	M	265	0	42.8	17.8	21.6	19.7	144	0	0	0	0	0
195	10	0	A	U	249	0	0	28	24.6	26.3	141	1	0	0	0	0
195	10	0	A	M	270	2.3	39	22.1	16.1	19.1	141	0	0	0	0	0
199	10	3	A	M	281	3.9	40.3	27.6	20.8	24.2	146	0	0	0	0	0
199	10	0	A	M	249	0	43.7	19.9	21.9	20.9	143	2	0	0	0	0
199	10	2	A	M	292	0	34.9	16.8	21.3	19.05	146	0	0	0	0	0
199	10	0	A	F	241	0	38.9	23	21.3	22.15	147	0	0	0	0	0
199	10	1	A	F	241	0	40.4	28	25	26.5	141	1	0	0	0	0

Appendix V

Raw data of all Least Auklets (*Aethia pusilla*) caught during the breeding season in 2009 and 2010. All louse specimens are mounted and ID by Ricardo Palma of Museum of New Zealand Te Papa Tongarewa. Day= numeric date from 1 January of the respective year; Yr= year; A= adult; S= sub-adult; Knob= height of bill knob; Plumage= plumage colouration (the degree of blackness in the breast plumage on a scale of 0 – 4;Jones 1990); Web= score of 0-2(0-no holes in either foot web;1- individuals had a single circular hole in either foot web; and 2- had greater than one hole); Tick= number of *Ixodes uriea*; Lice= number of *Quadraceps aethereus*.

						Auricular plume length						
Day	Yr	Age	Mass	Knob	Plumage	Left	Right	Mean	Wing	Web	Tick	Lice
160	10	A	81	1	2	14.1	12	13.05	91	0	12	0
178	09	A	81	.	.	.	.	.	.	.	6	0
153	09	A	82	1	2	12.2	14	13.1	99	1	3	0
167	09	A	83	1.3	2	12.4	11.6	12	97	0	1	2
161	09	S	78	1.6	2	11	10	10.5	96	0	1	1
167	09	A	82	0.9	3	11.6	8.8	10.2	95	1	1	1
182	09	S	79	0.8	2	10.3	8.7	9.5	96	0	1	1
152	10	A	79	1	2	11.9	13.4	12.65	98	0	1	1
152	10	S	81	1.4	3	14.1	15.2	14.65	96	0	1	1
153	09	A	82	1	3	13.1	12.3	12.7	95	1	1	0
156	09	A	85	1.4	2	11.8	12	11.9	98	0	1	0
161	09	A	80	1.5	3	8.5	8.9	8.7	98	0	1	0
161	09	A	80	1.4	2	12.6	12.1	12.35	98	0	1	0
170	09	A	89	0.8	2	16	19.3	17.65	95	1	1	0

Day	Yr	Age	Mass	Knob	Plumage	Auricular plume length Left	Right	Mean	Wing	Web	Tick	Lice
178	09	A	81	.	.	.	.	.	.	.	1	0
182	09	A	75	0.8	2	11	11	11	96	0	1	0
185	09	S	79	0.8	3	11.3	10.9	11.1	97	0	1	0
192	09	A	84	1	2	18.9	16.5	17.7	97	0	1	0
192	09	A	81	0.4	2	19.2	16.4	17.8	101	2	1	0
192	09	A	84	0.4	2	9.7	10.3	10	97	2	1	0
197	09	A	75	0.2	2	15.8	16.7	16.25	104	0	1	0
152	10	A	85	2.8	3	17.4	13.2	15.3	95	0	1	0
164	10	A	95	0.9	2	16.6	12.9	14.75	95	0	1	0
191	10	A	97	0.8	2	11.8	11.5	11.65	97	0	1	0
167	09	A	75	0.9	2	8.2	5.7	6.95	94	0	0	3
154	10	S	93	1	2	16.9	15	15.95	96	0	0	3
180	10	A	84	1.5	2	12.4	11.3	11.85	91	0	0	3
161	09	A	89	2.2	2	15.2	13.1	14.15	95	1	0	2
153	09	S	76	1	3	16.9	15	15.95	92	1	0	1
159	09	A	85	2.6	3	12	13	12.5	96	0	0	1
167	09	A	88	1.6	3	14.1	15.5	14.8	94	2	0	1
167	09	A	84	.	.	.	.	.	.	.	0	1
167	09	A	79	1.7	2	9.1	8.5	8.8	96	0	0	1
167	09	S	79	1	3	12.4	11.2	11.8	97	1	0	1
167	09	A	85	0.7	2	14.1	14.6	14.35	96	0	0	1
182	09	A	75	1.1	2	13.6	16.9	15.25	97	1	0	1
185	09	A	81	0.5	1	16.7	15.7	16.2	95	0	0	1

						Auricular plume length						
Day	Yr	Age	Mass	Knob	Plumage	Left	Right	Mean	Wing	Web	Tick	Lice
197	09	A	76	1.8	2	12.9	9.2	11.05	97	1	0	1
157	10	A	72	1.2	3	13.1	13.3	13.2	96	0	0	1
173	10	S	79	1.1	3	10.2	8.7	9.45	96	0	0	1
177	10	S	76	0.7	3	14.4	13.4	13.9	96	0	0	1
191	10	A	83	0.6	1	11.1	11.8	11.45	97	2	0	1
153	09	A	90	0.9	2	18.4	16.2	17.3	98	0	0	0
153	09	A	90	1.7	3	14.1	12.5	13.3	99	0	0	0
153	09	A	83	1.5	2	15.4	15.1	15.25	112	0	0	0
153	09	A	82	1.8	3	12.6	13.4	13	96	1	0	0
153	09	A	78	1.4	2	10.4	10.2	10.3	98	0	0	0
153	09	S	76	0.3	2	11.6	11.8	11.7	97	0	0	0
153	09	A	81	1.5	2	5.4	4.9	5.15	95	1	0	0
153	09	A	79	2.1	2	17.9	17	17.45	98	0	0	0
153	09	A	76	1.1	3	12.3	13.6	12.95	91	0	0	0
153	09	A	82	1.4	2	12.8	11.8	12.3	95	1	0	0
153	09	A	73	0.9	2	13	12.7	12.85	96	0	0	0
153	09	A	76	0.7	2	10.8	10.7	10.75	97	1	0	0
153	09	A	86	2.2	2	10.1	11.8	10.95	98	0	0	0
153	09	A	81	1.8	2	10.9	11.3	11.1	99	1	0	0
153	09	A	78	0.5	3	15.5	13	14.25	90	2	0	0
153	09	A	81	1.7	3	17.9	12	14.95	94	0	0	0
153	09	S	76	0.8	3	8.8	9.3	9.05	96	1	0	0
156	09	S	75	1.4	2	10.9	8.5	9.7	93	1	0	0

						Auricular plume length						
Day	Yr	Age	Mass	Knob	Plumage	Left	Right	Mean	Wing	Web	Tick	Lice
156	09	S	74	1.8	2	11.6	11.8	11.7	96	0	0	0
156	09	A	.	0.6	2	17.7	13.5	15.6	90	1	0	0
156	09	A	86	1.2	2	15.1	12.6	13.85	97	0	0	0
156	09	A	90	1.3	2	12.7	13.1	12.9	98	0	0	0
156	09	S	76	1.2	3	13.4	16	14.7	96	0	0	0
156	09	A	74	1.9	2	13.1	13.4	13.25	95	1	0	0
156	09	A	74	1.7	2	12.4	13.9	13.15	94	0	0	0
156	09	A	86	1.2	3	15.5	16.2	15.85	96	1	0	0
156	09	S	74	0.6	3	9.6	11.9	10.75	93	2	0	0
159	09	A	77	1.1	2	12.1	11.1	11.6	94	1	0	0
159	09	S	77	0.6	2	11.8	10.5	11.15	95	0	0	0
159	09	A	78	0.7	2	17.8	17.1	17.45	93	0	0	0
159	09	A	81	0.9	2	10	10.2	10.1	99	1	0	0
159	09	S	78	0.9	3	14.7	16	15.35	100	0	0	0
161	09	A	79	1.6	3	11.6	8.2	9.9	95	0	0	0
161	09	A	91	1.3	2	14.7	8.5	11.6	94	0	0	0
161	09	A	86	.	.	.	.	.	.	.	0	0
161	09	A	94	1.8	2	12.8	13	12.9	100	1	0	0
161	09	A	87	.	.	.	.	.	.	.	0	0
161	09	A	85	1	2	11.5	11.6	11.55	97	0	0	0
161	09	S	72	1.6	3	10.1	12.2	11.15	97	0	0	0
161	09	A	94	.	.	.	.	.	.	.	0	0
161	09	A	88	.	.	.	.	.	.	.	0	0

Day	Yr	Age	Mass	Knob	Plumage	Auricular plume length			Wing	Web	Tick	Lice
						Left	Right	Mean				
161	09	A	83	1.6	2	11	12.6	11.8	98	1	0	0
161	09	A	90	1.2	2	13.8	15	14.4	97	0	0	0
161	09	A	79	1.8	2	15.2	13	14.1	97	1	0	0
164	09	A	79	.	.	.	.	.	.	.	0	0
164	09	S	83	0.2	3	15	13.1	14.05	101	0	0	0
164	09	A	78	.	.	.	.	.	.	.	0	0
167	09	A	.	.	.	.	.	.	.	.	0	0
167	09	S	81	0.3	3	5	6.9	5.95	95	1	0	0
167	09	S	80	0.9	2	11.8	10.1	10.95	97	0	0	0
167	09	A	94	.	.	.	.	.	.	.	0	0
167	09	S	77	1.3	1	10.6	10.3	10.45	98	0	0	0
167	09	A	76	1.5	3	16.8	16.4	16.6	96	0	0	0
167	09	A	85	.	.	.	.	.	.	.	0	0
167	09	A	77	1.4	2	10.6	11.2	10.9	92	0	0	0
167	09	A	79	1.3	3	13.4	10.1	11.75	92	0	0	0
167	09	S	75	1.9	2	15.2	13.5	14.35	96	1	0	0
167	09	S	.	1.4	2	17.2	15.1	16.15	97	0	0	0
170	09	A	81	3.3	2	13	12.6	12.8	98	0	0	0
170	09	A	82	0.5	2	15.9	13.1	14.5	94	0	0	0
170	09	A	79	2.1	2	8.9	7.1	8	93	0	0	0
170	09	S	91	1.9	2	11.1	14	12.55	99	0	0	0
170	09	A	79	2.3	2	15.8	12.1	13.95	101	0	0	0
170	09	A	81	0.4	2	16.5	12.4	14.45	97	0	0	0

Day	Yr	Age	Mass	Knob	Plumage	Auricular plume length			Wing	Web	Tick	Lice
						Left	Right	Mean				
170	09	S	78	0.8	2	17.5	16.6	17.05	101	1	0	0
170	09	A	84	2.6	1	12.5	11.1	11.8	97	0	0	0
170	09	S	83	0.9	3	10	6.4	8.2	94	0	0	0
170	09	A	76	1	2	8.2	8.7	8.45	91	0	0	0
170	09	A	79	1	2	15	14.3	14.65	95	0	0	0
170	09	S	75	0.4	2	13.7	15.4	14.55	94	0	0	0
170	09	S	79	1.1	2	9.4	11.8	10.6	95	0	0	0
170	09	A	88	1.3	2	16.7	17.5	17.1	97	0	0	0
174	09	S	74	0.7	2	18.2	11	14.6	96	0	0	0
174	09	A	82	.	.	.	.	.	.	.	0	0
174	09	A	83	0.9	2	16.7	15.7	16.2	97	0	0	0
174	09	A	80	1.4	3	7.5	6.4	6.95	97	0	0	0
174	09	A	83	1.1	2	14.6	14.1	14.35	94	0	0	0
174	09	S	84	1.1	3	8	7.1	7.55	96	1	0	0
178	09	S	79	1.8	3	8	9.9	8.95	95	0	0	0
178	09	A	85	1.5	3	15.7	14.6	15.15	98	1	0	0
178	09	A	97	.	0	.	.	.	.	.	0	0
178	09	A	86	.	.	.	.	.	.	.	0	0
178	09	A	82	1.2	2	8.1	9.2	8.65	94	0	0	0
178	09	A	75	0.8	2	10.3	13.6	11.95	96	0	0	0
178	09	A	.	.	.	.	.	.	.	.	0	0
182	09	A	79	.	.	.	.	.	.	.	0	0
182	09	A	83	.	.	.	.	.	.	.	0	0

						Auricular plume length						
Day	Yr	Age	Mass	Knob	Plumage	Left	Right	Mean	Wing	Web	Tick	Lice
182	09	A	78	0.5	2	11.4	12	11.7	99	0	0	0
182	09	S	80	0.9	3	15	17.4	16.2	93	0	0	0
182	09	A	82	1.5	2	12.1	9.2	10.65	99	1	0	0
182	09	A	82	0.1	2	14.4	15	14.7	95	1	0	0
182	09	A	82	1.8	3	14.7	13.1	13.9	97	1	0	0
182	09	A	75	0.1	1	14.9	15.2	15.05	97	0	0	0
185	09	A	77	1.3	2	13.5	15.1	14.3	97	0	0	0
185	09	A	82	.	.	.	.	.	.	.	0	0
185	09	A	81	0.3	2	11.3	8.8	10.05	94	0	0	0
185	09	A	80	0.5	2	10.1	10.5	10.3	97	2	0	0
185	09	A	82	0.6	2	14.8	11.7	13.25	100	0	0	0
185	09	A	85	0.6	2	10.4	8	9.2	102	0	0	0
185	09	A	76	.	.	.	.	.	.	.	0	0
185	09	S	77	1	2	8.4	7.8	8.1	97	0	0	0
185	09	A	79	0.5	1	9	10.2	9.6	94	0	0	0
185	09	A	78	1.6	2	17.4	19.9	18.65	94	1	0	0
185	09	A	73	1.3	2	14.5	13.1	13.8	97	0	0	0
185	09	A	75	1	3	12.3	13	12.65	96	0	0	0
185	09	A	83	1.6	2	13.5	17	15.25	96	0	0	0
185	09	A	77	0.5	2	16	13.2	14.6	97	0	0	0
192	09	A	83	0.5	2	11.8	14.1	12.95	101	0	0	0
192	09	A	75	1.4	2	8.9	10	9.45	95	0	0	0
192	09	A	86	0.4	2	18.1	16.8	17.45	99	0	0	0

Day	Yr	Age	Mass	Knob	Plumage	Auricular plume length Left	Right	Mean	Wing	Web	Tick	Lice
192	09	A	89	0.8	2	18.4	20.2	19.3	.	0	0	0
192	09	A	77	0.1	2	11.4	9.6	10.5	98	1	0	0
192	09	A	86	0.4	2	17.5	20.7	19.1	102	1	0	0
197	09	A	88	0.2	2	11.2	15.1	13.15	96	0	0	0
197	09	A	79	0.8	2	10.7	9.2	9.95	100	2	0	0
197	09	A	82	0.4	2	13.9	10	11.95	94	0	0	0
197	09	A	74	1.2	2	11.6	8.7	10.15	97	0	0	0
197	09	A	78	0.3	2	12.7	13.5	13.1	92	1	0	0
198	09	A	85	0.5	2	17.3	13.1	15.2	92	0	0	0
198	09	A	95	1.2	2	18.7	18.9	18.8	103	0	0	0
201	09	A	77	0.8	2	12.3	14.1	13.2	96	0	0	0
201	09	A	84	0.1	2	10.9	13.9	12.4	102	1	0	0
201	09	A	85	0.4	2	10.1	12.2	11.15	96	0	0	0
201	09	A	80	1.2	2	13.5	13.8	13.65	94	0	0	0
152	10	A	78	0.2	2	15.3	18.6	16.95	92	0	0	0
152	10	A	78	1.9	2	11.5	11.4	11.45	97	0	0	0
152	10	A	82	1.2	2	12.1	11.3	11.7	96	1	0	0
152	10	A	84	1.5	3	15.8	15.4	15.6	96	0	0	0
152	10	A	86	2.2	2	11.5	14.6	13.05	98	0	0	0
152	10	A	73	1.8	2	13.7	13.8	13.75	95	0	0	0
152	10	A	80	1.8	3	14	13.2	13.6	95	1	0	0
152	10	A	80	1.1	2	13.3	13.3	13.3	95	0	0	0
152	10	A	93	1.1	3	11.6	14.1	12.85	104	0	0	0

Day	Yr	Age	Mass	Knob	Plumage	Auricular plume length Left	Right	Mean	Wing	Web	Tick	Lice
152	10	A	81	1	2	16	16.9	16.45	97	0	0	0
152	10	A	75	1.3	3	14.5	10.6	12.55	98	0	0	0
152	10	S	83	1.2	.	10.3	11.3	10.8	99	0	0	0
152	10	A	78	1.4	3	9.9	12	10.95	96	0	0	0
152	10	A	81	1.7	3	9.6	13.1	11.35	102	0	0	0
154	10	A	82	1.6	3	13.8	11.5	12.65	97	2	0	0
154	10	S	75	2	2	11.1	10.5	10.8	94	0	0	0
154	10	S	73	1.6	2	14.7	14.5	14.6	97	0	0	0
154	10	S	80	1.5	2	8.4	9.1	8.75	91	0	0	0
154	10	S	83	1.9	4	10.1	12.9	11.5	96	0	0	0
154	10	A	79	0.9	2	16.8	5.7	11.25	97	0	0	0
154	10	A	79	1.5	3	9	8.6	8.8	97	0	0	0
154	10	A	80	0.9	2	7.2	7.4	7.3	96	0	0	0
154	10	S	70	1.3	2	12.8	12.4	12.6	93	1	0	0
154	10	S	84	1.6	2	11.7	13.5	12.6	104	0	0	0
154	10	A	81	2.2	3	12.3	15.1	13.7	96	0	0	0
154	10	A	87	2.1	3	15.5	13.8	14.65	97	1	0	0
154	10	S	86	1.5	3	11.1	14.1	12.6	99	0	0	0
154	10	A	80	1.6	3	8.6	7	7.8	98	2	0	0
154	10	S	75	1	3	9.3	10.4	9.85	98	0	0	0
154	10	A	84	1.9	2	18.5	19	18.75	96	0	0	0
157	10	A	84	1.4	3	14.3	15.8	15.05	94	0	0	0
157	10	S	80	1.1	3	13.7	12.4	13.05	96	1	0	0

Day	Yr	Age	Mass	Knob	Plumage	Auricular plume length Left	Auricular plume length Right	Auricular plume length Mean	Wing	Web	Tick	Lice
157	10	A	90	1.4	3	18.1	18.6	18.35	99	0	0	0
157	10	A	83	2.8	2	14.7	12.4	13.55	96	0	0	0
157	10	A	82	1.1	3	11.3	11.9	11.6	94	0	0	0
157	10	A	78	1.4	2	9.4	11.6	10.5	99	0	0	0
157	10	A	79	1.1	2	8.7	8.3	8.5	96	0	0	0
157	10	A	77	0.8	2	8.7	10.1	9.4	97	0	0	0
157	10	A	79	1.2	2	15.2	13	14.1	96	1	0	0
157	10	A	78	2.1	3	13.9	13.1	13.5	97	0	0	0
157	10	A	75	1.9	3	18.2	19.2	18.7	98	0	0	0
157	10	A	84	1.2	1	12.1	13.5	12.8	93	0	0	0
157	10	A	78	1.3	3	15	12.4	13.7	98	0	0	0
160	10	A	88	1.2	3	16.1	16.6	16.35	96	0	0	0
160	10	S	81	1.2	3	9.4	10.6	10	97	0	0	0
160	10	A	85	1.6	2	8.7	9.4	9.05	105	0	0	0
160	10	A	81	1.1	3	14.1	16.5	15.3	98	0	0	0
160	10	S	86	0.5	3	14.6	14.4	14.5	95	0	0	0
160	10	A	77	0.8	3	13.3	10.2	11.75	91	0	0	0
160	10	S	79	1	2	9	9.2	9.1	91	0	0	0
164	10	A	82	2.4	2	11.3	7.5	9.4	95	1	0	0
164	10	A	97	0.4	2	17.5	15.1	16.3	96	0	0	0
164	10	S	77	0.9	3	13.4	13.9	13.65	95	0	0	0
164	10	A	87	1.5	2	14.1	13.4	13.75	98	0	0	0
164	10	A	87	1.6	2	10.4	9.5	9.95	99	1	0	0

						Auricular plume length						
Day	Yr	Age	Mass	Knob	Plumage	Left	Right	Mean	Wing	Web	Tick	Lice
164	10	A	83	1.1	3	11	11.3	11.15	96	0	0	0
164	10	S	77	0.8	2	13.6	12.2	12.9	94	0	0	0
164	10	S	82	0.5	3	11.5	11.9	11.7	96	0	0	0
164	10	S	82	1	2	12	13.5	12.75	98	0	0	0
164	10	S	80	1.1	3	8.4	7.3	7.85	93	1	0	0
167	10	A	78	1.9	2	13.1	12.8	12.95	90	0	0	0
167	10	A	78	1	2	12.6	12.5	12.55	94	0	0	0
167	10	A	115	1.1	2	11.7	11	11.35	98	3	0	0
167	10	A	93	1.1	2	11	12	11.5	93	1	0	0
167	10	S	85	0.7	3	12.6	13.2	12.9	100	0	0	0
167	10	S	71	0.5	3	11	8.7	9.85	94	0	0	0
167	10	A	84	1.7	3	16.6	12.9	14.75	94	0	0	0
173	10	A	81	0.8	2	14.8	11.5	13.15	95	0	0	0
173	10	A	87	1.7	2	10.4	12.6	11.5	98	0	0	0
173	10	S	70	0.9	3	13.2	12.3	12.75	97	1	0	0
173	10	A	81	0.6	2	12	12.9	12.45	96	0	0	0
173	10	A	75	1.6	2	9.8	8.8	9.3	96	0	0	0
175	10	A	77	0.8	1	14.9	14	14.45	96	0	0	0
175	10	A	82	1.5	2	10.4	12.1	11.25	94	0	0	0
175	10	S	74	1	3	12.9	11.5	12.2	97	0	0	0
175	10	A	86	0.9	2	14.1	13.2	13.65	96	0	0	0
175	10	A	76	0.5	1	13.4	14.8	14.1	96	0	0	0
175	10	A	84	1.7	3	14.8	14.5	14.65	101	0	0	0

Day	Yr	Age	Mass	Knob	Plumage	Auricular plume length			Wing	Web	Tick	Lice
						Left	Right	Mean				
177	10	A	92	1.5	2	9	10.9	9.95	98	0	0	0
179	10	A	85	0.5	2	14.3	13.5	13.9	99	0	0	0
179	10	A	85	0.4	2	12.8	12	12.4	98	0	0	0
179	10	A	86	1.3	2	12.3	7.4	9.85	95	0	0	0
179	10	S	87	1.1	2	13.3	16.4	14.85	101	0	0	0
179	10	A	87	0.2	3	17	17.1	17.05	102	0	0	0
179	10	A	85	0.9	3	17.6	14.7	16.15	95	0	0	0
179	10	S	83	1.1	3	12.9	10.8	11.85	99	2	0	0
179	10	A	86	1.4	2	11.6	10.2	10.9	98	0	0	0
179	10	A	84	1.7	3	13.8	13	13.4	95	1	0	0
180	10	A	94	1.2	2	9.5	9.5	9.5	98	0	0	0
180	10	A	85	1.1	2	15.4	15.4	15.4	97	0	0	0
183	10	A	86	1	1	14.6	14.7	14.65	99	0	0	0
183	10	S	79	0.9	3	11.6	10.9	11.25	97	0	0	0
183	10	S	74	1.6	2	13.3	13.6	13.45	97	0	0	0
183	10	A	83	0.4	2	16	15	15.5	98	0	0	0
183	10	A	83	1.6	2	12.6	11	11.8	98	0	0	0
186	10	A	86	1.3	2	14.4	13.1	13.75	97	0	0	0
186	10	A	80	0.4	2	12.1	10.3	11.2	100	0	0	0
186	10	S	81	0.8	3	8.6	8.7	8.65	96	1	0	0
186	10	A	93	1.3	2	8.6	10.1	9.35	100	0	0	0
186	10	S	71	1.3	1	11.7	11.3	11.5	93	0	0	0
188	10	A	84	1.2	3	12.3	11	11.65	98	0	0	0

Day	Yr	Age	Mass	Knob	Plumage	Auricular plume length			Wing	Web	Tick	Lice
						Left	Right	Mean				
191	10	A	84	0.5	2	12.1	9.3	10.7	100	0	0	0
195	10	A	100	1.1	1	13.1	10.6	11.85	96	0	0	0
199	10	A	79	0.8	1	15	25.9	20.45	99	0	0	0