Taxonomic, Ecological and Quantitative Examination of Chewing Lice (Insecta: Phthiraptera) on Canada Geese (*Branta canadensis*) and Mallards (*Anas platyrhynchos*) in Manitoba, Canada

By

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Abstract

Over 19 years chewing lice data from Canada geese and mallards were collected. From Canada geese (n=300) 48,669 lice were collected, including *Anaticola anseris, Anatoecus dentatus, Anatoecus penicillatus, Ciconiphilus pectiniventris, Ornithobius goniopleurus,* and *Trinoton anserinum*. The prevalence of all lice on Canada geese was 92.3% and the mean intensity was 175.6 lice per bird. From mallards (n=269) 6,986 lice were collected which included: *Anaticola crassicornis, A. dentatus, Holomenopon leucoxanthum, Holomenopon maxbeieri* and *Trinoton querquedulae.* The prevalence of lice on mallards was 55.4% and the mean intensity was 42.0 lice per bird. Based on CO1, *A. dentatus* and *Anatoecus icterodes* were synonymised as *A. dentatus*. *Anatoecus* was found exclusively on the head, *Anaticola* was found predominantly on the wings, *Ciconiphilus, Holomenopon* and *Ornithobius* were observed in several body regions and *Trinoton* was found most often on the wings of mallards.

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Dedication

This thesis is dedicated to my grandfather, George Adams.

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CHAPTER 1: General Introduction

When you look at a bird, you should see beyond a warm-blooded vertebrate covered in feathers and see a mobile island of parasites. A parasite is an organism that obtains part or all of its nutrition from another host organism and causes some degree of damage to its host (Price 1980). Even though the majority of parasites are inconspicuous, there are actually more parasitic organisms then non-parasitic organisms on earth (Roberts and Janovy 2005). These parasitic organisms can be divided into two categories: ectoparasitic, those that live on their hosts and endoparasitic, those that live in their host.

The publication, *Arthropod ectoparasites of vertebrates in Canada* (Galloway and Danks 1991), was the motivation for a survey on ectoparasites infesting birds and mammals in Manitoba, Canada. This survey has continued over the years (1994-2012) and has produced a substantial dataset with over 237 species of birds and 44 species of mammals examined. The family Anatidae, which consists of ducks, geese and swans in the order Anseriformes, makes up 29 species in this dataset. Canada Geese (*Branta canadensis* (Linnaeus)) and mallards (*Anas platyrhynchos* (Linnaeus)) are the most abundant of the Anatidae that come through the lab and will be the focus of this thesis.

Canada geese and mallards are ecologically and economically important in many parts of the world. Waterfowl play an important part in the management of wetlands with regards to nutrient levels and water quality (Baschuk *et al.* 2012; Post *et al.* 1998), and have a substantial economic impact as game birds. In 2004, hunters in Canada spent $91.7 million on hunting migratory birds (Environment Canada 2010).

Canada geese and mallards are hosts of chewing lice (Phthiraptera: Menoponidae, Philopteridae). Chewing lice are ectoparasites that spend their entire life upon their hosts.

This close association, coupled with the fact that chewing lice have a certain level of host specificity, has led to co-speciation events. Host-induced selective pressures and rates of evolution can be used to test hypotheses about host-parasite co-speciation (Johnson *et al.* 2002).

Some species of lice are found only on one host species, such as *Geomydoecus subgeomydis* Price and Emerson on plains pocket gophers (*Geomys bursarius attwateri* (Merriam)) (Price and Emerson 1971). Therefore, if their host goes extinct, so does the louse. Other lice may have more than one host; *Menacanthus eurysternus* (Burmeister) is an extreme example found on at least 118 species of birds within the order Passeriformes (Price 1975). Infestations can also be examined from the host's perspective; there are hosts with only one species of louse. The yellow-eyed flycatcher warbler (*Seicercus burkii* (Burton)) is host only to *Ricinus balati* Rheinwald, yet other host species can be host to several species of lice, such as the common pheasant (*Phasianus colchicus* Linnaeus) which is host to 11 species of lice (Price *et al.* 2003), though probably not all at the same time.

Part of being a parasite is that it causes harm to its host. This creates a fine line for chewing lice since they are not able to survive off of their host (Marshall 1981a). Chewing lice are known to cause damage to feathers, which impacts the insulative properties of the plumage (Booth *et al.* 1993). Chewing lice also impact sexual selection in their hosts. Females of some species of birds, such as the barn swallow (*Hirundo rustica* (Linnaeus)), will avoid lousy males based on feather characteristics (Kose *et al.* 1999). Large populations of lice can have detrimental effects to their host (Barbosa *et al.*

2002; Booth *et al.* 1993; Brown *et al.* 1995); however, louse populations are usually kept under control by host preening (Clayton 1991).

Canada geese have seven species of chewing lice recorded from them: *Anaticola anseris* (Linnaeus), *Anatoecus dentatus* (Scopoli), *Anatoecus icterodes* (Nitzsch), *Ciconiphilus pentiniventris* (Harrison), *Holomenopon leucoxanthum* (Burmeister), *Ornithobius goniopleurus* Denny and *Trinoton anserinum* (Fabricius) (Price *et al.* 2003). Mallards have seven species of chewing lice recorded from them: *Anaticola crassicornis* (Scopoli), *Anatoecus dentatus* (Scopoli), *Anatoecus icterodes* (Nitzsch), *Holomenopon leucoxanthum* (Burmeister), *Holomenopon maxbeieri* Eichler, *Holomenopon transvaalense* (Bedford) and *Trinoton querquedulae* (Linnaeus) (Price *et al.* 2003). *Holomenopon transvaalense* has only been recorded from Africa and was not observed on any of the mallards examined in this survey.

Ciconiphilus, Holomenopon, Ornithobius and *Trinoton* have all gone through recent revisions and are taxonomically stable (Arnold 2005; Eichler and Vasjukova 1980; Price 1971; Price and Beer 1965). The last time *Anatoecus* was revised was in 1960 by Kéler. Since then, louse researchers have questioned the validity of recognizing *A. dentatus* and *A. icterodes* as separate species (Emerson 1972; Ledger 1980). *Anatoecus dentatus* and *A. icterodes* are found co-inhabiting the head and neck of their hosts (Chapter 4). Males of these species are easily distinguishable by characteristics of their genitalia (Cummings 1916); however, females are morphologically indistinguishable (Ledger 1980). This inability to separate female *A. dentatus* from *A. icterodes* has led to uncertainty about their taxonomic status. I predicted that *A. dentatus* and *A. icterodes* are the same species. In order to test this hypothesis, the mitochondrial gene, cytochrome c

oxidase I, was sequenced from *A. icterodes, A. dentatus, Anatoecus penicillatus* Kéler and *Anatoecus cygni* (Denny).

Each louse species spatially partitions its host in its own characteristic way (Marshall 1981a). Louse body shape can be used to help predict what areas of the body of the host a louse will inhabit. Therefore different species of lice from the same genus should inhabit the same body regions across different hosts. Strilchuk (1976) examined the niche association of the louse fauna on two mallards and showed that for each species of louse there appeared to be site specificity for different areas of the host's body. However, these results could be an artifact of small sample size. Therefore my second objective was to examine the different body regions of Canada geese and mallards to determine if specific lice are associated with certain body regions.

Quantitative data about infestation parameters on Anseriformes are sparse. The majority of data on Anseriformes come from host-parasite lists (*e.g.*, Spencer (1948) and Threlfall *et al*. (1979)). The only record of chewing lice on Anseriformes in Manitoba is from Buscher (1965). He looked at 11 different species of hosts, including mallards, and reported that 46.2% of the 13 mallards examined had ectoparasites. Since mallards can be infested by several species of lice and are host to mites as well as other ectoparasites, Buscher's results give little insight to their infestation parameters.

Infestation parameters of Canada geese and mallards were determined from the available 19-year dataset. These included prevalence, mean intensity, seasonal fluctuations, and dispersal patterns of chewing lice from adult to juvenile hosts. This information created a baseline for comparison to other Canada goose and mallard populations, as well as other species of Anseriformes.

This thesis is arranged in a manuscript style, with each of the three chapters being its own stand-alone manuscript. However, all references are at the end of the thesis instead of at the end of each chapter because many references are repeated in each chapter. Chapters follow guidelines for authors for The Canadian Entomologist.

CHAPTER 2: Review of the Pertinent Literature

Biology and Ecology

Lice (Insecta: Phthiraptera) are small, wingless, hemimetabolous, ectoparasitic insects that spend their entire life upon a host (Marshall 1981a). There are four suborders of lice: Anoplura, Amblycera, Ischnocera and Rhynchophthrina. These suborders can be divided into two groups, sucking lice, which includes Anoplura and chewing lice, that is made up of Amblycera, Ischnocera and Rhynchophthrina.

Anoplura are commonly referred to as sucking lice because of their modified mouthparts, which are used to feed on blood. These highly specialized mouthparts are made up of a piercing instrument that is formed by three protrusible stylets that are retractable (Ferris 1951). Their legs have modified claw-like clasping apparati formed by a thumb-like process on the tibia (Marshall 1981a). They use these claws to grasp the hair of their host; there is usually a correlation between claw size and hair diameter (Marshall 1981a). Anoplura are found living exclusively in the hair of mammals. They cement their eggs to the hair of their host, with the exception *Pediculus humanus humanus* Linnaeus, the human body louse, which attaches its eggs to clothing (Ferris 1951).

Chewing lice are distinguishable from sucking lice by their head being as wide or wider than their prothorax, with the exception of Rhynchophthrina, which have their own distinctive anatomy. The head of sucking lice is narrower than the prothorax (Durden and Musser 1994). Chewing lice also lack the modified claws.

Chewing lice, once referred to as Mallophaga, consist of Rhynchophthrina, Amblycera, and Ischnocera, and are named for their mandibular mouthparts. Rhynchophthrina is the smallest suborder of the chewing lice with only three species that

parasitize elephants, warthogs and bush pigs (Price *et al.* 2003). Rhynchophthrina have a weevil-like appearance because their mouthparts are borne on the end of a long proboscis (Price *et al.* 2003). Amblycera, and Ischnocera are parasites of practically all birds and some mammals (Marshall 1981a). For the purposes of this literature review, Amblycera and Ischnocera will be the focus, with references primarily to parasites of birds.

Eggs of Amblycera and Ischnocera are glued to the basal region of feathers with cement secreted by females (Marshall 1981a; Peters 1928). Eggs can be laid individually or in clumps (Johnson and Clayton 2003). *Hohorstiella lata* (Piaget) lays its eggs one on top of the other, while *Columbicola columbae* (Linnaeus) lays its eggs in the furrows between the barbs of the flight feathers (Nelson and Murray 1971). Depending on the species, eggs can incubate from four to ten days before they hatch (Marshall 1981a). Chewing lice go through three nymphal instars with each instar lasting two to 12 days (Marshall 1981a). Adults live for approximately 20 to 30 days with females producing on average one egg per day (Marshall 1981a). Female lice are often 20% larger than males (Price *et al.* 2003) and sex ratios tend to be female biased (Choe and Kim 1988; Marshall 1981b). In a review of 50 collections of lice, 38% did not differ significantly from unity and the other 62% were predominately female (Marshall 1981b). However, male biases have been infrequently reported. In a survey of 125 louse metapopulations infesting neotropical birds, four had a significant male bias, while nine had a significant female bias, and the majority did not significantly differ from unity (Clayton *et al.* 1992).

Amblycera and Ischnocera are dorsoventally flattened with a horizontally positioned head with large mandibles. The mandibles in Amblycera are closer to the anterior margin of the head and parallel to the ventral surface (Marshall 1981a). The

antennae of Amblycera are also concealed in lateral grooves (Johnson and Clayton 2003). While the mandibles of Ischnocera are centrally located and inserted at approximately at a right angle to the head (Marshall 1981a), Ischnocera also have antennae that are visible and in some species, the male's antennae are enlarged and used for clasping the female during copulation (Johnson and Clayton 2003).

Amblycera and Ischnocera also have different diets. Amblycera are known to feed on feathers, blood, body exudates, skin and debris (Eveleigh and Threlfall 1976; Marshall 1981a; Nelson 1972). *Menacanthus stramineus* (Nitzsch), the chicken body louse, has been observed puncturing the quill of young feathers with its mandibles; this causes blood to flow from the quill (Wilson 1933). Some species, such as *Colpocephalum turbinatum* Denny, are cannibalistic and will eat their own eggs and nymphs in laboratory cultures (Nelson and Murray 1971). Ischnocera have a more restricted diet and only consume feather, skin and debris (Ash 1960; Marshall 1981a).

Feathers are found in the diets of both Amblycera and Ischnocera; however, not all feather types are equally consumed by all species. Feather consumption may be very specific. A louse will thrive when fed the correct feather type, from a certain area of the body, but if the same louse is fed a feather type from another area of the host body, it will fail to breed and soon dies (Ash 1960). Crutchfield and Hixson (1943) examined the crop of different species of lice infesting the domestic chicken (*Gallus allus* (Linnaeus)). The crops of *Lipeurus caponis* (Linnaeus) contained almost entirely hooklets from the primary and secondary feathers of the wings, while mostly barbs and some barbules were found in the crops of *Goniocotes* gigas Taschenberg. When the chewing lice of rock pigeons (*Columba livia* Gmelin) were fed feathers from different parts of the body,

Campanulotes compar (Scopoli), *Hohorstiella lata* (Piaget), *C. columbae*, and *C. turbinatum* only survived on feathers from fluffy parts of body feathers (Nelson and Murray 1971). However, upon closer examination of rock pigeons, not all of these species were found exclusively in the body feathers. When the host body was broken down into different regions, *C. compar* was found mostly on the neck, back, sides, breast and vent; while its eggs were found in all of these body regions, they were also seen on the wings in large numbers (Nelson and Murry 1971). *Hohorstiella lata* was found scattered over all regions of the body; however, their eggs were found almost solely on the head. *Columbicola columbae* and its eggs were seen predominately on the wings, but a few were also found on the other regions of the body. *Colpocephalum turbinatum* was mainly found on the wings, but also seen on the tail and vent. The eggs of *C. turbinatum* were also mainly found on the wings, but could be also found on the tail (Nelson and Murry 1971). Therefore, just because a species lays its eggs in one area of the host's body, that does not mean it also consumes those feathers, as seen with *C. columbae*.

Dubinin (1947) was the first to document that different species of chewing lice upon the same avian host each have their own distinct spatial distribution, with his now famous illustration of the glossy ibis (*Plegadis falcinellus*, Linnaeus). Since then, many researchers have examined the spatial distribution of chewing lice (Ballard and Ring 1979; Choe and Kim 1988; Clay 1974; Nelson and Murray 1971; Strilchuk 1976; Wheeler and Threlfall 1986). From these studies, a few general patterns have emerged. Amblycera are fast moving, less site specific and have been seen running across the skin of their hosts, while Ischnocera have more defined distributions and are less mobile (Ash 1960; Marshall 1981a). In addition, ischnoceran lice found in the same body regions on

different hosts have similar morphological structures, which are highly correlated to grooming escape behaviours (Johnson *et al.* 2012). Along with this, Ischnocera are highly specialized for moving through feathers; therefore, they rarely venture onto the skin or leave their host after its death. Conversely, species of Amblycera have been observed to abandon their host after its death (Ash 1960; Marshall 1981a).

The main way birds combat chewing lice is through preening, which is the manipulation of plumage with the bill, and to a lesser extent with foot scratching (Clayton 1991; Clayton *et al.* 2005). There are generally four morphological/behavioural combinations in lice; these correspond to the body region in which the louse is found: head, wing, body or generalist. Lice located on the head of their host are usually short, round-bodied and generally not so dorsoventrally flattened (Clay 1949). Some lice avoid preening by remaining in body regions birds cannot preen. Although foot scratching is still a concern for lice found on the head of their host, these lice have enlarged mandibles which they use to grip feather barbs as a form of attachment (Clay 1951). Wing lice possess a long slender body form (Johnson *et al.* 2012). When wing lice are disturbed by light, air flow, or simulated preening, they will do one of three things. The lice will either immediately stop moving and flatten themselves against the vein, move towards the base of the feather where they are concealed by the under coverlets, or remove themselves from the surface of the feather by inserting themselves between the barbs of the feather (Clayton 1991). Body lice are short and round; they escape preening by dropping from one feather to another or burrowing into the downy region of the feathers (Clayton 1991; Johnson *et al.* 2012). Finally, generalists have an intermediate body form, and they can be

found in all body regions and escape preening by moving quickly through the feathers (Clay 1949; Johnson *et al.* 2012).

When a bird is not able to preen effectively due to bill deformities or lethargy, its louse populations are usually greater than for birds that are able to preen properly (Boyd 1951; Clayton 1991; Ledger 1970; Pomeroy 1962; Rothschild and Clay 1952). Clayton (1991) observed a house sparrow (*Passer domesticus* (Linnaeus)) with a deformed bill that was host to over 1200 *Brueelia subtilis* (Nitzsch), compared to ten normal house sparrows which had a mean intensity of 20 lice (range 0-56). This has been experimentally confirmed by using beak-clipping and bits which prevent the mandibles from completely closing, to prevent lice being removed during preening (Clayton 1991). Deformed and missing feet can also cause louse populations on the head and upper body of the bird to increase. An elevated number of eggs was observed on a one-legged sanderling (*Calidris alba* Pallas) compared to 78 two-legged birds examined at the same site (Clayton 1991).

When louse populations become large, they can have a negative impact on their host's fitness (Barbosa *et al.* 2002; Brown *et al.* 1995; Hoi *et al.* 2012). Large louse populations have been shown to reduce a bird's feather mass by 23-28% (Bush and Malenke 2008; Clayton 1990; Clayton 1991). Booth *et al.* (1993) compared the feather damage and metabolic rate of rock pigeons with bits versus those without in a wild population. Upon recapture, bitted pigeons had a mean intensity of 450 lice and showed a significant reduction in feather mass compared to non-bitted pigeons, which had a mean intensity of 104 lice. Feather damage in high-load pigeons is thought to have decreased the insolative effectiveness of the plumage due to increased whole-body thermal

conductance (Booth *et al.* 1993) . The body temperature of high-load pigeons did not differ significantly from low-load pigeons; however, the metabolic rate of high-load birds was 8.5% higher than low-load birds. From these results, Booth *et al.* (1993) proposed that high-load birds maintain a constant body temperature, despite increased thermal conductance, by elevating their metabolic rates.

Lice have also been shown to impact mate selection in their hosts (Kose *et al.* 1999). Hamilton and Zuk (1982) hypothesized that bright ornamentation has evolved as a way to signal parasite resistance to potential mates. Since lice feed mainly of feathers, they may impact the appearance of the plumage. When female rock pigeons were given the choice between lousy males and clean males (no lice present), females chose clean males in 16 of 21 trials (Clayton 1990). In addition to this, the presence of lice also had an impact on male display behaviour. The mean per cent display time of clean males was 15%, compared to 8% for lousy males (Clayton 1990).

Large louse populations reduce feather mass and affect mate selection; however, normal louse populations appear to have very little effect on their hosts (Ash 1960). The majority of species of lice have an aggregated distribution across their host populations; therefore, many hosts will have few lice while a few host have many lice (Anderson and Gordon 1982). It is these smaller populations of lice that are believed to allow lice to persist. If a small louse population has little to no effect on its host, the host has little to gain by removing it (Clayton 1991). However, there are few species of lice known to be vectors of parasitic nematodes, in the Charadriiformes, Anseriformes, Gruiformes and Podicipediformes (Bartlett 1993; Bartlett and Anderson 1987; Bartlett and Anderson 1989; Cohen *et al.* 1991; Seegar *et al.* 1976).

In order to be a successful vector, a louse must be able to disperse to new hosts. Chewing lice disperse mainly through direct contact. Vertical transmission is usually how uninfected individuals become infested with chewing lice (Brooke 2010; Clayton and Tompkins 1994; Darolova *et al.* 2001; Harbison *et al.* 2008; Marshall 1981a). Black-headed gull chicks (*Chroicocephalus ridibundus* (Linnaeus)) less than a day old had adult *Saemundssonia lari* (Fabricius) on them (Broek 1967). On other bird species, such as common swifts (*Apus apus* (Linnaeus)), lice are not observed on nestlings until several days after hatching; *Dennyus hirundinis* (Linnaeus) was not observed on nestlings until 12-14 day after hatching (Lee and Clayton 1995). Ash (1960) proposed that Amblycera are first to appear on nestlings, since they would be able to find food before feathers were present. However, *S. lari,* which appears on gull chicks within the first few hours after hatch, is an ischnoceran. Therefore, generalizations about when or what species of lice disperse first are not possible. Even the developmental stage at which lice disperse depends on the species of louse. On gull chicks, only adult *S. lari* were found (Broek 1967), but Lee and Clayton (1995) observed mainly nymphs of *D. hirundinis* on two-week old swift nestlings; louse eggs were not observed on nestlings until after five weeks of age, which is a three week gap from when lice were first observed to when eggs were present. Interestingly, approximately three weeks is the time it takes many species of lice to mature from first instar nymphs into adults (Marshall 1981a). Lice also disperse horizontally through direct contact, such as during mating, fighting or roosting (Brooke and Nakamura 1998; Darolova *et al*. 2001; Harbison *et al.* 2008; Hillgarth 1996). Horizontal dispersal has been shown experimentally between European bee-eaters (*Merops apiaster* Linnaeus) (Darolova *et al.* 2001). One member of a wild mating

pair was deloused, and of the eight birds recaptured four to five weeks later, all of them were infested with lice. Cuckoos also accrue lice through horizontal transmission (Brooke and Nakamura 1998; Lindholm and Venter 1998). The common cuckoo (*Cuculus canorus* Linnaeus) lays its eggs in the nest of passerines and does not return. When cuckoo chicks from passerines nests were inspected, they had no cuckoo-specific lice (Brooke and Nakamura 1998; Lindholm and Venter 1998); however, birds within their first year on their way to the breeding grounds were infested before breeding with cuckoo-specific lice (Brooke and Nakamura 1998).

Both of these modes of dispersal rely on contact, but how often do lice become dislodged during flight or some other amount of vigorous movement? The wing louse, *C. columbae* on rock pigeons, was studied by outlining a 1cm square on the fifth primary feather with Scribbles® paint to create a ridge that prevented lice from crawling outside the defined area and then two lice were placed inside the square and the bird was allowed to fly a distance of 50-100m (Clayton *et al*. 2003). Of the 40 trials, 95% of the lice remained attached during flight. In addition, the same procedure was done to plucked feathers by attaching them to a fan for 20 minutes to simulate a racing pigeon flying at a velocity of 85 km/h (Bush *et al.* 2006). From this, 91% of the lice remained attached. Therefore, the probability that lice disperse by being shed from their host is minimal.

Another way lice disperse horizontally is through phoresy (Harbison *et al.* 2008; Marshall 1981a). The main phoretic host used by chewing lice is hippoboscids; Keirans (1975b) reviewed all know cases of phoresy involving chewing lice and 405 of them involved hippoboscids. Of these cases, 44% of them involved flies carrying more than one louse. Peters (1935) recorded 31 lice from one hippoboscid. In addition to

hippoboscids, lice have been observed on fleas, flies, dragonflies, bees, butterflies and mosquitoes (Keirans 1975a). There are several documented observations of hippobosicds carrying pigeon lice (Ansari 1947; Clayton *et al.* 2004; Harbison *et al.* 2008; Macchioni *et al.* 2005; Martin 1934; Ward 1953); however, all of these refer to wing lice. The proportion of body and wing lice dispersing by the pigeon fly (*Pseudolynchia canariensis* (Macquart)) was experimentally examined. Clean rock pigeons were caged individually on one side of a shed and pigeons seeded with 50 wing and 50 body lice were individually caged on the other side (Harbison *et al.* 2008). Of the 80 clean pigeons, 45 become infested with wing lice and one became infested with a body louse. Of the pigeons infested with wing lice, 44% were infested with more than one louse.

It is also important to consider how lice are dispersed on a larger geographic scale. The distribution of lice depends solely on the distribution of the host; if the host is absent, the louse is not going to be present (Clay 1976). There are also cases when the louse is absent even when the host is present. In British Columbia, the bald eagle (*Haliaeetus leucocephalus* (Linnaeus)) is infested with *Laemobothrion vulturis*; however, in Manitoba *L. vulturis* has never been observed on bald eagles (Galloway, unpublished). There are a couple possible explanations for this: missing the boat, and abiotic environmental conditions. When hosts are introduced or colonize a new geographic region, they may not bring any lice with them, due to the aggregated nature of louse infestation; therefore, lice are "missing the boat" (Paterson and Gray 1997; Paterson *et al.* 1999). A potential example of this is the house sparrow, which was introduced into North America from Europe. In Europe, the house sparrow is host to 11 species of lice (Brown and Wilson 1975); however, in North America, it is host to only four (Brown and Wilson

1975). However, it is not known if these species truly missed the boat or if they were "lost overboard," which is when the host and its lice are introduced to a new region, but only the host colonizes the new region successfully (MacLeod *et al.* 2010). There are a number of reasons why a louse species would fail to become established in a new region when its host does so successfully. Perhaps a small number of lice were introduced or lice were not transmitted to different hosts. In addition, abiotic environmental conditions, such as relative humidity, greatly impact lice (Rudolph 1983). Lice acquire moisture using a water vapour uptake system (Rudolph 1983). If lice were introduced into a region that had a different relative humidity than their native region, this could be the cause of their failed introduction. Different species of lice will thrive at different humidity levels; this impacts how lice are globally distributed. When louse populations on mourning doves (*Zenaida macroura* (Linnaeus)) and inca doves (*Columbina inca* (Lesson)) in Arizona (arid region) were compared to populations in Texas (humid region), there were significantly fewer lice on doves in Arizona than Texas (Moyer *et al.* 2002). To insure other factors were not the cause of this difference in population structure, controlled experiments were conducted in which all other factors were held constant and only ambient humidity was manipulated. These experiments produced similar results to what was seen in Arizona and Texas populations, with lice surviving longer in more humid conditions (Moyer *et al.* 2002). Experiments were also conducted to see if the plumage buffered the humidity, and it did not; humidity under the plumage was highly correlated to ambient humidity (Moyer *et al.* 2002). This geographical displacement of lice based on humidity is also seen in scrub-jays, and chickens (Bush *et al.* 2009; Fabiyi 1996).

In addition to geographical differences in population structure, louse populations also fluctuate throughout the year. There is a general trend for lice to become more numerous just prior to the host's breeding season. This increase then continues until chicks hatch, followed by a reduction in louse populations after offspring have hatched. This trend is seen on numerous British passerines (Ash 1960). It is seen in *Menacanthus eurysternus* (Burmeister) on starlings (*Sturnus vulgaris* Linnaeus) in England (Kettle 1983), in *Brueelia nebulosa* and *M. eurysternus* on starlings in North America (Boyd 1951), *Brueelia vulgata* (Kellogg) on house sparrows (Woodman and Dicke 1954), in *Ricinus picturatus* (Carriker), *Menacanthus* sp., and *Philopterus* sp., on orange-crowned warblers (*Oreothlypis celata* (Say)) (Foster 1969), and in *Menacanthus alaudae* (Schrank) and *Ricinus microcephalus* (Kellogg) on house finches, *Carpodacus mexicanus* (Müller) (Hamstra and Badyaev 2009). Louse populations increase when their hosts are most frequently coming into contact with others (mates and offspring), and therefore when the chance for successful louse dispersal is at its highest (Woodman and Dicke 1954). Louse populations of some species, such as *Brueelia nebulosa* and *M. eurysternus* on starlings, appear to overwinter as eggs (Boyd 1951). In the summer, the prevalence of *B. nebulosa* was 68.3% and in the winter it was 25.0%; however, when eggs are included, the summer prevalence was 76.6% and the prevalence in winter rose to 66.7%; the same pattern is seen in *M. eurysternus*. From this it would seem that both for these species, their reproductive cycle is reduced at lower temperatures (Boyd 1951; Peters 1928).

The conventional acceptance about host specificity in regards to lice has changed over time. When early taxonomists first started to identify lice, some tended to believe that each species of host had its own species of lice. This is no longer considered

acceptable for modern taxonomic revisions (Clayton *et al.* 1992). Approximately 67% of lice infest only one host (Johnson *et al.* 2011). Nevertheless, there are other species of lice that infest several hosts. *Menacanthus eurysternus,* for example, has been recorded at least from 118 bird species from 20 families (Price 1975).

Chewing lice with reference to Canada geese, mallards and other Anseriformes

There is not a lot of information about the chewing lice on Anseriformes. The majority of information comes from checklists such as: *A list of the chewing lice (Insecta: Mallophaga) from birds in New Zealand* (Pilgrim and Palma 1982) and *A checklist of lice of Hungary (Insecta: Phthiraptera)* (Vas *et al.* 2012). However, the checklist that has had the greatest influence on louse workers is *The Chewing Lice: World Checklist and Biological Overview* (Price *et al*. 2003). These lists do not contain any information about the global or regional distribution of different louse species; they are strictly lists of hosts on which each species of louse has been recorded (some also contain lists of synonyms). To get a better idea about the distribution of louse species, host-parasite lists from different locations should be consulted. For instance, to examine the distribution of lice on Canada geese and mallards in Canada, information was published by Baker *et al.* (1919), Brown and Wilk (1944), Peters (1934), Spencer (1948) and Threlfall *et al.* (1979). In Manitoba, there are two records of chewing lice on Anseriformes (Buscher 1965; Twinn 1935), unfortunately only one contains the species of direct interest in my thesis. Buscher (1965) examined 13 mallards infested by *Anaticola crassicornis* (Scopoli), *Anatoecus dentatus* (Scopoli) and *Trinoton querquedulae* (Linnaeus). He also recorded the prevalence of birds infested; 46.2% of mallards were infested with

ectoparasites; regrettably this includes not only chewing lice but feather mites as well. The chewing lice of Canada geese have never been reported in Manitoba.

Quantitative information on the infestation parameters of chewing lice on Anseriformes is scarce. The most comprehensive data are published in a three part series from Texas in which the prevalence and mean intensity of ectoparasites infesting northern cinnamon teals (*Anas cyanoptera* Vieillot) (Wilkinson *et al.* 1977), northern shovelers (*Anas clypeata* Linnaeus) (Broderson *et al.* 1977) and green-winged teals (*Anas crecca* Gmelin) (Canaris *et al.* 1981) were examined. The prevalence and mean intensity of chewing lice on mallards was reported by Rékási *et al.* (1997), who examined 70 mallards as part of a study to compare the infestation parameters of the lice on 15 different hosts.

In the literature there is disproportionally more information/records about the chewing lice infesting mallards than there is for Canada geese. There are no reported infestation parameters for any of the lice on Canada geese, which is surprising, since Canada geese are more frequently becoming residents of urban centres (Conover and Chasko 1985).

It is surprising that there is not more quantitative and ecological information on the ectoparasites of Anseriformes, especially ducks, since their internal parasites have been extensively studied, *e.g.*, Bush and Holmes (1986), Caver (2006), Mahoney and Threlfall (1978), Turner and Threlfall (1975). Hopefully this thesis will create a baseline of information about Canada geese and mallards, which others can use as a starting point when studying the chewing lice of Anseriformes.

CHAPTER 3: *Anatoecus* Species (Phthiraptera: Philopteridae) From Anseriformes in North America and Taxonomic Status of *Anatoecus dentatus and Anatoecus icterodes*

Abstract

Anatoecus is a genus of chewing lice (Phthiraptera: Philopteridae) with four species infesting Anseriformes in North America: *Anatoecus cygni* (Denny), *Anatoecus dentatus* (Scopoli), *Anatoecus icterodes* (Nitzsch), and *Anatoecus penicillatus* Kéler. Males of *A. dentatus* and *A. icterodes* are distinguishable by their genitalia; however, there are no known anatomical characteristics to distinguish females. *Anatoecus dentatus* and *A. icterodes* are recorded from at least 55 of the same host species worldwide. I examined the mitochondrial gene cytochrome c oxidase subunit I from the four *Anatoecus* spp. found infesting Anseriformes in North America, specifically with the intention of examining the taxonomic status of *A. dentatus* and *A. icterodes*. When sequences from these species were analysed using neighbour joining analysis, *A. dentatus* and *A. icterodes* were recovered in a well-supported monophyletic clade. However, *A. dentatus* and *A. icterodes* were paraphyletic with respect to each other. The average interspecific genetic distance of *A. dentatus* and *A. icterodes* (0.04%) was almost the same as the average intraspecific genetic distances of *A. dentatus* and *A. icterodes* 0.02% and 0.05%, respectively. Therefore, we formally synonymize *A. dentatus* and *A. icterodes* as *Anatoecus dentatus* (Scopoli, 1763) (new synonymy). In addition two new hosts for *A. penicillatus* were recorded: Canada goose (*Branta canadensis* (Linnaeus)) and snow goose (*Chen caerulescens* (Linnaeus)).

Introduction

Obligate ectoparasites must maintain a delicate balance between taking enough nutrition from their host to survive while not causing excessive or fatal harm. Chewing lice (Insecta: Phthiraptera) are permanent ectoparasites found on birds and mammals (Marshall 1981a). Since parasites can have detrimental effects on their hosts, it is important to understand their biology. In order to make accurate interpretations, confident identifications of all members of the community under study must be achieved.

Species of *Anatoecus* (Phthiraptera: Philopteridae) infest ducks, geese, swans (Anseriformes) and flamingoes (Phoenicopteriformes) (Price *et al.* 2003). There are six species of *Anatoecus* recorded from Anseriformes worldwide; however, two of these species, *Anatoecus clayae* (Kéler) and *Anatoecus regina* Ansari, are only recorded from hosts found outside of North America. The four species found on hosts that have at least part of their distribution in North America are *Anatoecus cygni* (Denny), *Anatoecus dentatus* (Scopoli), *Anatoecus icterodes* (Nitzsch), and *Anatoecus penicillatus* Kéler.

The majority of *Anatoecus* species infest one to three closely related host species. For example, *A. penicllatus* infests mute swans (*Cygnus olor* (Gmelin)), and *A. cygni* infests tundra swans (*Cygnus columbianus* (Ord)), trumpeter swans (*Cygnus buccinator* Richardson) and whooper swans *(Cygnus cygnus* (Linnaeus)). *Anatoecus dentatus* and *A. icterodes* are found on at least 67 and 70 host species, respectively, and co-infest at least 55 of the same host species worldwide (Price *et al.* 2003). Co-infestations among species of lice from the same genus are not unusual; however, co-infestations usually only occur on one or a small number of host species (Price *et al.* 2003). The extent to which *A. dentatus* and *A. icterodes* are found co-infesting the same species is extraordinary.

Females of all species of *Anatoecus* can be identified by the shape of the clypeal plate and characteristics of the terminal segments, except *A. dentatus* and *A. icterodes* (Kéler 1960). Interestingly, females of *A. dentatus* and *A. icterodes* are morphologically indistinguishable. However, males of all *Anatoecus* species are separable by characteristics of the genitalia (Fig. 3-1). Male *A. dentatus* have an effractor, which is an oval piece of dark-shiny chitin on the posterior margin of the endomeral plate, described by Cummings (1916) as resembling a "tin-opener without the handle" (Fig. 3-1A). Males of *A. dentatus* also have a conspicuous reticular comb on the hypoineral area (Cummings 1916) (Fig. 3-1A). *Anatoecus icterodes* lacks both the effractor and the reticular comb (Fig. 3-1B, *cf.* 3-1A.). The lack of distinction between females of *A. dentatus* and *A. icterodes*, coupled with both species co-infesting the head and neck of their host (Ash 1960; Strilchuck 1976) and being found together on at least 55 species of hosts, has raised questions about the validity of these two species (Emerson 1972).

DNA barcoding using the mitochondrial gene cytochrome c oxidase subunit I (COI) has been developed to assign specimens to species as well as to identify cryptic species in insects (Hebert *et al.* 2003). Specimens can be assigned to different species by using neighbour joining analysis in which species form monophyletic groups on a tree and by the presence of a barcoding gap between species that forms when interspecific and intraspecific genetic distances are compared. The barcoding gap appears when interspecific genetic variation exceeds intraspecific genetic variation (Barrett and Hebert 2005; Hebert *et al.* 2004). A barcoding gap threshold of the interspecific genetic distance being at least 10 times greater than the distance within samples has been proposed; therefore, if the interspecific genetic divergence is below the threshold, this would

support the taxonomic similarity among the samples and if the interspecific genetic divergence is above the threshold, the samples are distinct (Hebert *et al.* 2004). In the past, a 383 base pair (bp) portion of COI has been successfully used to differentiate species of chewing lice (Clayton *et al.* 2006; Johnson *et al.* 2001; Price and Johnson 2009; Price *et al.* 2008; Valim *et al.* 2011). Here we compare DNA sequence divergence of COI of *A. cygni*, *A. dentatus*, *A. icterodes* and *A. penicillatus* to assess the taxonomic status of *A. icterodes* and *A. dentatus.*

Material and Methods

Lice were collected from salvaged birds collected in Manitoba, Canada, from 1994 to 2012. The majority of birds came from wildlife rehabilitation centres where they were either euthanized or died in their care. A few birds were provided by Manitoba Conservation and by hunters. All birds have been salvaged under a Wildlife Scientific Permit (WB12483) issued by Environment Canada, Canadian Wildlife Service.

Each bird was individually bagged as soon as possible after death and frozen for a minimum of 48 hours in order to kill all ectoparasites. Birds were allowed to thaw at room temperature until the wings and legs were movable. To remove ectoparasites, birds were washed twice with warm water and liquid soap and once with just warm water. The contents of each washing were poured through a 90 μm mesh screen and rinsed into a plastic 400mL storage container with either 70% or 95% ethanol to preserve the contents. Specimens were originally stored in 70% ethanol but were subsequently switched to 95% ethanol when the necessary of DNA analysis became apparent. Lice from each sample were sorted under a dissecting microscope.

In order to see the genitalia clearly, lice were cleared and mounted onto microscope slides. Mounting can be done after DNA extraction; however, this would have lead to hundreds of unnecessary extractions. Instead, half the louse was cleared and mounted onto a slide. If the louse was male the abdomen was mounted and if the louse was female the head was mounted; the other half of the louse was placed into an Eppendorf tube for DNA extraction. From this procedure, specimens were identified to species and selected for DNA extraction. All slides were prepared using the method described by Richards (1964) and vouchers were deposited in the J.B. Wallis - R.E. Roughley Museum of Entomology, University of Manitoba.

DNA was extracted from the portion of the louse placed in the Eppendorf tube using the DNeasy™ Tissue Kit (Qiagen, Valencia, California) following the manufacturer's protocol for animal tissue using spin columns. The DNA extract was used for PCR amplification of the COI gene using primers LCO1490 and HCO2198 (Folmer *et al.* 1994). Each PCR reaction mixture included 20.0-50.0 ng/µl of DNA template, 1X Buffer (0mM Tris-HCl, 550mM KCL, 1.5mM $MgCl_2$, ph 8.3@25°C) (New England Biolabs (NEB)), 0.2mM dNTP (NEB), 4.0uM MgSO4, 0.4µM of each primer, one unit of *Taq* (NEB) and enough purified water to reach a final volume of 25µL. Amplification was carried out using a MyCycler Thermal Cycler (BioRad -170-9701EDU). The thermal regime consisted of an initial denaturation of one minute at 95°C followed by 35 cycles of 15 seconds at 95°C, 15 seconds at 46°C and 45 seconds at 72°C, with a final extension of four minutes at 72°C. Sequences were obtained using an ABI3730 sequencer from the University of Kentucky, Advanced Genetics Technology Center (refer to Table 2 for accession numbers).

Sequences were aligned by eye using BioEdit 7.2.0 (Hall 1999). As there were no indels, alignment was trivial and the ends were trimmed to minimize missing data across taxa. Genetic distances were calculated using Kimura's two-parameter model (K2P) (Kimura 1980) for base substitutions in MEGA v. 5.1 software (Kumar *et al.* 2004), following the Barcode of life data system (BOLD) protocol (Ratnasingham and Hebert 2007). A neighbour-joining (NJ) analysis was performed based on these distances using MEGA software. MEGA was also used to perform bootstrap analysis for the NJ analysis (1000 replications) (Kumar *et al.* 2004). *Anaticola crassicornis* (Scopoli), a common chewing louse infesting ducks, was selected as the outgroup and sequences for this species were obtained from GenBank (Accession numbers: NC015998.1 and DQ007339).

Results

In the 19 years that birds were examined for ectoparasites, 28 species of anseriform birds were examined and 17 of them were infested with *Anatoecus* spp. in Manitoba, Canada (Table 3-1). In all host species examined in which *A. dentatus* and *A. icterodes* were present, *A. icterodes* was more frequently observed than *A. dentatus* with an average of nine *A. icterodes* to one *A. dentatus.*

DNA was sequenced from 60 specimens of *Anatoecus,* which were collected from 18 hosts, representing seven species (Table 3-2). Hosts from which lice were acquired for sequencing were salvaged from 1999 to 2012; 10 were from Winnipeg, four were from within 360km of Winnipeg and four had no locality data, but all came from within the province of Manitoba, Canada.

The final alignment of COI was 519bp in length of which 189 sites were variable and 189 were parasimony informative and the genetic distances of all specimens are presented in Table 3-3. The average interspecific genetic distance between *A. icterodes* and *A. dentatus* was 0.04%, which equates to less than 1 substitution per 519 bp. The next lowest interspecific genetic distance was 18.2% between *A. icterodes* and *A. cygni*. The average intraspecific genetic distances for *A. icterodes* and *A. dentatus* were 0.05% and 0.02%, respectively. These average intraspecific genetic distances are comparable to the other *Anatoecus* spp. which range from 0 to 0.1%. The average interspecific genetic distance between *A. icterodes* and *A. dentatus* does not meet the barcoding gap threshold of being 10 times greater than the average intraspecific genetic distances. The average interspecific genetic differences between all other combinations of *Anatoecus* spp. exceed the 10 times barcoding gap threshold for the intraspecific genetic differences of those species and therefore support specific distinctness for *A. penicillatus* and *A. cygni.* All specimens of *A. icterodes* and *A. dentatus* were recovered in a well supported monophyletic clade (bootstrap support = 1000) regardless of host (Fig. 3-2). However, *A. dentatus* and *A. icterodes* were recovered as paraphyletic with respect to each other, which is not surprising given the extremely low interspecific distances between these species.

I have also observed two new host records for *Anatoecus penicillatus.* In 1995, *A. penicillatus* was first collected from a Canada goose (*Branta canadensis* (Linnaeus)). Since then, it has been recorded from 27 Canada geese. *Anatoecus penicillatus* was found on a snow goose (*Chen caerulescens* (Linnaeus)) in 1998 and has been recorded from two additional snow geese. Specimens were sent to Ricardo Palma for identification and

we compared our specimens to the syntype of *A. penicillatus,* which was borrowed from the K.C. Emerson Entomology Museum, Oklahoma State University. **Material Collected:** 113 ♂, 211♀, *ex* Canada geese from Winnipeg, Stony Mountain, Selkirk, Headingley, Hecla Island, Pine Falls, Oakbank and East St. Paul, Manitoba, Canada; 18 ♂, 7♀, *ex* snow geese, from Winnipeg and Winnipeg Beach, Manitoba, Canada. Some vouchers of *A. penicillatus* (not specimens used for this study) were also deposited in the Canadian National Collection of Insects, Arachnids and Nematodes.

Anatoecus penicillatus has been collected from hosts that were also infested with *A. dentatus* and *A. icterodes.* Of the 30 geese from which *A. penicllatus* was collected, 14 Canada geese also had *A. icterodes,* one Canada goose was infested with both *A. dentatus* and *A. icterodes,* and one snow goose was also infested with both *A. dentatus* and *A. icterodes.*

Discussion

There is good genetic evidence based on the lack of a barcoding gap (Table 3-3), that *A. dentatus* and *A. icterodes* are conspecific. The average interspecific genetic distance between *A. dentatus* and *A. icterodes* was 0.04%, considerably smaller then the next smallest interspecific distance of 18.2% between *A. icterodes* and *A. cygni.* In other studies on lice, the genetic divergences between species were greater than 14.5% for *Myrsidea* spp. (Phthiraptera: Menoponidae) (Price and Johnson 2009) and greater than 7.0% for *Dennyus spp.* (Phthiraptera: Menoponidae) (Clayton *et al.* 2006).

Hosts of *A. dentatus* and *A. icterodes* are found around the world; however, we have only sampled birds within Manitoba. Since these hosts are migratory in North America, and some, such as the Canada goose, may travel from Canada to northern

Mexico to overwinter (Saunders and Saunders 1981), this allows different populations to interact. Although only birds collected from Manitoba were examined, because of their migratory behaviour, they should contain a reasonable representation of the population diversity of louse fauna that occurs over a wide area of North America. Therefore we formally propose the synonymy of *A. icterodes* and *A. dentatus*, as *Anatoecus dentatus* (Scopoli) (new synonymy).

The effractor and reticular comb are fascinating structures, although their function is unknown. *Anatoecus dentatus* (new syn.) without the effractor and reticular comb outnumbered those with the effractor and reticular comb nine times to one. In the course of this study, hundreds of male *A. dentatus* (new syn.) were mounted onto slides. All of the lice examined, with the exception of one, were clearly distinguishable as either expressing the effractor and reticular comb or not. In one louse from a brant goose (*Branta bernicla* (Linnaeus)), the reticular comb was not completely developed (Fig. 3-3). However, an effractor was present so it was initially identified as *A. dentatus*. This was not the only male *Anatoecus* on this host; it was also infested with nine males that lacked an effractor and reticular comb.

The effractor and the reticular comb are always expressed together; however, it is not known what triggers the expression of these structures or how many genes are involved. Expression could also be based on environmental cues, or stress caused by resource availability or competition. Since the effractor and reticular comb are located in the same region as the male genitalia, they could possibly serve some function during mating or reproduction. If would be interesting to see if females are biased when offered a choice between a male with an effractor and reticular comb versus a male without.

Anatoecus penicllatus was previously recorded only from the mute swan (Price *et al.* 2003). Mute swans are native to Eurasia and were introduced to North America from the mid 1800s through the early 1900s as embellishments to parks and large estates as well as exhibits in zoos (Ciaranca *et al.* 1997). Since then, the mute swan has escaped captivity and the greatest concentration of them can be found along the Atlantic coast from Maine all the way to South Carolina (Ciaranca *et al.* 1997). There are also populations of mute swans along the northern shores of Lake Erie and Lake Ontario as well as on Vancouver Island and the Fraser River delta of British Columbia (Cadman *et al.* 1987; Campbell *et al.* 1990). There are no known established populations of mute swans in Manitoba (Parsons 2003) and none have come through the rehabilitation centres in Manitoba during the time this study was conducted. For this reason, it is unlikely that the specimens of *A. penicillatus* found on Canada geese and snow geese were the result of contamination in the rehabilitation centres.

Anatoecus penicillatus has invaded hosts that have a smaller body size than its native host. This is opposite to what Bush and Clayton (2006) found when they transferred *Columbicola columbae* (Linnaeus) (Phthiraptera: Philopteridae) and *Campanulotes compar* (Burmeister) (Phthiraptera: Philopteridae) from rock pigeons (*Columba livia* Gmelin) to smaller, novel Columbiformes. When birds were able to preen normally, introduced louse populations were reduced to near zero. *Columbicola columbae,* a wing louse, was not able to insert itself fully between the furrows in the barbs of the contour feathers. *Campanulotes compar*, a body louse, was not able to burrow into the downy feathers as successfully when on the smaller exotic hosts due to the smaller amount of downy feathers. Therefore, *C. columbae* and *C. compar* were more

susceptible to preening by smaller, novel host birds. However, *A. penicillatus* is found on the head of its hosts (Grossi and Galloway, unpublished), where preening may be less efficient, therefore feather size may not be a restricting factor.

Over the past seven years (2006-2012), *A. penicillatus* has been found regularly on Canada geese and snow geese. Therefore, it appears *A. penicillatus* has expanded its host range and has established populations on these novel hosts. Canada geese have also been introduced to Europe, where the mute swan is native. It would be very interesting to see if *A. penicillatus* has also made this transition to Canada geese in Europe.

The mute swan, in addition to being host to *A. penicillatus*, is host to *A. dentatus*, which is also recorded from Canada geese and snow geese (Price *et al.* 2003). In our study, *A. dentatus* and *A. penicillatus* were recorded co-infesting 15 Canada geese and have been observed together on the head and neck of their hosts (Grossi and Galloway, unpublished).

Finding two species of louse from the same genus recorded from the same host is not uncommon. For example, *Columbicola baculoides* (Paine) and *Columbicola macrourae* (Wilson) can be found together on mourning dove, *Zenaida macroura* (Linnaeus) (Galloway and Palma 2008). There is even one bird, the sora (*Porzana carolina* (Linnaeus)), which is host to two pairs of species of lice within the same genus (Galloway 2004): *Fulicoffula americana* Emerson, and *Fulicoffula distincta* Emerson, and *Rallicola mystax* (Giebel) and *Rallicola subporzanae* Emerson. The ability for two species of the same genus to co-exist on one host seems counterintuitive to the competitive exclusion principle (Gause's law), where two species with the same resource requirements cannot occupy the same niche (Gause 1934; Hardin 1960). By this

principle, either competition will drive one species to extinction or the species will evolve adaptations that allow them to exploit non-overlapping niches. The majority of sampling techniques only capture a snapshot of the louse population and do not monitor its change over time. It seems *A. penicillatus* and *A. dentatus* (new syn.) are able to co-exist, suggesting they inhabit at least, in part, non-overlapping niches.

To conclude, *A. icterodes* and *A. dentatus* are formally synonymised as *Anatoecus dentatus* (Scopoli) (new synonymy), and Canada geese and snow geese are identified as new hosts for *A. penicillatus.* Nevertheless, we encourage others to replicate this study in other locations outside of North America to further test this synonymy. We also encourage louse workers to examine anseriform birds to see if *A. penicillatus* has established populations on novel hosts elsewhere.

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Tables and Figures

Table 3-1. Male *Anatoecus dentatus* and *A. icterodes* collected from anseriform birds from 1994 to 2012 in Manitoba, Canada. The numbers in brackets represent total lice collected. Where both species were collected from the same bird, the first number in brackets is *A. dentatus* and the second is *A. icterodes*.

Host Species	No. of Hosts examined	No. of hosts with only *A. dentatus*	No. of hosts with only *A. icterodes*	No. of hosts with *A. dentatus* and *A. icterodes*
Anatinae				
Anas crecca	9	0	2 (4)	1 (1;1)
Anas clypeata	3	0	0	1 (2; 31)
Anas discors	15	1 (1)	2 (3)	3 (4; 9)
Anas platyrhynchos	295	10 (13)	30 (149)	28 (104; 296)
Aix sponsa	38	0	6 (7)	4 (10; 15)
Branta bernicla	2	0	0	1 (1; 9)
Branta canadensis	293	5 (5)	87 (714)	19 (53; 691)
Branta hutchinsii	11	0	4 (67)	0
Chen caerulescens	20	0	5 (11)	3 (16; 114)
Chen rossii	3	0	1 (3)	0
Aythyinae				
Aythya affinis	4	0	2 (10)	0
Aythya americana	5	0	2 (6)	0
Aythya collaris	1	0	1 (1)	0
Aythya valisineria	14	0	2 (2)	2 (15; 71)
Merginae				
Bucephala clangula	13	1 (1)	0	1 (6; 11)
Lophodytes cucullatus	26	0	1 (1)	1 (2; 11)
Oxyurinae				
Oxyura jamaicensis	5	0	0	1 (2; 7)
Total	733	17 (20)	145 (978)	65 (217; 1267)

Table 3-2. *Anatoecus* specimens chosen for sequencing with corresponding GenBank accession numbers and host from which they were collected from in Manitoba, Canada. Case number: the first four letters are the bird species, the number indicates the hospital case number, the next letters represent the source from which the host came (CEN = Wildlife Haven, PWRC = Prairie Wildlife Rehabilitation Centre, MC = Manitoba Conservation) and the last two numbers represent the year the bird was collected.

Host	Case Number	Louse sp.	Sex	Voucher #	Accession number
Anas crecca	AGWT/144/CEN/11	*A. dentatus*	♂	954	KF754407
		A. icterodes	♂	955	KF754415
Anas discors	BWTE/380/PWRC/11	*A. dentatus*	♂	957	KF754416
Anas platyrhynchos	MALL/405/PWRC/11	*A. dentatus*	♂	005	KF754376
				006	KF754391
				010	KF754393
				011	KF754380
		A. icterodes	♂	001	KF754394
				002	KF754381
				003	KF754382
				004	KF754383
				009	KF754395
				012	KF754384
		A. dentatus or *A. icterodes*	♀	013	KF754385
				015	KF754386
				016	KF754388
				017	KF754390
				018	KF754387
				019	KF754392
				020	KF754389
	MALL/1055/CEN/11	*A. dentatus*	♂	110	KF754378
				111	KF754376
		A. icterodes	♂	118	KF754409
				124	KF754410
	MALL/1543/CEN/11	*A. dentatus*	♂	367	KF754374
				375	KF754372
				376	KF754396
		A. icterodes	♂	369	KF754411
				370	KF754412
				373	KF754399
Aythya affinis	LESC/1/MC/11	*A. icterodes*	♂	951	KF754408
Branta canadensis	CAGO/1130/CEN/11	*A. dentatus*	♂	604	KF754402
				609	KF754375

				613	KF754400
		A. icterodes	♂	568	KF754406
				589	KF754414
	CAGO/1611/CEN/11	*A. dentatus*	♂	782	KF754398
				790	KF754373
		A. icterodes	♂	792	KF754404
				794	KF754403
				795	KF754405
	CAGO/41/PWRC/11	*A. icterodes*	♂	884	KF754401
		A. penicillatus	♂	882	KF754363
				883	KF754360
				885	KF754364
	CAGO/001/CEN/12	*A. icterodes*	♂	552	KF754379
	CAGO/1562/CEN/09	*A. penicillatus*	♂	913	KF754365
				914	KF754366
	CAGO/1557/CEN/09	*A. penicillatus*	♂	910	KF754358
				911	KF754359
	CAGO/381/PWRC/11	*A. penicillatus*	♂	880	KF754361
				881	KF754362
				879	KF754367
	CAGO/397/PWRC/11	*A. icterodes*		246	KF754397
Bucephala clangula	COGO/1/MC/11	*A. icterodes*	♂	963	KF754417
Cygnus columbianus	TUSW/211/CEN/09	*A. cygni*	♂	895	KF754368
				905	KF754371
	TUSW/1/MC/10	*A. cygni*	♂	888	KF754370
				900	KF754369

Table 3-3. Average interspecific and intraspecific genetic distances (K2P) of CO1 (519bp) with a bootstrap analysis (1000 replications) and corresponding standard errors (standard errors for average intraspecific genetic distance in brackets). Data are based on 62 sequences from five species of lice collected from seven species of Anseriformes in Manitoba, Canada. Two sequences of *Anaticola crassicornis* were downloaded from GenBank (NC015998.1 and DQ007339) and used as an outgroup taxon.

	Anatoecus icterodes	*Anatoecus dentatus*	Females	*Anatoecus penicillatus*	*Anatoecus cygni*	*Anaticola crassicornis*
Anatoecus icterodes (n=22)	**0.005 (0.0003)**	0.00018	0.00015	0.02085	0.01989	0.02542
Anatoecus dentatus (n=17)	0.00036	**0.0002 (0.0002)**	0.00011	0.02104	0.01994	0.02548
Females* (n=08)	0.00027	0.00011	**0.000 (0.000)**	0.02102	0.01988	0.02546
Anatoecus penicillatus (n=10)	0.18363	0.18566	0.18585	**0.0008 (0.0007)**	0.02295	0.03104
Anatoecus cygni (n=04)	0.18198	0.18335	0.18291	0.21289	**0.001 (0.001)**	0.02860
Anaticola crassicornis (n=02)	0.26961	0.27134	0.27062	0.34107	0.33570	**0.000 (0.000)**

*Females are either *A. icterodes* or *A. dentatus* since they are indistinguishable. All other lice listed are males.

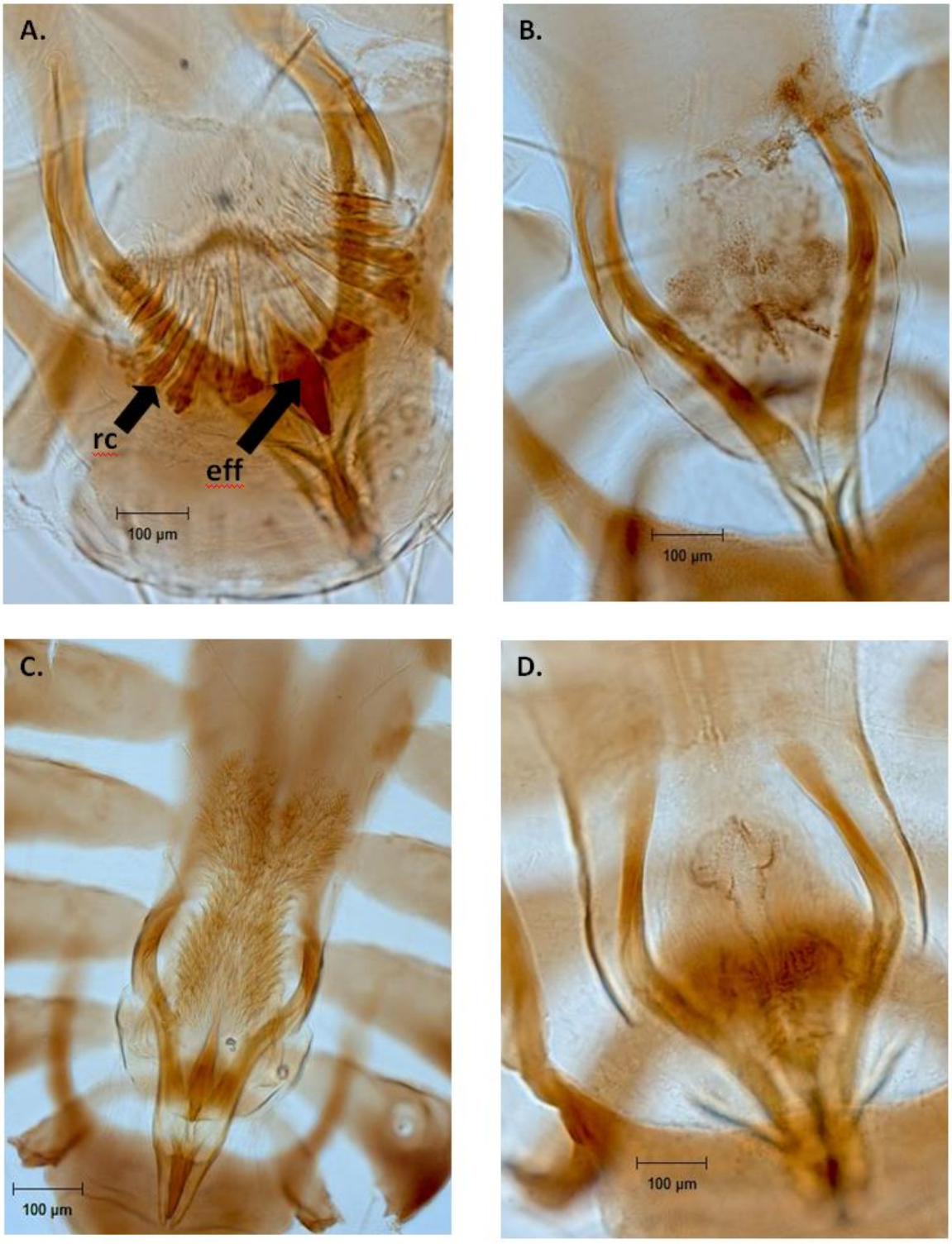

Fig. 3-1. The male genitalia of *Anatoecus* spp. (A) *Anatoecus dentatus*, (B) *Anatoecus icterodes*, (C) *Anatoecus penicillatus*, (D) *Anatoecus cygni* ; (eff = effractor; rc = reticular comb).

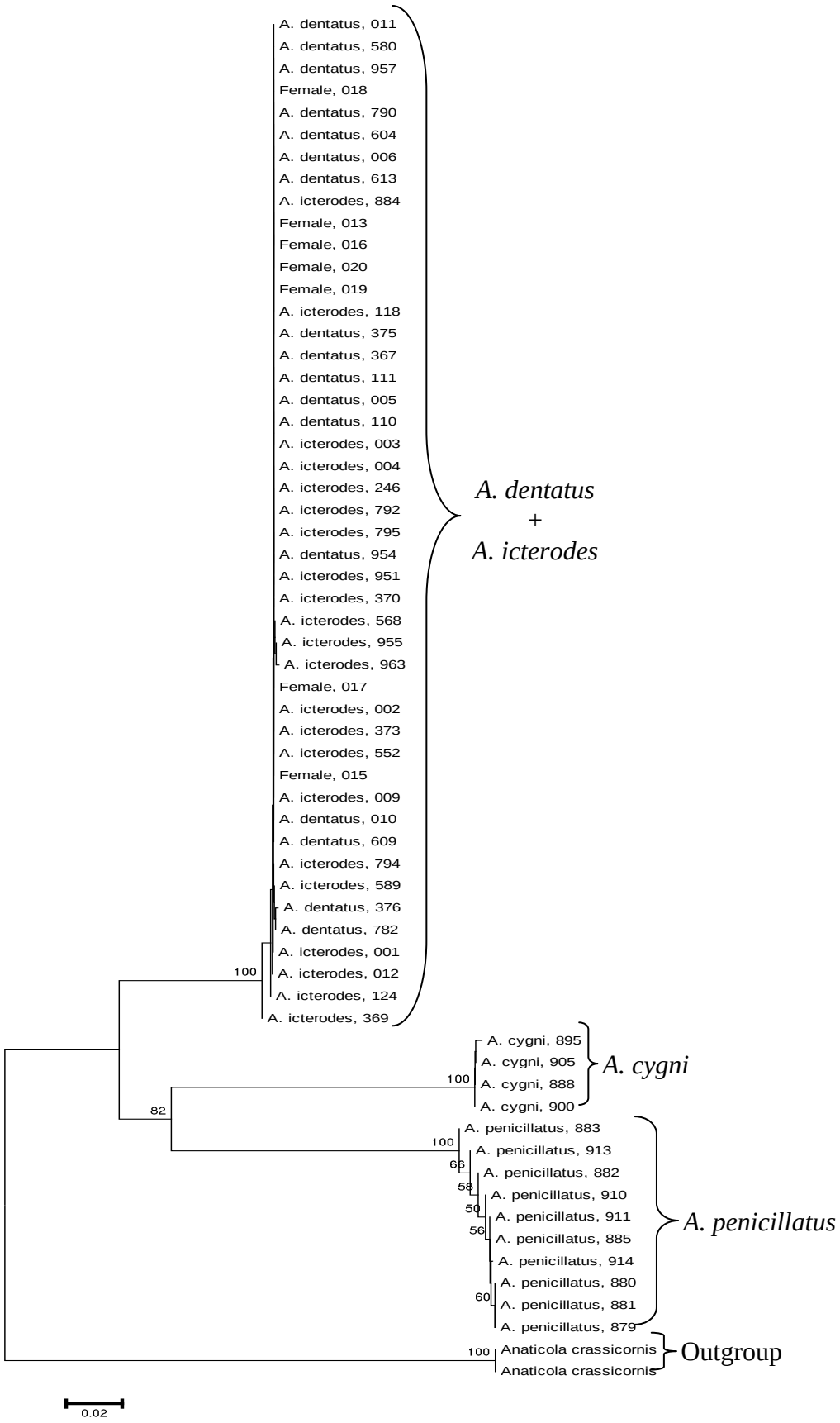
A. dentatus, 011
A. dentatus, 580
A. dentatus, 957
Female, 018
A. dentatus, 790
A. dentatus, 604
A. dentatus, 006
A. dentatus, 613
A. icterodes, 884
Female, 013
Female, 016
Female, 020
Female, 019
A. icterodes, 118
A. dentatus, 375
A. dentatus, 367
A. dentatus, 111
A. dentatus, 005
A. dentatus, 110
A. icterodes, 003
A. icterodes, 004
A. icterodes, 246
A. icterodes, 792
A. icterodes, 795
A. dentatus, 954
A. icterodes, 951
A. icterodes, 370
A. icterodes, 568
A. icterodes, 955
A. icterodes, 963
Female, 017
A. icterodes, 002
A. icterodes, 373
A. icterodes, 552
Female, 015
A. icterodes, 009
A. dentatus, 010
A. dentatus, 609
A. icterodes, 794
A. icterodes, 589
A. dentatus, 376
A. dentatus, 782
A. icterodes, 001
A. icterodes, 012
A. icterodes, 124
A. icterodes, 369
A. dentatus
+
A. icterodes
A. cygni, 895
A. cygni, 905
A. cygni, 888
A. cygni, 900
A. cygni
A. penicillatus, 883
A. penicillatus, 913
A. penicillatus, 882
A. penicillatus, 910
A. penicillatus, 911
A. penicillatus, 885
A. penicillatus, 914
A. penicillatus, 880
A. penicillatus, 881
A. penicillatus, 879
A. penicillatus
Anaticola crassicornis
Anaticola crassicornis
Outgroup
100
82
100
66
58
50
56
60
100
0.02

Fig. 3-2. Neighbour-joining tree (K2P) based on COI with bootstrap values over 50 (1000 replications) indicated at the relevant nodes. Data based on 63 sequences from four *Anatoecus* species. Only bootstrap values greater than 50% were included. Female specimens that are not distinguishable as *A. dentatus* or *A. icterodes* are labeled "Female". After the louse species name is the voucher number.

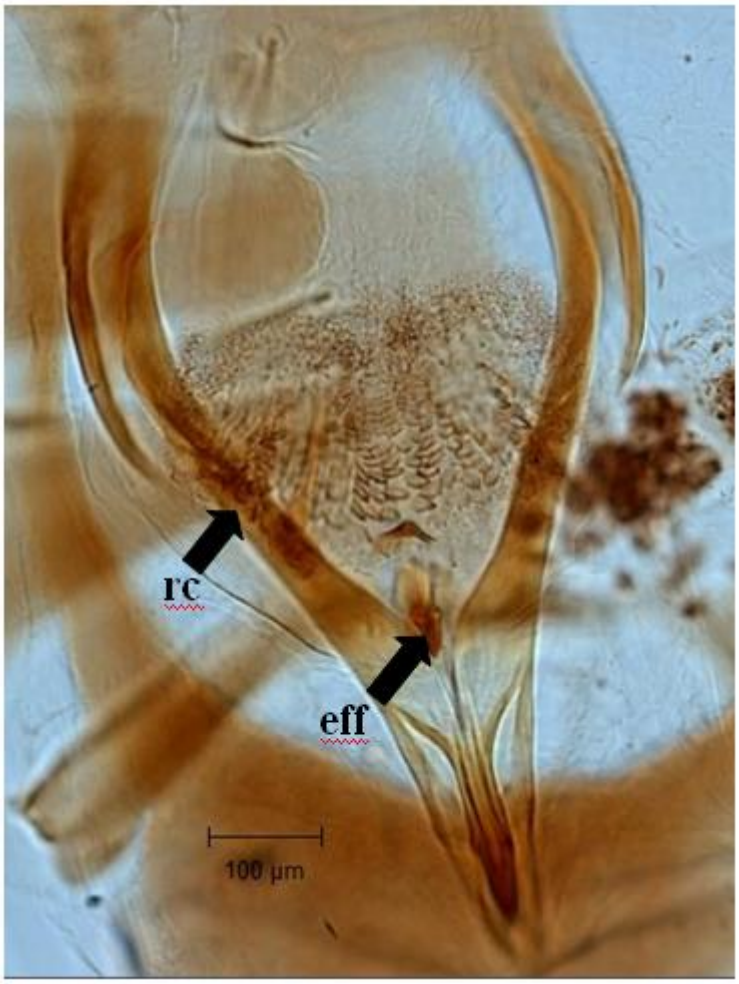

Fig. 3-3. *Anatoecus dentatus* from a brant goose (*Branta bernicla*) with an incompletely formed reticular comb; (eff = effractor; rc = reticular comb).

CHAPTER 4: Spatial Distribution of Chewing Lice (Phthiraptera: Menoponidae, Philopteridae) on Canada Geese (*Branta canadensis*) and Mallards (*Anas platyrhynchos*) (Aves: Anatidae)

Abstract

The spatial distribution of chewing lice on Canada geese (*Branta canadensis* (Linnaeus)) and mallards (*Anas platyrhynchos* Linnaeus) was examined with the hypotheses that Ischnocera will have more restricted distributions, that their body shape will be correlateed with where on the host body they are found and that Amblycera are going to be more widely distributed on the body of their hosts. Twenty Canada geese and eight mallards were dissected into five body regions: head and neck, wings, back, underside, and tail. Canada geese were infested with six species of lice (n=4214). *Anaticola anseris* (Gurlt) (n=628) were located mostly on the wings (86.0%), while *Anatoecus* spp. (n=510) were almost exclusively located on the head (98.2%). Adult *Ornithobius goniopleurus* Denny (n=469) were mainly located on the wings (58.8%) and the underside (21.7%), while nymphs (n= 1672) were more evenly spread across the head and neck (34.5%), underside (30.3%) and wings (21.3%). *Ciconiphilus pentiniventris* (Harrison) (n=930) was found on the wings (53.9%), back (20.2%) and underside (24.8%). *Trinoton anserinum* (Fabricius) (n=2) was present, but in insufficient numbers to make any conclusions about their distribution. Mallards were infested with four species of lice (n=556): *Anaticola crassicornis* (Scopoli) (n=201) was mostly located on the wings (82.9%), and *Anatoecus dentatus* (Scopoli) (n=234) was almost exclusively found on the head (99.6%). *Holomenopon maxbeieri* Eichler (n=55) was found on the

back (20.0%) and underside (49.1%) and *Trinoton querquedulae* (Linnaeus) (n=56) was located mostly on the wings (85.7%). *Anaticola* spp., *Anatoecus* spp., *Ciconiphilus pentiniventris,* and *Holomenopon* spp. had distributions that were typical of their suborder and body shape. *Ornithobius goniopleurus* is a generalist Ischnocera and *Trinoton querquedulae* is a site specific.. Therefore conventional hypotheses about louse distribution based on suborder and body shape do not always hold true.

Introduction

Host parasite systems are complex; one aspect of this interaction is how a parasite arranges itself in or on its hosts. There are many examples of ectoparasites spatially partitioning their hosts. The classic avian example was cited by Dubinin, where he mapped out the distribution of four genera of chewing lice infesting the glossy ibis (*Plegadis falcinellus* Linnaeus) (Dubinin 1947). Another well known example is the rock pigeon (*Columba livia* Gmelin), which is infested with eight species of chewing lice worldwide (Price *et al.* 2003); two of these, *Campanulotes compar* (Burmeister) and *Columbicola columbae* (Linnaeus), infest the body and wings, respectively (Nelson and Murray 1971). When studying how ectoparasites interact with one another, the spatial scale at which a study is conducted has to be taken into account, considering different species of feather mites can even partition a single feather (Mestre *et al.* 2011). Host partitioning also occurs among different stages of the same species. South American sea lion pups (*Otaria flavescens* Shaw) are infested with the sucking louse, *Antarctophthirus microchir* (Trouessart and Neumann). On the dorsal surface of the host, significantly more eggs and gravid females were found compared to the ventral surface, where

significantly more males, nongravid females and second and third instar nymphs were found (Leonardi *et al.* 2012).

Chewing lice (Insecta: Phthiraptera) are obligate ectoparasites of birds and mammals (Marshall 1981a) and rely predominantly on direct contact to disperse. The feathers of a bird are not all uniform, and this impacts how lice distribute themselves on their avian hosts. There are two suborders of chewing lice found on birds and they each have different strategies related to spatial distribution. Ischnocera are thought to be more site specific than Amblycera, which are more mobile and less restricted to a specific area of the host's body (Ash 1960; Marshall 1981a).

Host defence also impacts distribution among feather lice (Bush and Malenke 2008). Preening is the primary mechanism a host uses to defend itself against feather lice (Clayton *et al.* 2010). Each species of louse will exhibit certain behaviours to escape preening; these escape behaviours are highly correlated with louse body shape (Johnson *et al.* 2012). There are generally four behaviour/body shape combinations found in lice, each corresponding to the inhabited region of the host's body: head, wing, body and generalist. The louse body shape correlated to a region on the host applies primarily to Ischnocera because of their site specificity (Johnson *et al.* 2012; Marshall 1981a).

Lice found on the head usually have stout, round bodies which are not as dorsoventrally flattened as seen in chewing lice found elsewhere on the body (Clay 1949). Since birds primarily use their bills to preen, the head is usually not accessible by this method; therefore, having a slightly less dorsoventrally flattened body is not a disadvantage. However, feathers found on the head and neck are often narrower than elsewhere on the host's body (Clay 1949). Lice adapted to this feather structure have

large mandibles which are used to grip feather barbs as a form of attachment (Clay 1951). Lice inhabiting the wing usually have an elongated body and avoid preening by inserting themselves between the barbs of the flight feathers (Clayton 1991; Marshall 1981a). They also lay their eggs in the furrows between the barbs of the flight feathers (Nelson and Murray 1971). Lice that occupy the body of the host usually have rounded bodies and rounded head margins (Johnson *et al.* 2012). *Campanulotes compar* will avoid preening by dropping from one feather to another or by burrowing into the downy region on the feathers (Clayton 1991). Some lice are generalists and escape preening by actively moving about the feathers. These lice are not associated with any particular body region and have an intermediate body shape.

It is important to determine the spatial distribution of lice on different hosts, so that invasion events are accurately interpreted. Within at least the last ten years, *Anatoecus penicillatus* Kéler has expanded its distribution in North America and is now found regularly on Canada geese (*Branta canadensis* (Linnaeus)) and snow geese (*Chen caerulescens* (Linnaeus)) (Chapter 3). Previously, *A. penicillatus* was only recorded from mute swans (*Cygnus olor* (Gmelin)) (Price *et al.* 2003). Mute swans were introduced to North America from the mid 1800s through the early 1900s (Ciaranca *et al.* 1997).

In 2012, the spatial distribution of chewing lice on Canada geese and mallards (*Anas platyrhynchos* Linnaeus) was studied as part of an ongoing ectoparasite survey at the University of Manitoba. Strilchuk (1976) also examined the spatial distribution of lice on mallards but he had a sample size of two. The objective of the present study was to describe the spatial distribution of different species of chewing lice infesting Canada geese and mallards. The hypotheses are that Ischnocera will have more restricted

distributions, that their body shape will correlate with where on the host body they are found and that Amblycera are going to be more widely distributed on the body of their hosts. Three genera of lice infest both of these hosts: *Anaticola, Anatoecus* and *Trinoton.* I predicted that each of these three genera would be found in similar body regions on Canada geese and mallards despite some being different species. Mallards are also host to *Holomenopon* spp. and Canada geese are host to *Ciconiphilus pectiniventris* (Harrison). Since *Holomenopon* spp. and *C. pectiniventris* have similar body shapes, I predicted they would be found in comparable body regions of Canada geese and mallards.

Material and Methods

Hosts were salvaged from wildlife rehabilitation centres or provided by hunters, under Wildlife Scientific Permit (CWS99-M023) issued by Environment Canada, Canadian Wildlife Service. Once euthanized or shot, birds were placed immediately into plastic bags and frozen for at least 48 hours at -20°C, in order to kill all ectoparasites. Birds were then thawed at room temperature.

Once the bird's appendages were easily movable, it was dissected into six body regions: head and neck, left wing, right wing, back, underside and tail. The head and neck were removed where the neck meets the clavicle. Each wing was then separated from the body where the head of the humerus meets the scapula. The back was skinned off, then the underside. The underside includes the breast, sides, flanks, belly, tibial feathers and vent. The tail was then removed; this included the uppertail and undertail coverlets. The bench was thoroughly examined for any lice that had fallen off during the dissection.

Each body region was then washed separately and lice were collected according to the procedure outlined in Chapter 3. Some lice were mounted on slides following the process outlined by Richards (1964) and all lice collected were deposited in the J.B. Wallis - R.E. Roughley Museum of Entomology, University of Manitoba, Winnipeg, Manitoba, Canada. *Anatoecus dentatus* (Scopoli) and *Anatoecus icterodes* (Nitzsch) are referred to as *A. dentatus,* according to the synonymy proposed in Chapter 3.

To visualize and compare different species or life stages of lice, CANOCO 4.5 bundled with CanoDraw for Windows was used to perform principle component analysis with a square root transformation.

Results

From March to December 2012, 20 adult Canada geese and eight adult mallards, were broken down into six body regions: head and neck, left wing, right wing, back, underside and tail. Since the left and right wing represent the same feather structure, they were combined and will be referred to as wings.

Canada geese (*Branta canadensis*)

Six species of lice were collected: *Anaticola anseris* (Gurlt), *A. dentatus, A. penicillatus, C. pentiniventris, Ornithobius goniopleurus* Denny and *Trinoton anserinum* (Fabricius). A total of 4214 lice was collected and had a rage of 0 - 1374 lice per bird. The majority of lice were found on the wings (39.9%), head (26.7%) and underside (20.9%); for spatial distribution of each species, refer to Table 4-1.

Anaticola anseris (n=628) was found primarily on the wings (80.6%). Adults and nymphs of *A. anseris* had a similar distribution on their host; this is illustrated on a principle component biplot (Fig. 4-1) by the vectors for the adults and nymphs pointing in the same direction and having a similar length. *Anatoecus* spp. (n=510) were found almost exclusively on the head and neck (98.2%). *Anatoecus penicillatus* (n=2 adults) was only observed on one Canada goose. This goose was also infested with *A. dentatus* (n=19 adults) and both species were only found on the head and neck of this bird. *Ciconiphilus pectiniventris* (n=930) was mainly found on the wings (53.9%) but not to the same extent as *A. anseris*; in addition to the wings, *C. pectiniventris* was found on the underside (24.8%) and the back (20.2%). Even though *C. pectiniventris* was found in several body regions, the adults and nymphs had a similar distribution across the host's body; this is supported by the vectors for adults and nymphs for *C. pectiniventris* being beside each other on the principle components biplot (Fig. 4-1). *Ornithobius goniopleurus* (n=2141) was mainly found on the underside (28.4%), head and neck (28.2%) and wings (26.5%). There is a large difference in distribution of adults and nymphs; adults were found predominantly on the wings (58.8%), while nymphs were found mainly on the head and neck (34.5%) and underside (30.3%). This is also reflected on the principle component biplot (Fig. 4-1); the vector for adults points towards the wings, while the vector for nymphs is influenced more by the head and neck, which results in the vector being located between the head and wings. Only two *T. anserinum* were collected, both from the head and neck; however, no conclusions about the spatial distribution of this species can be reached.

Mallard (*Anas platyrhynchos*)

Four species of chewing lice were collected: *Anaticola crassicornis* (Scopoli), *A. dentatus, Holomenopon maxbeieri* Eichler, and *Trinoton querquedulae* (Linnaeus). A total of 556 lice was collected, with a range of 4 - 213 lice per bird. The majority of lice were collected from the head and neck (45.0%) and wings (41.7%); for spatial distribution of each species refer to Table 4-2.

Anaticola crassicornis (n=201) was found primarily on the wings (82.9%), and the principle component biplot supports that the adults and nymphs had similar spatial distributions, with both species vectors pointing in the same direction (Fig. 4-2). *Anatoecus dentatus* (n=234) was almost exclusively found on the head (99.6%).

Both *H. maxbeieri* and *Holomenopon leucoxanthum* (Burmeister) have been recorded from mallards (Price *et al.* 2003). In this study, only three mallards were infested with *Holomenopon*; two mallards were infested with only adult *H. maxbeieri*, and one mallard was infested with only nymphs. No attempt was made to identify *Holomenopon* nymphs; however, the prevalence the *H. leucoxanthum* on mallards (n=87) was 2.0%, compared to *H. maxbeieri,* 10.8% (Chapter 5). *Holomenopon* (n=55) was most prevalent on the underside (49.1%) and back (20.0%). However, adults of *H. maxbeieri* were mostly found on the underside (51.6%) and wings (29.0%), while *Holomenopon* nymphs were found on the underside (45.8%), back (33.3%) and head (20.5%). This difference in spatial distribution between the adults and nymphs is illustrated in the principle component biplot (Fig. 4-2) with the vector for the adults being more influenced by the wings than the vector for the nymphs. *Trinoton querquedulae* (n=56) was

collected predominantly from the wings (85.7%) and there was no difference in distribution between the adults and nymphs (Fig. 4-2).

Comparison between lice on Canada geese and mallards

When *Anaticola* spp. and *Anatoecus* spp. from Canada geese and mallards are compared on a principle component biplot (Fig. 4-3), all *Anaticola* spp. vectors point towards the wings, while all *Anatoecus* spp. vectors point towards the head, indicating that they occupy similar body regions on both hosts.

Ciconiphilus pectiniventris and *H. maxbeieri* from Canada geese and mallards, respectively, were plotted on a principle component biplot (Fig. 4-4). Adult vectors for each species are plotted in similar directions, while vectors for nymphs of each species are almost 90° to each other. The biplot also shows that the wings have a greater influence on nymphs of *C. pectiniventris,* while the underside is more often occupied by the *Holomenopon* nymphs.

Discussion

Ischnoceran lice are known for being site specific (Ash 1960; Marshall 1981a); this was true for *Anaticola* spp. and *Anatoecus* spp. *Anaticola* spp. and *Anatoecus* spp. also fit the stereotypical distributions for their body shape; *Anaticola* is a long slender louse that is found predominantly on the wings and *Anatoecus* a short globular louse found almost exclusively on the head. However, *O. goniopleurus,* an ischnoceran on Canada geese was not confined to a specific area and had a distribution that resembles generalist species of Amblycera. *Ornithobius* also has an intermediate body shape that is long but not slender, with rounded head margins, which is seen in generalist Ischnocera.

Holomenopon and *C. pectiniventris,*amblyceran lice, also displayed generalist distributions. The majority of *Holomenopon* were found on the body, conversely the majority of *Ciconiphilus* were found on the wings. Ischnoceran and amblyceran lice both feed on feathers and skin debris; in addition to this, many species of amblyceran are known to feed on blood (Marshall 1981a). It is thought that this ability to feed on blood, coupled with being more mobile, allow Amblycera lice to avoid competition by moving around the host's body since they are not restricted to a specific feather structure (Choe and Kim 1988; Marshall 1981a). In the course of conducting this study, a red substance assumed to be blood was frequently observed in the gut of adults and nymphs of *O. goniopleurus.* The ability of *O. goniopleurus* to feed on blood may allow it to be more of a generalist in where it is found on the body of its host. *Trinoton querquedulae* on the other hand, which is an amblyceran, did not display a generalist distribution with 85.6% found on the wings on mallards.

In addition to *O. goniopleurus* being more of a generalist, its adults and nymphs had different spatial distributions. There are other examples of different life stages of chewing lice infesting different body regions of their host. *Quadraceps obliquus* (Mjöberg), on the common murre (*Uria aalge* (Pontoppidan)) also has this segregated distribution, with the breast and belly supporting most adults while the crissum and tail supported most nymphs (Choe and Kim 1988). On Canada geese, adult *O. goniopleurus* were mainly located on the wings (58.8%) and the underside (21.7%), while nymphs were more evenly distributed across the head and neck (34.5%), underside (30.3%) and wings (21.3%); adults were not found on the head and neck very often (5.8%). A large percentage of nymphs were found on the head and neck; however, this could be an

artefact of how the geese were dissected. The neck was removed right where it meets the body and not where the feather structure changes from narrow head feathers to downy feathers. Therefore the basal portion of the neck was covered in contour and downy feathers. Approximately one third of *O. goniopleurus* nymphs were found on the underside of the goose, which is also covered in contour and downy feathers. As a result, it is possible nymphs of *O. goniopleurus* found on the head and neck, as defined here, were located on the basal portion that was covered in contour and downy feathers and not the dorsal portions that were covered in narrow head feathers.

Adults and nymphs of *H. maxbeieri* also differed in their distribution, but not to the extent seen for *O. goniopleurus.* Adult *H. maxbeieri* were found on the wings (29.0%) and underside (51.6%), while nymphs were found on the head and neck (20.8%), back (33.3%), and underside (45.8%). The variation in distribution for adults and nymphs could be caused by lice using various body regions for different purposes. *Columbicola columbae* lays its eggs on the undercoverlets of the wings of pigeons; however, it feeds on the fluffy portion of the body feathers (Nelson and Murray 1971). To understand better how lice utilize different body regions, the spatial distribution of eggs should be examined.

Examining smaller sections of each bird may be helpful to determine better how species interact. One interaction that warrants closer examination is between *A. dentatus* and *A. penicillatus* on Canada geese. Previously, the mute swan was the only recorded host for *A. penicillatus* (Price *et al.* 2003); however, *A. penicillatus* has established itself on Canada geese and snow geese in North America (Chapter 3). *Anatoecus dentatus* and *A. penicillatus* were observed together on the head and neck. If the head and neck were

examined in smaller sections, it may be possible to determine what level of interaction occurs between these two species. It would also be interesting to compare where on the head and neck *A. penicillatus* is found on its original host, the mute swan, and compare that to their location on Canada geese and snow geese to see if they have made any modifications to their behaviour with their establishment onto Canada geese and snow geese.

Canada geese and mallards share three of the same genera of lice, *Anaticola, Anatoecus* and *Trinoton*; these three genera are also found on flamingos (Price *et al.* 2003). Strilchuk (1976) examined the spatial distribution of chewing lice on two mallards and Palma *et al.* (2002) looked at the spatial distribution of chewing lice on 250 live greater flamingo chicks (*Phoenicopterus roseus* Pallas). From the distribution of *Anaticola* spp. from these two publications as well as from the present study, it is apparent that *Anaticola* is a wing specialist. In Manitoba, 86.0% and 82.9% of all *Anaticola* were found on the wings on Canada geese and mallards, respectively. *Anaticola* from the two mallards that Strilchuk examined did not have such a clear preference for the wings; on these birds 34.5% where found on the wings and 65.5% were found on the back; however, 97.7% of the *Anaticola* eggs were found on the wings. On the greater flamingo, 70.2% of *Anaticola* were observed on the wings. *Anatoecus* is almost exclusively found on the head and neck, regardless of host. In the present study, 98.2% and 99.6% of all *Anatoecus* were found on the head of Canada geese and mallards, respectively. Strilchuk (1976) observed 92.3% of *Anatoecus* on the head and neck on mallards and Palma *et al.* (2002) observed 94.3% of *Anatoecus* on the head of the greater flamingo. *Trinoton* does not have such a clear pattern observed across different host

species. Peters (1928) described *Trinoton* as "very agile and strong of foot, infests the back and breast of most ducks"; however, *Trinoton* was on the wings of mallards 75% and 85.7%, respectively, in Strilchuk (1976) and in the present study. On flamingos, *Trinoton* was predominantly observed on the flanks (61.5%). On Canada geese in the present study, it was only found on the head; however, only two specimens were collected from Canada geese.

In some other studies in which spatial distribution of lice upon their hosts was also examined, paper towel was placed between the body and wings to prevent movement between these body regions (Nelson and Murray 1971; Strilchuk 1976). This was not done in the present study, so movement between the wings and body cannot be ruled out. However, after the hosts are placed in the freezer, if movement did occur, it would probably be from the wings to the body as the lice tried to escape the cold.

Ciconiphilus and *Holomenopon* have similar body shapes and because of this, it was predicted they would have comparable spatial distributions on Canada geese and mallards. Their distributions are both spread out over several body regions; however, their proportions in those regions differ between species. *Ciconiphilus* was found predominantly on the wings of Canada geese (53.9%), while *Holomenopon* was mainly on the underside (49.1%) on mallards. Even though these lice have very similar body shapes, they are not found in the same body regions on their hosts, therefore factors other than body shape may play a role in how a species distributes itself on its host.

In summary, *Anaticola* and *Anatoecus*, both ischnocerans, have clearly defined distributions on the wings and head, respectively; in addition, their body shapes are consistent with what you would expect to find in lice that occupy these regions.

Ornithobius goniopleurus is a generalist ischnoceran and *C. pectiniventris* and *Holomenopon* spp. are generalist amblycerans. However, even though *C. pectiniventris* and *Holomenopon* spp. have similar body shapes, their distributions are different. Even though *Trinoton querquedulae* is an amblyceran, its distribution is confined mostly to the wings. Therefore, what is currently known about the distribution Ischnocera and Amblycera on their host are generalizations of what is seen most commonly and should not be assumed to occur for all species. More detailed studies are needed to examine smaller sections of each host as well as egg distribution to gain a better understanding of how these species of lice interact.

Acknowledgments

This work would not have been possible without the staff at Wildlife Haven and Prairie Wildlife Rehabilitation Centre and the care they gave in processing hosts for this study. Thanks to John Christie for providing some Canada geese and to S. Repa and D. Dunlop for their technical support in washing birds. Funding was provided by a Discovery Grant held by Terry D. Galloway from the Natural Sciences and Engineering Council of Canada.

Tables and Figures

Table 4-1. Spatial distribution of chewing lice infesting 20 Canada geese (*Branta canadensis*) in 2012, Manitoba, Canada. Total numbers of lice collected from each body region are in brackets.

	Head and Neck	Wings	Back	Underside*	Tail
Anaticola anseris					
Adults	0.8% (2)	84.5% (207)	2.5% (6)	6.1% (15)	6.1% (15)
Nymph	1.6% (6)	86.9% (333)	4.2% (16)	6.5% (25)	0.8% (3)
Total	1.3% (8)	86.0% (540)	3.5% (22)	6.3% (40)	2.9% (18)
Anatoecus* spp.*					
Adults	97.5% (302)	1.9% (6)	0.6% (2)	0	0
Nymphs	99.5% (199)	0	0	0.5% (1)	0
Total	98.2% (501)	1.2% (6)	0.4% (2)	0.2% (1)	0
Ciconiphilus pectiniventris					
Adults	2.3% (5)	64.2% (138)	11.2% (24)	21.4% (46)	0.9% (2)
Nymph	0.4% (3)	50.8% (363)	22.9% (164)	25.9% (185)	0
Total	0.9% (8)	53.9% (501)	20.2% (188)	24.8% (231)	0.2% (2)
Ornithobius goniopleurus					
Adults	5.8% (27)	58.9% (276)	10.0% (47)	21.7% (102)	3.6% (17)
Nymphs	34.5% (578)	21.3% (357)	10.7% (180)	30.3% (507)	3.2% (53)
Total	28.2% (605)	29.5% (633)	10.6% (227)	28.4% (609)	3.3% (70)
Trinoton anserinum					
Adults	100% (1)	0	0	0	0
Nymphs	100% (1)	0	0	0	0
Total	100% (2)	0	0	0	0
Total	26.7% (1124)	39.9% (1680)	10.4% (439)	20.9% (881)	2.1% (90)

* Underside includes: breast, sides, flanks, belly, tibial feathers and vent.

** Includes *Anatoecus dentatus* and *Anatoecus penicillatus.*

Table 4-2. Spatial distribution of chewing lice infesting eight mallards (*Anas platyrhynchos*) in 2012, Manitoba, Canada. Total numbers of lice collected from each body region are in brackets.

	Head and Neck	**Wings**	**Back**	**Underside***	**Tail**
Anaticola crassicornis					
Adults	6.5% (6)	72.8% (67)	3.3% (3)	7.6% (7)	9.8% (9)
Nymphs	3.4% (4)	90.7% (108)	4.2% (5)	0	1.7% (2)
Total	4.8% (10)	82.9% (175)	3.8% (8)	3.3% (7)	5.2% (11)
Anatoecus dentatus					
Adults	98.7% (74)	0	0	1.3% (1)	0
Nymphs	100% (159)	0	0	0	0
Total	99.6% (233)	0	0	0.4% (1)	0
Holomenopon maxbeieri*					
Adults	3.2% (1)	29.0% (9)	9.7% (3)	51.6% (16)	6.5% (2)
Nymphs	20.8% (5)	0	33.3% (8)	45.9% (11)	0
Total	10.9% (6)	16.4% (9)	20.0% (11)	49.1% (27)	3.6% (2)
Trinoton querquedulae					
Adults	4.2% (1)	87.4% (21)	4.2% (1)	4.2% (1)	0
Nymphs	0	84.4% (27)	12.5% (4)	3.1% (1)	0
Total	1.8% (1)	85.7% (48)	8.9% (5)	3.6% (2)	0
Total	45.0% (250)	41.7% (232)	4.3% (24)	6.7% (37)	2.3% (13)

* Underside includes: breast, sides, flanks, belly, tibial feathers and vent.

**May include nymphs of *Holomenopon leucoxanthum.*

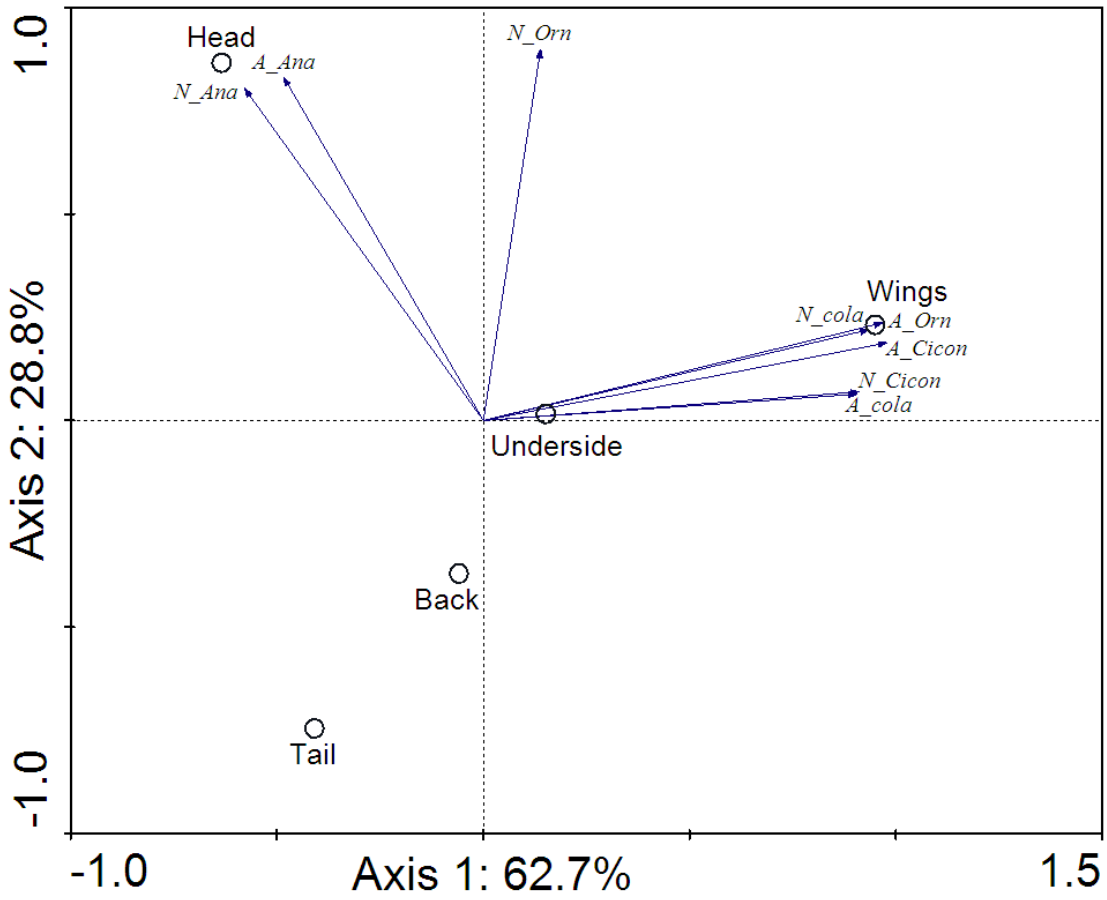

Fig. 4-1. Biplot of the distribution of chewing lice infesting Canada Goose (*Branta canadensis*) (n=20), collected in 2012, Manitoba, Canada. Data were transformed with a square root transformation and analysed using a principle component analysis. The point Head represents the head and the neck and the point Underside represents the breast, sides, flanks, belly, tibial feathers and vent of the host. Species labels that have an "A" in front of them represent adults and those with an "N" represent nymphs. Species abbreviations: cola = Anaticola anseris, Ana = Anatoecus spp. (includes A. dentatus and A. penicillatus), Cicon = Ciconiphilus pectiniventris, Orn = Ornithobius goniopleurus, and Tri = Trinoton anserinum.

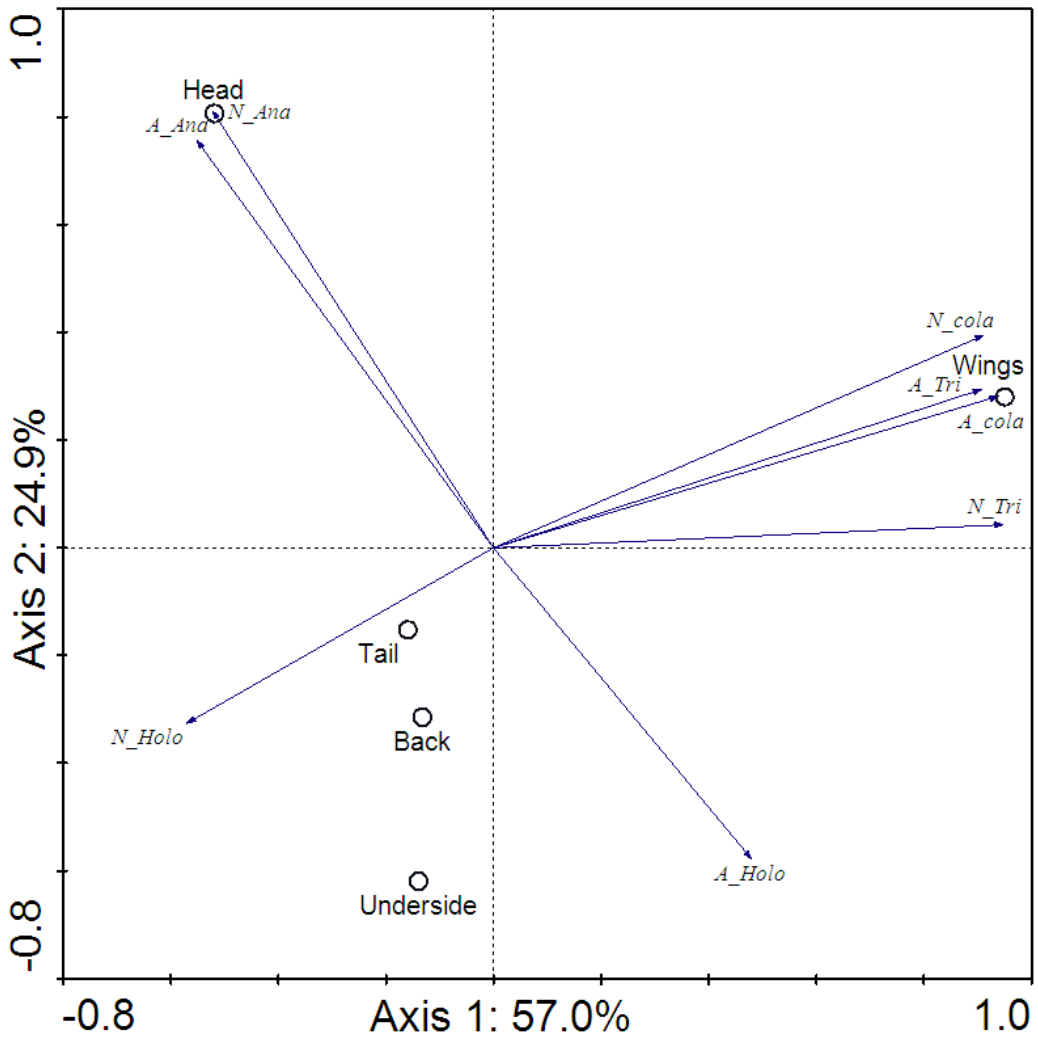

Fig. 4-2. Biplot of the distribution of chewing lice infesting mallards (*Anas platyrhynchos*) (n=8), collected in 2012, Manitoba, Canada. Data were transformed with a square root transformation and analysed using a principle component analysis. The point Head represents the head and the neck and the point Underside represents the breast, sides, flanks, belly, tibial feathers and vent of the host. Species labels that have an "A" in front of them represent adults and those with an "N" represent nymphs. Species abbreviations: cola = Anaticola crassicornis, Ana = Anatoecus dentatus, Holo = Holomenopon maxbeieri (may include nymphs of Holomenopon leucoxanthum) and Tri = Trinoton querquedulae.

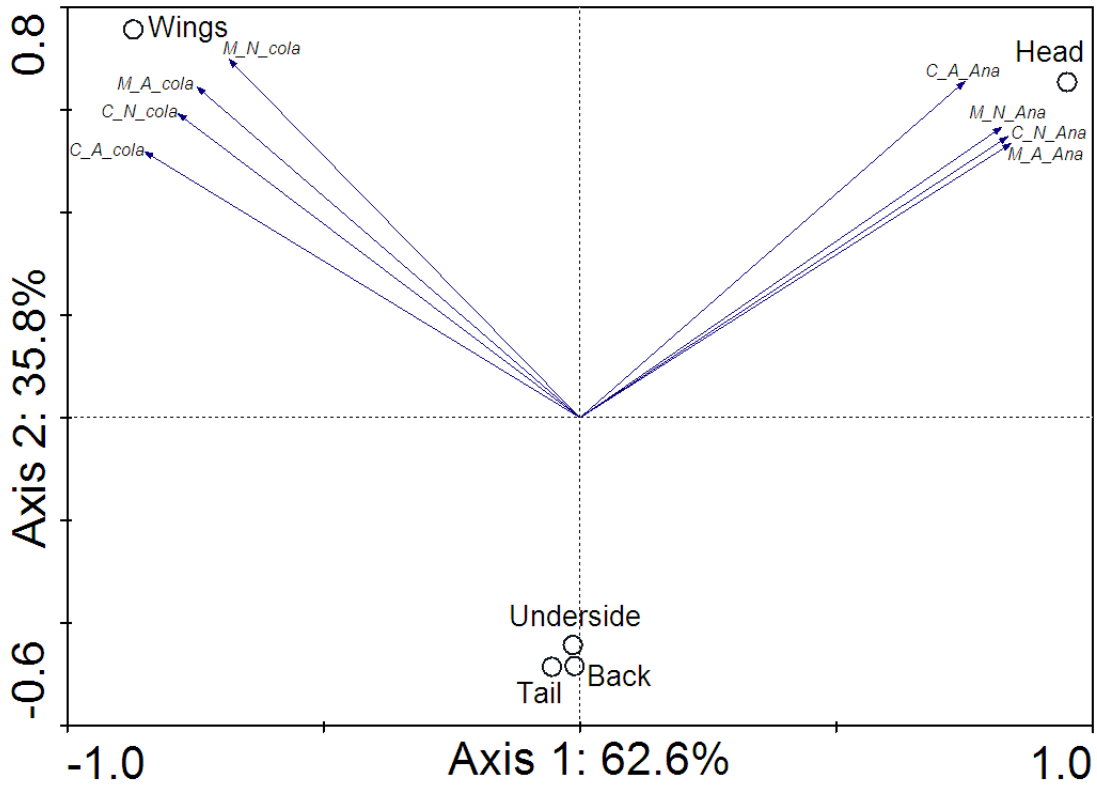

Fig. 4-3. Biplot of the distribution of chewing lice infesting Canada geese (*Branta canadensis*) (n=20) and mallards (*Anas platyrhynchos*) (n=8), collected in 2012, Manitoba, Canada. Data were transformed with a square root transformation and analysed using a principle component analysis. The point Head represents the head and the neck and the point Underside represents the breast, sides, flanks, belly, tibial feathers and vent of the host. The first letter in the species name represents the host, "C" is Canada goose and "M" is mallard. The second letter represents the developmental stage, "A" is adults and "N" is nymphs. Species abbreviations: cola = Anaticola, Ana = Anatoecus.

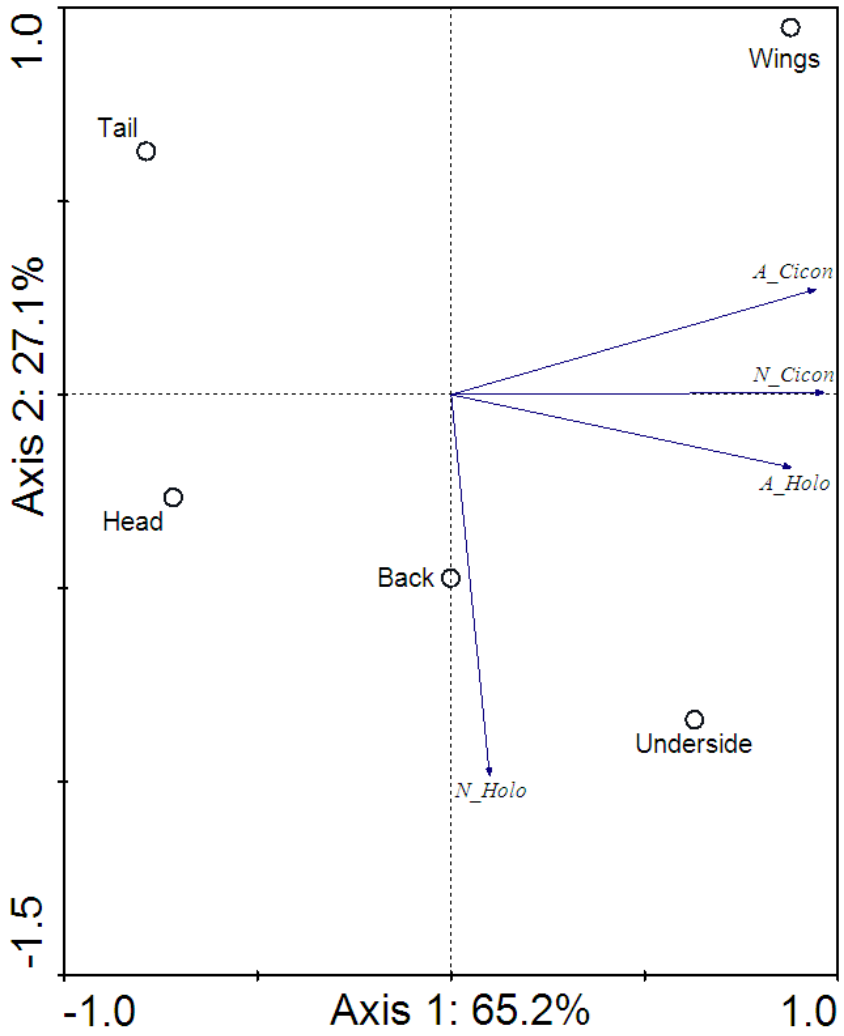

Fig. 4-4. Biplot of the distribution of chewing lice infesting Canada geese (*Branta canadensis*) (n=20) mallards (*Anas platyrhynchos*) (n=8), collected in 2012, Manitoba, Canada. Data were transformed with a square root transformation and analysed using a principle component analysis. The point Head represents the head and the neck and the point Underside represents the breast, sides, flanks, belly, tibial feathers and vent of the host. The letter represents the developmental stage, "A" is adults and "N" is nymphs. Species abbreviations: Cicon = Ciconiphilus pectiniventris and Holo = Holomenopon maxbeieri (may include nymphs of Holomenopon leucoxanthum).

CHAPTER 5: Infestation Parameters of Chewing Lice (Insecta: Phthiraptera) on Canada Geese (*Branta canadensis*) and Mallards (*Anas platyrhynchos*) in Manitoba, Canada

Abstract

Long term quantitative information about chewing louse (Insecta: Phthiraptera) infestations is scarce. Canada geese (*Branta canadensis* (Linnaeus)) (n=300) and mallards (*Anas platyrhynchos* Linnaeus) (n=290) have been examined for ectoparasites since 1994 to determine prevalence and intensity of chewing louse infestations. Sex ratio and seasonal distribution of chewing lice were also determined. Dispersal of lice from adult to juvenile mallards was also examined. Canada geese were infested with *Anaticola anseris* (Gurlt), *Anatoecus dentatus* (Scopoli), *Anatoecus penicillatus* Kéler, *Ciconiphilus pectiniventris* (Harrison), *Ornithobius goniopleurus* Denny, and *Trinoton anserinum* (Fabricius), and mallards were infested with *Anaticola crassicornis* (Scopoli), *A. dentatus*, *Holomenopon leucoxanthum* (Burmeister), *Holomenopon maxbeieri* Eichler, and *Trinoton querquedulae* (Linnaeus). On Canada geese, *O. goniopleurus* was the most prevalent (87.2%) and *C. pectiniventris* had the highest mean intensity (84.7), while on mallards, *A. crassicornis* had the highest prevalence (60.9%) and *A. dentatus* had the highest mean intensity (38.1). All species of lice showed a significant female bias except *Trinoton* spp. Different genera of lice infested mallard ducklings at different times. Nymphs of *A. anseris* and *Holomenopon* spp. first appeared on ducklings that weighed 20-30g; however, adults were not consistently collected until ducklings weighed 500-600g. Adults and nymphs of *A. dentatus* started appearing when chicks weighed 20-30 g

and *T. querquedulae* appeared steadily after chicks reached 500g. From April to November, the prevalence on Canada geese was greater than 90%, but from May to November the prevalence on Mallards varied from 53% to 100%. On Canada geese, the prevalence for *A. anseris,* and *C. pectiniventis* dropped in May and June and peaked in September. The prevalence of *O. gonipleurus* was greater than 70% from May to November and the prevalence of *Anatoecus* spp. showed no distinguishable pattern. On mallards, the prevalence of *A. dentatus* and *Holomenopon* spp. dropped in June and peaked in October. There was no distinguishable seasonal pattern for *A. crassicornis.* On Canada geese, the mean intensity of all louse species except *A.anseris* increased in July. On mallards, the mean intensity of all species increased in August.

Introduction

There are more parasitic organisms than non-parasitic organisms (Roberts and Janovy 2005). A parasite is an organism that lives in or on another organism, taking part or all of its nutrition from its hosts and causes damage to its host. Since parasites can have harmful effects on their hosts, it is important to understand all aspects of parasite infestations, not just what parasites infest a host, but how many are present. Parasites are known to have an aggregated distribution, where many hosts have few parasites and few hosts have many parasites (Anderson and Gordon 1982). This means large samples of hosts have to be examined to assess the infestation parameters of its parasites accurately.

One group of parasites for which comprehensive quantitative information is scarce is chewing lice (Insecta: Phthiraptera). Chewing lice are obligate ectoparasites of birds and mammals (Marshall 1981a). Most often host-parasite lists for various hosts in

different locations are reported, *e.g.*, Mourik and Horman (1985), Spencer (1948) and Threlfall *et al.* (1979). These lists provide little indication of how often or how intense louse infestations occur on specific hosts.

Anseriformes (ducks, geese and swans) especially have been neglected with regards to quantitative information on the chewing lice that infest them. This is surprising since anseriforms are ecologically and economically important. They play a significant role in wetland management with regard to nutrient levels and water quality (Baschuk *et al.* 2012; Post *et al.* 1998) and have an economic impact as game birds. Hunters in Canada spent $ 91.7 million on hunting migratory bird (Environment Canada 2010). In this study, the infestation parameters (prevalence, mean intensity, sex ratio, nymph to female ratio) of chewing lice infesting Canada geese (*Branta canadensis* (Linnaeus)) and mallards (*Anas platyrhynchos* Linnaeus), two of the top three harvested game birds in North America (Mowbray *et al.* 2002), were examined.

Buscher (1965) previously conducted a study to examine the ectoparasites of anseriforms, including mallards, at Delta Marsh, Manitoba, Canada. He reported the percentage of each host species infested with ectoparasites, including lice, fleas and mites. Rékási *et al*. (1997) also reported the infestation parameters of chewing lice on mallards; they examined each louse species separately and had a sample size of 72 birds. Astonishingly, no published quantitative data on Canada geese has been found.

It is important to know the infestation parameters of different species of lice so that changes and variations in population structure are recognized and correctly interpreted. The objective of this study was to establish a baseline of information on the infestation parameters of chewing lice infesting Canada geese and mallards in Manitoba,

so that any future changes can be recognized. In 1994, an ectoparasite survey of birds and small mammals was started at the University of Manitoba. This has created an 19 year dataset from which the prevalence, mean intensity, sex ratio, female/nymph ratio, index of discrepancy, seasonal variation and dispersal patterns were examined for each louse species infesting Canada geese and mallards.

Material and Methods

Canada geese and mallards were salvaged from 1994 to 2012 under Wildlife Scientific Permits issued by Environment Canada, Canadian Wildlife Service. The majority of birds came from wildlife rehabilitation centres (Wildlife Haven and Prairie Wildlife Rehabilitation Centre); some came from Manitoba Conservation, hunters and the general public.

As soon after death as possible, each bird was placed in its own plastic bag and frozen (-20°C) for at least 48 hours to kill all of the ectoparasites. Each bird then went through the washing process described in Chapter 3.

Some lice were mounted on microscope slides following Richards (1964). Mounted lice and those in ethanol were deposited in the J.B. Wallis-R.E. Roughley Museum of Entomology, University of Manitoba, Winnipeg, Canada. *Anatoecus dentatus* (Scopoli) and *Anatoecus icterodes* (Nitzsch) are here treated as *A. dentatus*, according to the synonymy proposed in Chapter 3.

Seasonal distribution of prevalence and mean intensity was calculated by pooling data from all years the study was conducted. The months March to November for Canada geese and April to November for mallards were examined. These months represent when each species of host was present in the province from spring to fall migration. March was

not included in the seasonal distribution of mallards because no mallards came through the laboratory in March.

Birds were separated into different groups based on their feather development extrapolated from body weight because feather development of each host was not recorded. Mallards were divided into three groups. Downy chicks have no visible contour feathers, only down present (<240g). Partly to fully feathered young, included birds that were just starting to develop contour feathers (240-800g) all the way to fully feathered birds that were unable to fly (>800g). Adult and flying young of the year (Y.O.Y.) included birds that were fully feathered and able to fly (>800g) (Lokemoen *et al.* 1990). However, separating Canada geese by weight was not possible because no attempt was made to differentiate between the lesser Canada goose (*Branta canadensis parvipes* (Cassin)) and the giant Canada goose (*Branta canadensis maxima* (Delacour)), which differ in size.

Infestation parameters and their confidence limits were obtained with the free software Quantitative Parasitology 3.0 (Reiczigel and Rózsa 2005). Prevalence was defined as " the number of hosts infected with 1 or more individuals of a particular parasite species (or taxonomic group) divided by the number of hosts examined for that parasite species" (Bush *et al.* 1997). Sterne's exact method was used to calculate confidence intervals (CI) for prevalence (Reiczigel 2003). Mean intensity was defined as "the average intensity of a particular species of parasite among the infected members of a particular host species. In other words, it is the total number of parasites of a particular species found in a sample divided by the number of hosts infected with that parasite"

(Bush *et al.* 1997). Confidence limits for mean intensity were calculated using a bootstrap procedure with 2000 replicates (Rózsa *et al.* 2000).

Results

Canada geese (*Branta canadensis*)

From 1994 to 2012, 300 Canada geese of all ages were examined for ectoparasites; refer to Table 5-1 for the distribution of when birds were sampled. Two hundred and thirty Canada geese were sampled from Winnipeg and the rest were collected from various places around the province. Over the 19 years Canada geese were examined, 48,669 lice were collected with a range of 1 - 3226 lice being collected per bird. The prevalence of all chewing lice on Canada geese was 92.3% (88.7 - 94.9, 95% CI) and the mean intensity was 175.6 (143.3 - 222.8, 95% CI). Six species of lice were collected, *Anaticola anseris* (Gurlt), *A. dentatus, Anatoecus penicillatus* Kéler, *Ciconiphilus pectiniventris* (Harrison), *Ornithobius goniopleurus* Denny, and *Trinoton anserinum* (Fabricius). All of these are new records for Manitoba and *C. pectiniventris* is a new record for Canada.

Prevalence and mean intensities were calculated for adult birds only (n=180) and are presented in Table 5-2. *Ornithobius goniopleurus* was the most prevalent species on Canada geese (87.2%, 84.5-91.5, 95% CI) and *T. anserinum* was the least prevalent (0.02%, 0.007-0.06, 95% CI). Of the 180 adult Canada geese sampled, only four were infested with *T. anserinum* and a total of six lice (3 males; 1 female; 1 nymph) were collected, resulting in *T. anserinum* having the lowest mean intensity. *Ciconiphilus pectiniventris* had the highest mean intensity (84.7, 45.9-161.7, 95% CI). Canada geese were infested with two species of *Anatoecus*: *A. dentatus* and *A. penicillatus.* Of the 180

adult Canada geese, 158 were infested with adult *A. dentatus*, 13 were infested with adult *A. penicillatus*, and 15 were infested with *A. dentatus* and *A. penicillatus*. No attempt was made to distinguish nymphs of these species; consequently, all *Anatoecus* data were pooled and analyzed as *Anatoecus* spp. (Table 5-2). To make robust comparisons between *A. dentatus* and *A. penicillatus*, the adults of each species were also analyzed: *A. dentatus,* prevalence 58.9% (51.4 - 65.8, 95% CI), mean intensity 5.0 (11.7 -24.5, 95% CI) and *A. penicillatus* prevalence 12.8% (5.8 - 18.5, 95% CI), mean intensity 13.3 (7.7 - 22.3, 95% CI). All species, with the exception of *O. goniopleurus,* exhibited high levels of aggregation (refer to the Index of Discrepancy in Table 5-2) (Poulin 1996).

The sex ratios for every species with the exception of *Trinoton* were significantly female biased, (Table 5-3). However, only four adult *T. anserinum* were collected. For *Anaticola anseris,* 57.9% of infested birds had a female bias, 29.4% had a male bias and 12.7% had an equal number of females and males. For *Anatoecus* spp., 72.7% had a female bias, 22.4% had a male bias and 4.9% had an equal number of females and males. For *Ciconiphilus pectiniventris,* 68.6% had a female bias, 21.6% had a male bias and 9.8% had an equal number of females and males. For *Ornithobius goniopleurus,* 58.0% had a female bias, 31.6% had a male bias and 10.4% had an equal number of females and males, and *Trinoton anserinum,* none had a female bias, 75% had a male bias and 25% had an equal number of females and males. The female to nymph ratio ranged from 1:2.6 for *Anatoecus* spp. to 1:6.0 for *O. goniopleurus*, (Table 5-3).

Prevalence of all chewing lice on Canada geese was greater than 85% in all months sampled (Fig. 5-1). From March to June, the seasonal distribution of mean intensity of all lice was consistent, with a peak in July (Fig. 5-2). For *A. anseris,*

prevalence dropped in April and May and then peaked in September (Fig. 5-3); the mean intensity was fairly consistent over the nine months, with slight increases in nymphs in March, July and November (Fig. 5-4). The prevalence of *Anatoecus* spp. does not have as clear a pattern as was seen with the other species on Canada geese. There are drops in prevalence in May, June and September and peaks in August, October and November (Fig. 5-6). The mean intensities over the season show a much clearer pattern; there were very low mean intensities in March through June and then there was an increase in July and August (Fig. 5-7). For *C. pectiniventris*, the prevalence dropped in April and there was a peak in September (Fig. 5-8) and there was a peak in the mean intensity in July and August for both adults and nymphs and a peak in October for nymphs (Fig. 5-9). *Ornithobius goniopleurus* had a very high prevalence from April to November (Fig. 5-10). There was a general increase in mean intensity for *O. goniopleurus* throughout the season with a large increase in nymphs in July (Fig. 10). The seasonal distribution for *Trinoton* was not calculated because of its small sample size.

Mallards (*Anas platyrhynchos*)

From 1995 to 2012, 296 mallards of all ages were examined for ectoparasites (Table 5-1). Of these, 140 were salvaged in Winnipeg, and the remainder were salvaged from various localities around the province. Over the 19 years mallards were examined, 6,986 lice were collected with a range of 1 - 672 lice being collected per bird. The prevalence of chewing lice on mallards was 55.4% (49.7 - 61.0, 95% CI) and the mean intensity was 42.0 (32.8 - 58.0, 95% CI). Five species of lice were collected, *Anaticola crassicornis* (Scopoli), A. *dentatus, Holomenopon leucoxanthum* (Burmeister),

Holomenopon maxbeieri Eichler and *Trinoton querquedulae* (Linnaeus). For *H. leucoxanthum* and *H. maxbeieri*, these are new records in Manitoba; in addition, this is a new record for *H. maxbeieri* in Canada.

Prevalence and mean intensities were calculated for adult birds only (n=87)(Table 5-4). *Anaticola crassicornis* was the most prevalent (60.9%) and *Holomenopon* spp. was the least prevalent (29.9%, 21.2-40.2, 95% CI). However, *A. dentatus* had the highest mean intensity (38.1, 25.1-59.6, 95% CI) and *T. querquedulae* had the lowest mean intensity (7.0, 4.8-10.2, 95% CI). Mallards were infested with two species of *Holomenopon: H. maxbeieri* and *H. leucoxanthum.* There are no known morphological characteristics that distinguish nymphs of these species, consequently all *Holomenopon* data were pooled and analysed as *Holomenopon* spp. (Table 5-4). Adult *H. leucoxanthum* and *H. maxbeieri* were found co-infesting one mallard, adult *H. leucoxanthum* were found infesting five mallards and adult *H. maxbeieri* were found infesting 31 mallards. The prevalence of adult *H. leucoxanthum* was 2.0% (0.9 - 4.3, 95% CI) and the mean intensity was 2.8 (1.2 - 4.8, 95% CI) and the prevalence of adult *H. maxbeieri* was 10.8% (7.7 - 15.0, 95% CI) and mean intensity of 5.2 (3.6 - 7.7, 95% CI). All species, with the exception of *T. querquedulae,* showed high levels of aggregation. Refer to the Index of Discrepancy in Table 5-4.

The sex ratios for every louse species, with the exception of *Trinoton,* were significantly female biased, (Table 5-3). The sex ratios for *Anaticola* were 46.2% female biased, 33.3% male biased and 20.5% had an equal number of females and males; for *Anatoecus,* 69.6% had a female bias, 20.6% had a male bias and 9.8% had an equal number of females and males; for *Holomenopon,* 64.3% had a female bias, 19.0% had a

male bias and 16.7% had an equal number of females and males, and for *Trinoton* 33.4% had a female bias, 48.7 had a male bias and 17.9 had an equal number of females and males. The female to nymph ratio was greatest in *Holomenopon* spp. (1:5.2) followed closely by *T. querquedulae* (1:4.9). The smallest ratio was seen in *A. dentatus* (1:2.8) (Table 5-3).

The 296 mallards examined varied in weight from 14.2 - 1360.8g, and therefore all feather development stages were represented (Table 5-5). There were 69 birds for which weight was not recorded and are therefore not included in these results. Partly to fully feathered young have the highest prevalence of the three age classes for every louse species found. Mean intensity was highest for partly to fully feathered young in all species except *Holomenopon* spp., in which adult and flying Y.O.Y. had the highest mean intensity. However, none of these are significantly different from the other two age classes with the exception of *Holomenopon* spp. in which *Holomenopon* spp. was significantly different from downy chicks. The male to female ratio for *A. crassicornis* increased as birds developed. Conversely, the female to nymph ratio decreased as ducks developed. *Anatoecus dentatus* had a steady male to female ratio during all development stages of their host. There were twice as many nymphs to females seen on downy chicks than in the other developmental stages. The male to female ratio for *Holomenopon* spp. was the highest for downy chicks. The female to nymph ratio for partly to fully feathered young was less than half the other two developmental stages. There were twice as many females to males of *T. querquedulae* for partly to fully feathered young than other developmental stages.

All four species of chewing lice were not collected on juvenile hosts at the same stage of host development (Fig. 5-13). *Anaticola crassicornis* and *Holomenopon* spp. have similar dispersal patterns, with a large increase in nymphs on small chicks (20-30g) with a plateau reached at 500 - 600g, when both nymphs and adults steadily increased. Numbers of adults and nymphs of *Anatoecus dentatus* steadily increased as mallard weight increased, first collected when chicks weighed 20-30g. *Trinoton querquedulae* were consistently observed on mallards that weighed >500g.

For seasonal distribution, the prevalence of total lice on mallards from April to November was not consistent (Fig. 5-14). Over the season, there was a drop in July and a peak in October. The mean intensity for total lice on mallards was similar from April to July and then there was an increase in August that continued through to November (Fig. 5-15). The prevalence of *A. crassicornis* was consistent; however, there is a drop in July and then again in September (Fig. 5-16). The mean intensity of *A. crassicornis* <10 lice per infested bird from April to July and then there was an increase in August through November (Fig. 5-17). The seasonal change in the prevalence of *A. dentatus* was very pronounced (Fig. 5-18). There was a gradual decrease from April to June and then from July to October there was a gradual increase. The mean intensity of *A. dentatus* was extremely low in April to June, there was a slight increase in nymphs in July and then there was a huge increase in adults and nymphs in August followed by a gradual decrease in September to November (Fig. 5-19). The prevalence for *Holomenopon* spp. changed drastically through the season (Fig. 5-20). No *Holomenopon* were collected in May or June, but then there was a gradual increase from July to October and then the prevalence dropped off again in November (Fig. 5-20). Mean intensity for *Holomenopon* spp. was

very low, for adults and nymphs <10, except in August and October, when nymphs increased to around 20 (Fig. 5-21).

Discussion

Anseriformes are an important group of birds because of the role they play in the hunting industry, as well as wetland management and ecology. In the past, their internal parasites have been studied extensively, *e.g.*, Bayssade-Dufour *et al.* (2006) and Turner and Threlfall (1975); however, their ectoparasites have not received the same amount of attention. This is the most comprehensive study on the infestation parameters of chewing lice infesting mallards and the first study on the infestation parameters of chewing lice infesting Canada geese.

There have been few studies in which prevalence and mean intensity of different species of lice on anseriforms have been reported; results from these studies have been compiled in Table 6. These few studies illustrate that even the same species can have a dramatically different prevalence and mean intensity depending on the host it is infesting. The prevalence for *A. crassicornis*, for example, can range from 39% to 100% and its mean intensity can range from 9.7 to 43.6, depending on the host. However, studies conducted on the same host species can also have variable results; Rékási *et al.* (1997) also studied mallards, but the prevalence they calculated for *A. crassicornis* was 6.7% lower from the one calculated in this study, and their mean intensity was 19.5 more lice per bird than was found in this study. Rékási *et al.* (1997) also observed *T. querquedulae* on mallards and they calculated the prevalence of *T. querquedulae* to be 25.4% less than what was found here and the mean intensity in the present study was 6.01 lice per infested host more than what Rékási *et al.* (1997) found (Table 5-6). There are many

factors to be considered when the quantitative results of different studies are compared, including sampling method, sample size, location, age of hosts, and time of year.

There are three sampling techniques for chewing lice on birds that are most frequently employed: visual inspection, fumigation and washing. Clayton and Drown (2001) compared these louse removal methods on rock pigeons (*Columba livia* Gmelin) which are host to *Columbicola columbae,* a wing louse and *Campanulotes compar,* a body louse. Visual inspection accounted for 8.8% of the wing lice and 10% of the body lice, fumigation removed >40% of the wing lice and <22% of the body lice and washing removed >88% of the body and wing lice. All of the studies in Table 6, with the exception of the present study, used visual inspection to sample for lice. Sampling method probably has a greater influence on reported mean intensity than it does prevalence. Prevalence is the percentage of hosts infested; it only takes one louse for a host to be considered infested, while mean intensity takes into account the whole louse population on the host.

Louse populations usually have an aggregated distribution, in which many hosts have few lice while few hosts have many lice (Anderson and Gordon 1982), therefore adequate sample sizes of hosts have to be examined. Of the studies in Table 6, the three hosts that have the smallest sample sizes (n=14, 6, 8) also have the highest prevalence (100%) (Naz *et al.* 2010), therefore this probably does not accurately represent the louse population on these host, because of their small sample size. Location can also influence louse populations, since lice are sensitive to temperature and humidity (Rudolph 1983). Moyer *et al.* (2002) showed that mourning doves (*Zenaida macroura* (Linnaeus)) and inca doves (*Columbina inca* (Lesson)) in Arizona (arid region) had significantly lower

prevalence and abundance of lice than those in Texas (humid region); these results were then validated with laboratory experiments (Moyer *et al.* 2002). While the present study was conducted in Manitoba, Canada, Rékási *et al.* (1997) worked in Hungary and Romania. This difference in locality could account for some of the differences in prevalence and mean intensity seen among louse species on mallards. Along with location, time of year can also influence prevalence and mean intensity. Some species of lice, such as *Menacanthus eurysternus* (Burmeister) on the European starling (*Sturnus vulgaris* Linnaeus), are believed to overwinter as eggs because in January the prevalence drops to zero; however, eggs are still present (Boyd 1951).

Canada geese and mallards have three of the same genera of lice: *Anaticola, Anatoecus,* and *Trinoton.* In addition, Canada geese are infested with *Ciconiphilus* and mallards are infested with *Holomenopon,* which are very similar in size and shape and might be considered ecologically equivalent genera. Canada geese are also infested with *Ornithobius*; however, there is no ecological equivalent of this on mallards. The genus *Acidoproctus* is found on other species of ducks (*Athya* spp.) and closely resembles *Ornithobius* in size and shape. It is possible that *Ornithobius* and *Acidoproctus* are ecologically equivalent genera. When the louse communities of Canada geese and mallards in Manitoba are compared, *Anatoecus* and *Ciconiphilus* were more prevalent on Canada geese, while *Anaticola* and *Trinoton* were more prevalent on mallards (Table 5-2 and 5-4). However, *Anaticola, Anatoecus,* and *Ciconiphilus* had a higher mean intensity on Canada geese and *Trinoton* had a higher mean intensity on mallards (Table5- 2 and 5-4). Canada geese can be two to three time larger than a mallard, which creates more surface area and could be the reason why infestations on Canada geese were more

intense. But, this does not hold true for *Trinoton*, which was hardly seen on Canada geese. Canada geese are also host to *Ornithobius,* which is not found on mallards. *Trinoton* and *Ornithobius* are the two largest lice found on anseriforms. On mallards, *Trinoton* was mainly found on the wings, while adult *Ornithobius* were mainly found on the wings of Canada geese (Chapter 4). *Ornithobius* may out-compete *Trinoton* on Canada geese on the wings and that is why *Trinoton* is not very prevalent on Canada geese, but on mallards, where *Ornithobius* is absent, *Trinoton* had a greater prevalence. Further research is required to understand the extent to which interspecific competition occurs among lice.

Sex ratios of ectoparasitic insects tend to be female biased (Marshall 1981b). Marshall reviewed 379 collections made up of at least a 100 individuals making up 250 different species of ectoparasites. His analysis included 50 collections of lice and of these, 38% did not differ significantly from unity; the other 62% were predominately female. Clayton *et al.* (1992) were the first to report a male bias in chewing lice. They found that 13 of the 125 metapopulations infesting neotropical birds they examined were significantly skewed. Nine of these had a female bias and four had a male bias. In Canada geese and mallards in Manitoba, all species had a significant female bias except *T. anserinum* and *T. querquedulae,* which did not significantly differ from unity.

When interpreting when lice disperse to new hosts, knowing how the host interacts with conspecifics, as well as other species, is critical. Anseriformes are precocial and therefore chicks leave the nest shortly after hatching. This affects the nature of the parent offspring interaction, which would facilitate louse transfer. However, in late summer and early fall, Canada geese migrate and mallards will travel in mixed-species

flocks, which may provide ample opportunity for dispersal. Many birds, such as the Columbiformes (pigeons and doves), are altricial. Chicks hatch naked and rely on their parents for food and warmth.

Therefore, precocial chicks may have more opportunities to acquire lice from sources other than their parents and siblings.

When lice first infest mallard chicks appears to depend on the species of louse. Adults and nymphs of *A. dentatus* and *Holomenopon* spp. were first collected on chicks that were approximately 20g. At 20g, chicks are about three days old and are completely covered in bright yellow down (Lokemoen *et al.* 1990). *Trinoton querquedulae* was not consistently seen on mallards until they were approximately 500g, at which time down was only visible in one or two small patches. *Anaticola crassicornis* was also observed on chicks that were 20g; however, only nymphs were found on young chicks. Adult *A. crassicornis* were first collected on chicks at approximately 100g, but were sporadic in their appearance until chicks reached 400g, at which time, prevalence of adult *A. crassicornis* was almost 100% on infested birds. At 100g, chicks are about nine days old and still covered completely with down; at 400g chicks are about 30 days old and are mostly feathered. The increase in prevalence of adult *A. crassicornis* at 400g could be caused by the increase of adult lice dispersing to ducklings of this weight; however, the generation time for most lice to develop from a first instar nymph to an adult is three weeks (Marshall 1981a), which is about the same time between when nymphs first started to appear on chicks to when adults were routinely found infested birds. Lee and Clayton (1995) found similar results with *Dennyus hirundinis* (Linnaeus) infesting swifts (*Apus apus* (Linnaeus)) as they dispersed from parents to nestlings. Nestlings were infested with

lice as early as two weeks after hatching. In addition, nestlings had significantly more nymphs than adult lice; this bias was not observed in older birds and the number of louse eggs on parent birds was significantly correlated with the number of nymphs on offspring. Louse eggs were not present on nestlings until they reached five weeks of age. This leaves a three week gap between when nymphs were first observed, and when eggs were observed, which according to Marshall (1981a), is the amount of time it takes a nymph to mature into a adult, which could then produce eggs.

Chewing lice are dynamic and so is their population structure over the year. A pattern has been suggested for seasonal variation in chewing lice on birds, in which there is an increase in the prevalence and intensity of lice just prior to the host's breeding season until the time when eggs are laid. This is then followed by a decrease in prevalence and intensity after chick hatch (Amaral *et al.* 2013; Bergstrand and Klimstra 1964; Chandra *et al.* 1990; Woodman and Dicke 1954). It is thought this seasonal pattern is to facilitate the dispersal of lice from parents to offspring and that the drop in prevalence and intensity on adult birds is because lice have dispersed to new, previously uninfested hosts. This pattern was not observed in the seasonal distribution of any louse species infesting Canada geese and mallards. The prevalence of infestation in Canada geese was continually high throughout March to November (>90%), whereas the prevalence of infestation in mallards varied depending on the month (ranging from 53% to 100%). A similar pattern for prevalence was seen at a species level between Canada geese and mallards. On Canada geese, the prevalence of *A. anseris* and *C. pectiniventris* dropped in April and May and peaked in September. The same pattern was observed on mallards for *A. dentatus* and *Holomenopon* spp., except everything happened one month

later, so prevalence dropped in June and peaked in October. This pattern is opposite to what has been observed in other louse/host interactions. There was an increase mean intensity of every louse species on Canada geese with the exception of *A. anseris* in July. The mean intensity in the months following July was greater than the months previous to it. The same pattern was observed with each louse species infesting mallards except the increase in mean intensity occurred in August. The increase in mean intensity coincided with the time flying Y.O.Y. appeared in the dataset. Since birds were aged based on their weight, adults and flying Y.O.Y. could not be separated. Therefore the increase in mean intensity may be an artefact created by the inclusion of flying Y.O.Y. When trying to interpret these data, one has to remember that birds from multiple years have been combined, therefore any variation that took place between years has been obscured.

Canada geese and mallards were only sampled in their breeding range; if sampling was continued through their migration to the overwintering grounds, a picture of what the true seasonal distribution would be gained. In addition to this, populations of Canada geese have started to change their behaviour and in same locations, are no longer migratory (Nelson and Oetting 1998). Efforts to re-establish the Canada geese in the midwestern United States has been so successful, populations have grown and expanded through the southern and southwestern United States (Nelson and Oetting 1998; Orr *et al.* 1998). Many of these populations are now found year round in the southern and southwestern United States, which was previously only used for overwintering. It would be very interesting to compare the seasonal dynamics of Canada geese that migrate to Canada geese that do not migrate.

Canada geese and mallards were only sampled in Manitoba, and therefore only one climatic area was included. Variations in population structure are influenced by climate specifically relative humidity; this impacts the distribution of certain louse species. Mourning doves (*Zenaida macroura* (Linnaeus)) are abundant in North America and are found in many diverse habitats and infested with two species of *Columbicola*. When mourning doves were sampled from across the United States, *Columbicola macrourae* (Wilson), a chewing louse was restricted to the more humid eastern part of the country and *Columbicola baculoides* (Paine) was restricted to the more arid western part, with some degree of overlap in the central United States (Malenke *et al.* 2011). Therefore multiple studies in different locations are needed to assess the infestation parameters of individual louse species. Particular attention should be given to *Holomenopon* spp. on mallards. In Manitoba, which is located centrally in the continent, *H. maxbeieri* is four times more prevalent than *H. leucoxanthum.* It would be interesting to see if humidity plays a role in the distribution of *Holomenopon* spp.; this could be done by sampling closer to the coasts where the humidity and temperature conditions are drastically different from Manitoba.

In summary, this is the first extensive study to examine the chewing lice of Canada geese and mallards in North America and provides a baseline for future comparisons. Hopefully there will be data on eggs as well as lice on Anseriformes from several locations across North America and elsewhere.

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Tables and Figures

Table 5-1. Number of Canada geese and mallards sampled each year. Three mallards included in the study did not have any data information.

	Canada Geese (*Branta canadensis*)	Mallards (*Anas platyrhynchos*)
1994	3	0
1995	5	12
1996	4	15
1997	3	14
1998	3	24
1999	3	10
2000	1	5
2001	0	3
2002	0	4
2003	3	6
2004	8	0
2005	1	0
2006	16	2
2007	17	8
2008	27	27
2009	51	44
2010	65	28
2011	61	76
2012	29	15
Total	300	287

Table 5-2. Infestation parameters of chewing lice on 180 adult Canada geese (*Branta canadensis*) (>2520g) from Manitoba, Canada examined from 1994 to 2012 (95% confidence intervals in brackets).

Species	No. of hosts infested	Range	Prevalence (%)	Mean intensity	Index of discrepancy (D)
Anaticola anseris	83	1 - 210	46.1 (38.9 - 53.6)	25.9 (18.2 - 35.2)	0.830
Anatoecus spp.**	129	1 - 1023	71.7 (64.5 - 77.8)	43.4 (30.1 - 71.5)	0.836
Ciconiphilus pectiniventris	101	1 - 2553	56.1 (48.6 - 63.3)	84.7 (45.8 - 161.7)*	0.909
Ornithobius goniopleurus	157	1 - 671	87.2 (81.5 - 91.5)	69.4 (55.0 - 89.3)	0.680
Trinoton anserinum	4	1 - 2	0.02 (0.007 - 0.06)	1.2 (1.0 - 1.5)	0.976
All Species	172	1 - 3226	95.6 (91.5 - 97.9)	157.7 (118.3 - 223.3)	0.713

* indicated 90% confidence intervals.

** includes *A. dentatus* and *A. penicillatus*.

Table 5-3. Sex ratios and female/nymph ratios for all ages of Canada geese (*Branta canadensis*) and mallards (*Anas platyrhynchos*) examined from 1994 to 2012, in Manitoba, Canada. P-vales for sex ratio calculated using chi-square test, p-vales >0.05 indicates a significant difference from 1:1.

Host species	Louse species	No. of hosts with adult lice	No. of males	No. of femals	Male: female	p-value	No. of nymphs	Female: nymph
Canada geese (n=300)	*Anaticola anseris*	102	385	493	1 : 1.3	<0.05	1721	1 : 3.5
	Anatoecus spp.*	205	1922	3253	1 : 1.7	<0.05	8356	1 : 2.6
	Ciconiphilus pectiniventris	155	1267	1960	1 : 1.5	<0.05	9081	1 : 4.6
	Ornithobius goniopleurus	231	2240	2585	1 : 1.1	<0.05	15409	1 : 6.0
	Trinoton anserinum	4	4	1	1 : 0.25	0.18	3	1 : 3.0
Mallard (n=296)	*Anaticola crassicornis*	78	256	305	1 : 1.2	<0.05	1322	1 : 4.3
	Anatoecus dentatus	92	577	870	1 : 1.5	<0.05	2439	1 : 2.8
	Holomenopon spp.**	42	94	145	1 : 1.5	<0.05	758	1 : 5.2
	Trinoton querquedulae	39	57	66	1 : 1.2	0.42	326	1 : 4.9

* included *A. dentatus* and *A. penicillatus.*

** included *H. maxbeieri* and *H. leucoxanthum.*

Table 5-4. Infestation parameters of chewing lice on 87 adult and flying young of the year mallards (*Anas platyrhynchos*) (>800g) examined from 1994 to 2012 in Manitoba, Canada. 95% confidence intervals in brackets.

Species	No. of hosts infested	Range	Prevalence (%)	Mean intensity	Index of discrepancy (D)
Anaticola crassicornis	53	1 - 119	60.9 (50.0 – 70.7)	18.9 (14.0 – 27.2)	0.733
Anatoecus dentatus	45	1 - 283	51.7 (41.2 – 62.1)	38.1 (25.1 – 59.6)	0.820
Holomenopon spp. **	63	1 - 75	29.9 (21.2 – 40.2)	16.5 (11.8 – 25.1)	0.840
Trinoton querquedulae	33	1 - 33	37.9 (28.1 – 48.8)	7.0 (4.8 – 10.2)	0.1719
All Species	65	1 - 328	74.7 (64.4 - 82.9)	52.0 (37.3 - 71.9)	0.719

** includes *H. maxbeieri* and *H. leucoxanthum.*

Table 5-5. Infestation parameters for mallards (*Anas platyrhynchos*) in Manitoba, Canada, based on feather development. Hosts were categorized by weight: downy chick <240g (n=170), partly to fully feathered young 240-800g (n=170) and adults and flying young of the year >800g (n = 87). 95% confidence intervals are in brackets and p-vales are based on a chi-square test.

Species / feather development	No. of hosts Infested	Prevalence (%)	Mean intensity	No. of males	No. of females	Male : female	p-value	No. of nymphs	Female: nymph
Anaticola crassicornis									
Downy Chick	43	25.3 (19.0 – 31.2)^{AB}	6.8 (4.4 – 11.8)^{I}	9	5	1 : 0.5	0.28	270	1 : 54
Partly to fully feathered young	24	61.5 (44.8 – 75.9)^{A}	24.4 (15.3 – 41.7)	97	97	1 : 1	1.0	391	1 : 4.0
Adult and flying Y.O.Y.	53	60.9 (50.0 – 70.7)^{B}	18.9 (14.0 – 27.2)^{I}	150	193	1 : 1.3	<0.05	661	1 : 3.4
Anatoecus dentatus									
Downy Chick	32	18.8 (13.5 – 25.5)^{CD}	8.9 (4.9 – 16.5)^{J}	32	54	1 : 1.7	<0.05	198	1 : 6.7
Partly to fully feathered young	28	71.8 (55.2 – 83.8)^{C}	67.7 (40.6 – 127.9)*	258	384	1 : 1.5	<0.05	1255	1 : 3.3
Adult and flying Y.O.Y.	45	51.7 (41.2 – 62.1)^{D}	38.1 (25.1 – 59.6)^{J}	290	439	1 : 1.5	<0.05	986	1 : 2.2
Holomenopon* spp.*									
Downy Chick	22	12.9 (8.4 – 18.8)^{EF}	4.4 (2.6 – 8.9)*^{KL}	5	16	1 : 3.2	<0.05	77	1 : 4.8
Partly to fully feathered young	15	38.5 (24.1 – 55.2)^{E}	15.4 (8.7 – 29.0)^{K}	38	67	1 : 1.8	<0.05	126	1 : 1.9
Adult and flying Y.O.Y	26	29.9 (21.2 – 40.2)^{F}	16.5 (11.8 – 25.1)^{L}	51	62	1 : 1.2	0.30	316	1 : 5.1
Trinoton querquedulae									
Downy Chick	3	1.8 (0.4 – 5.2)^{GH}	6.3 (1.0 – 8.7)*	3	3	1 : 1	1.0	13	1 : 4.3
Partly to fully feathered young	17	43.6 (28.6 – 59.5)^{G}	11.8 (5.0 – 29.2)*	19	36	1 : 2.0	<0.05	145	1 : 4.0
Adult and flying Y.O.Y.	33	37.9 (28.1 – 48.8)^{H}	6.97 (4.8 – 10.2)	35	27	1 : 0.8	0.30	168	1 : 6.2

* indicates *A. dentatus* and *A. penicillatus.*

** indicates *H. maxbeieri* and *H. leucoxanthum.*

Table 5-6. Summary of prevalence and mean intensity of chewing lice on Anseriformes from the literature and the present study.

Source	Host	Sample size (n)	Louse Species	Prevalence (%)	Mean Intensity
Present study	CAGO	180	*Anaticola anseris*	46.1	25.9
Present study	MALL	87	*Anaticola crassicornis*	60.9	18.9
(Rékási *et al.* 1997)	MALL	72	*Anaticola crassicornis*	54.2	37.4
(Canaris *et al.* 1981)	AGWT	70	*Anaticola crassicornis*	76	N/A
(Naz *et al.* 2010)	GRGO	14	*Anaticola crassicornis*	100	43.6
(Naz *et al.* 2010)	GWFG	6	*Anaticola crassicornis*	100	9.7
(Naz *et al.* 2010)	BHGO	8	*Anaticola crassicornis*	100	16.3
(Broderson *et al.* 1977)	NSHO	38	*Anaticola crassicornis*	39	N/A
(Wilkinson *et al.* 1977)	CITE	17	*Anaticola crassicornis*	5.9	N/A
Present study	CAGO	180	*Anatoecus* sp.	71.7	43.4
Present study	MALL	87	*Anatoecus dentatus*	51.7	38.1
(Rékási *et al.* 1997)	MALL	72	*Anatoecus dentatus*	20.8	3.49
(Rékási *et al.* 1997)	MALL	72	*Anatoecus icterodes*	16.7	8.18
(Canaris *et al.* 1981)	AGWT	70	*Anatoecus icterodes*	39	N/A
(Broderson *et al.* 1977)	NSHO	38	*Anatoecues icterodes*	13	N/A
(Broderson *et al.* 1977)	NSHO	38	*Anatoecus dentatus*	8	N/A
Present study	MALL	87	*Holomenopon* spp.	29.9	16.5
(Canaris *et al.* 1981)	AGWT	70	*Holomenopon setigerum*	16	N/A
(Broderson *et al.* 1977)	NSHO	38	*Holomenopon setigerum*	29	N/A
(Broderson *et al.* 1977)	NSHO	38	*Holomenopon clypeilargum*	8	N/A
Present study	CAGO	180	*Trinoton anserinum*	0.02	1.2
Present study	MALL	87	*Trinoton querquedulae*	37.9	6.97
(Rékási *et al.* 1997)	MALL	72	*Trinoton querquedulae*	12.5	0.96
(Canaris *et al.* 1981)	AGWT	70	*Trinoton querquedulae*	87	N/A
(Broderson *et al.* 1977)	NSHO	38	*Trinoton querquedulae*	84	N/A

CAGO = Canada goose (*Branta canadensis* Linnaeus)), MALL=mallard (*Anas platyrhynchos* Linnaeus), AGWT= American green-winged teal (*Anas crecca* Gmelin), GRGO= greylag goose (*Anser anser* (Linnaeus)), GWFG= greater white-fronted goose (*Anser albifrons*, (Scopoli)), BHGO=bar-headed goose (*Anser indicus* (Latham)), NSHO =northern shoveler (*Anas clypeata* Linnaeus), CITE= cinnamon teal (*Anas cyanoptera* Vieillot).

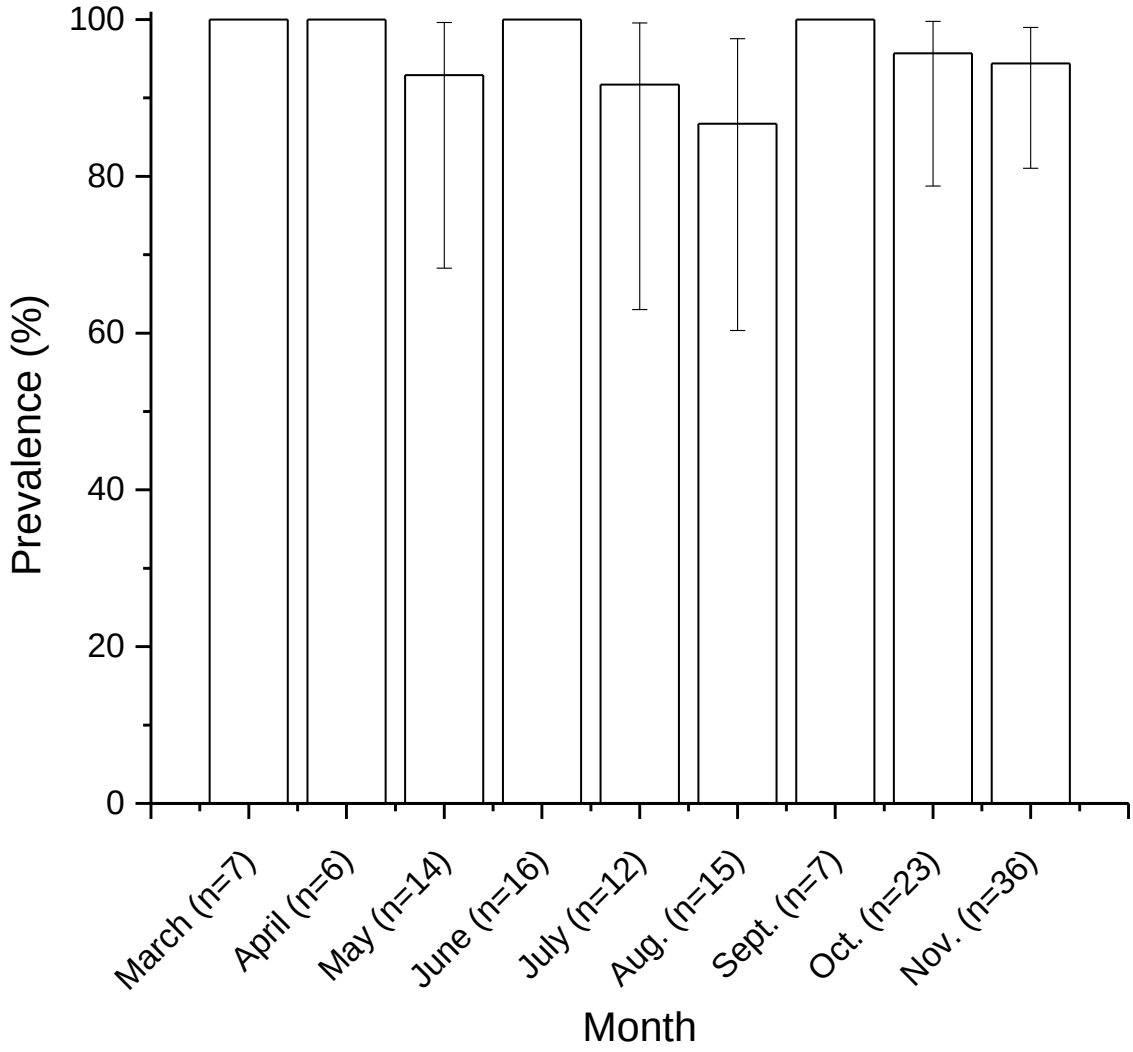

Fig. 5-1. Prevalence by month of all lice collected from adult Canada geese (>2520g) (n=136) examined from 1994 to 2012 in Manitoba, Canada, with 95% confidence intervals.

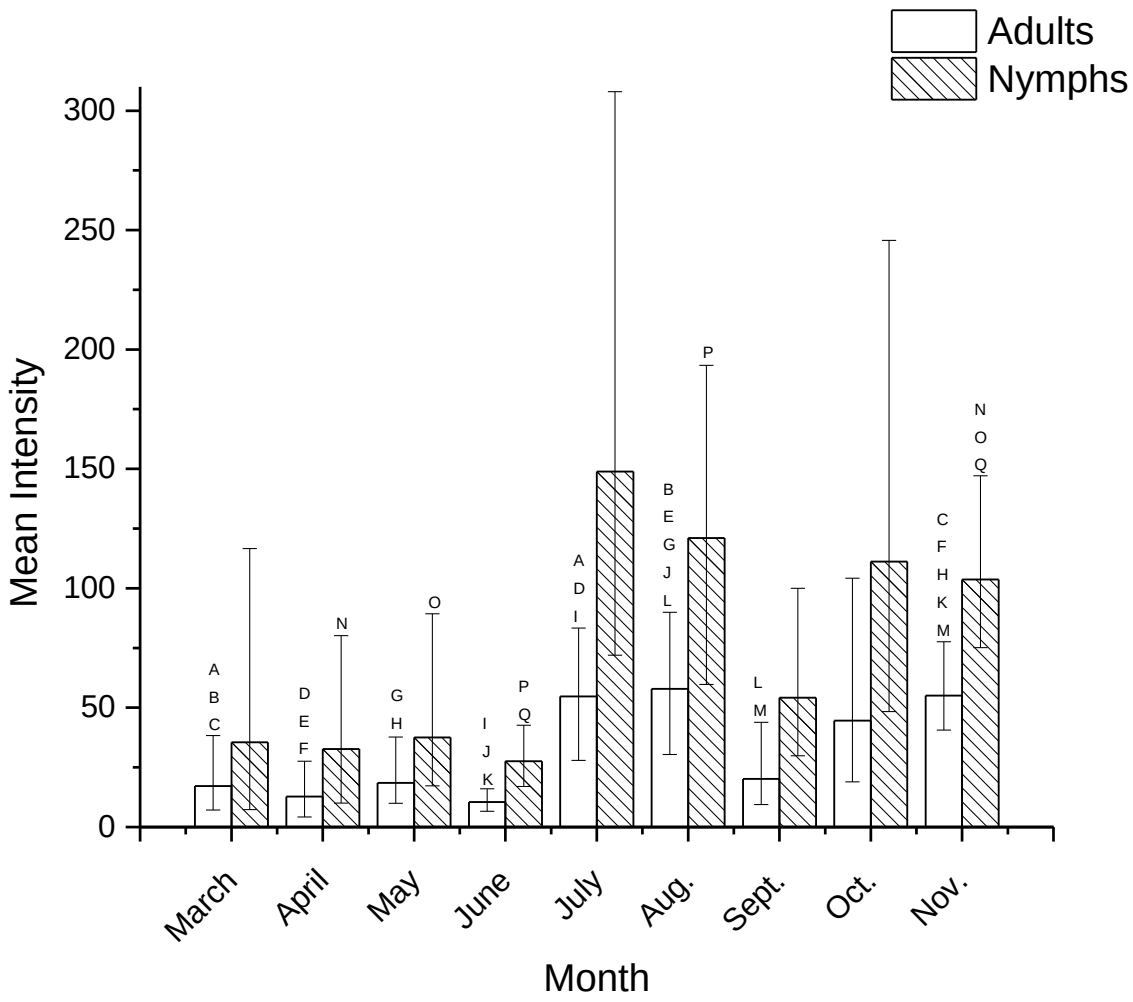

Fig. 5-2. Mean intensity by month of all lice collected from Canada geese (>2520g) (n=136) examined from 1994 to 2012 in Manitoba, Canada, with 95% confidence intervals. Matching letters indicate significant differences between pair-wise comparisons ($P<0.05$).

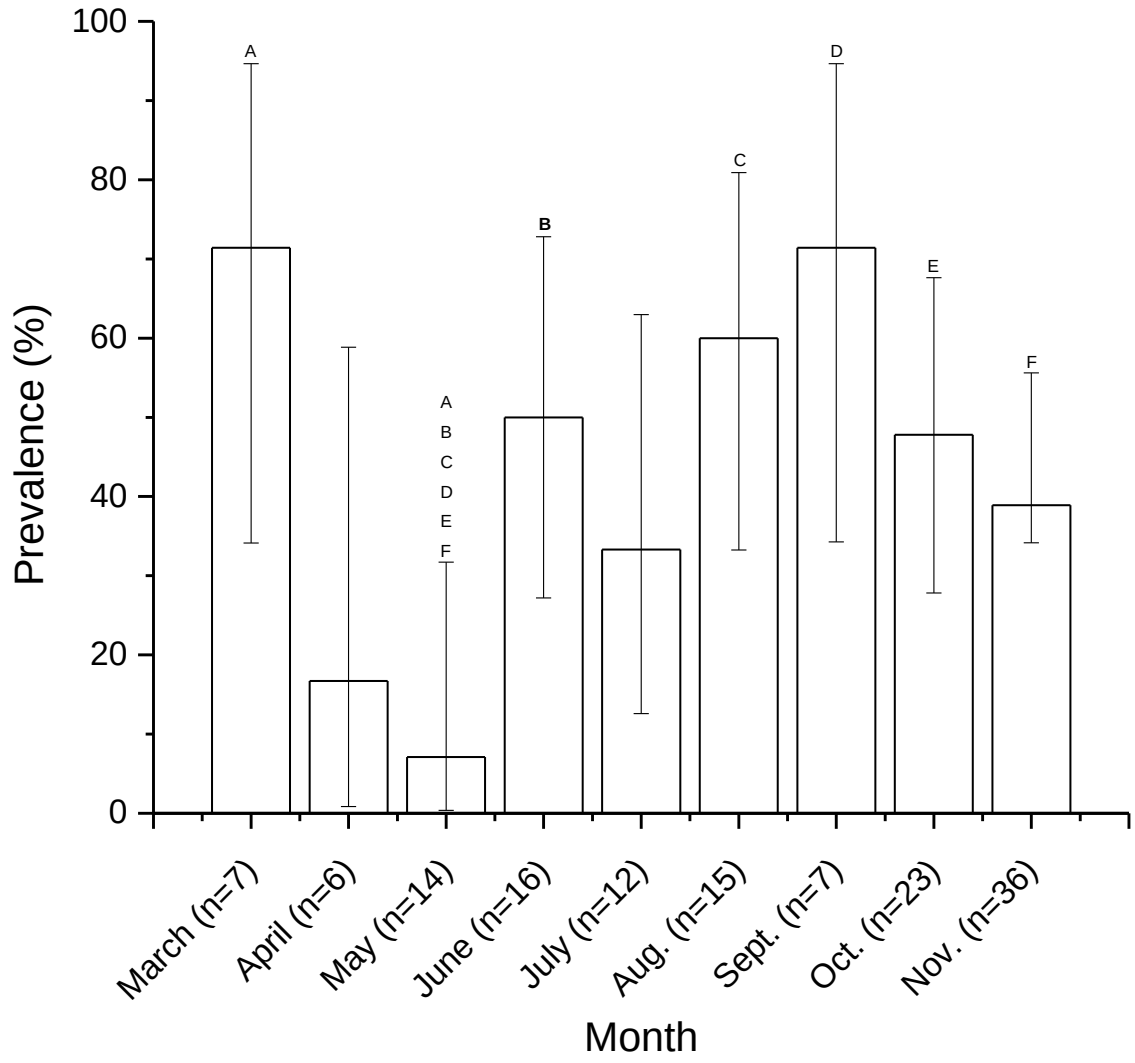

Fig. 5-3. Prevalence by month of *Anaticola anseris* collected from adult Canada geese (>2520g) (n=136) examined from 1994 to 2012 in Manitoba, Canada, with 95% confidence intervals. Matching letters indicate significant differences between pair-wise comparisons ($P<0.05$).

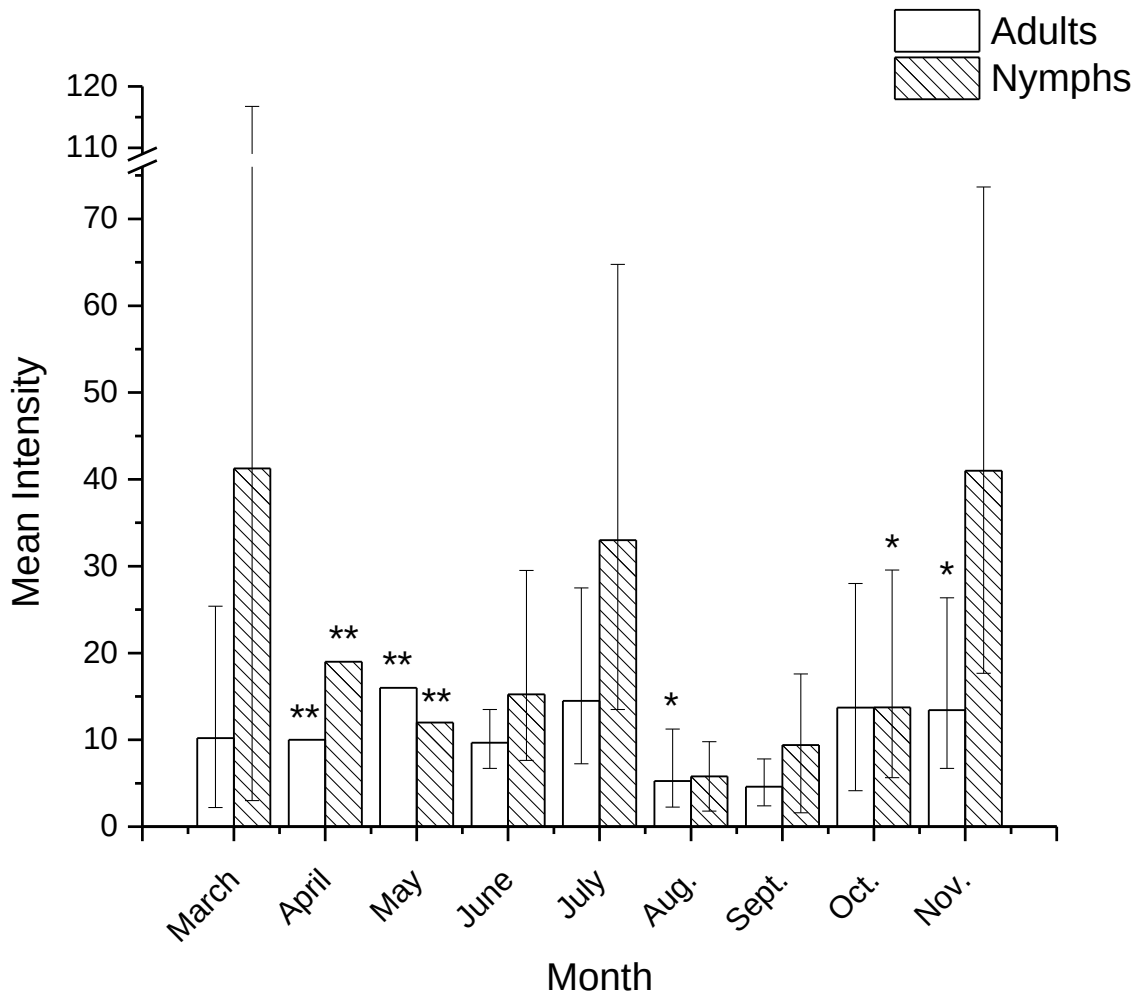

Fig. 5-4. Mean intensity by month of *Anaticola anseris* collected from Canada geese (>2520g) (n=136) examined from 1994 to 2012 in Manitoba, Canada, with 95% confidence intervals. * 90% confidence interval, ** Confidence limits are uncertain.

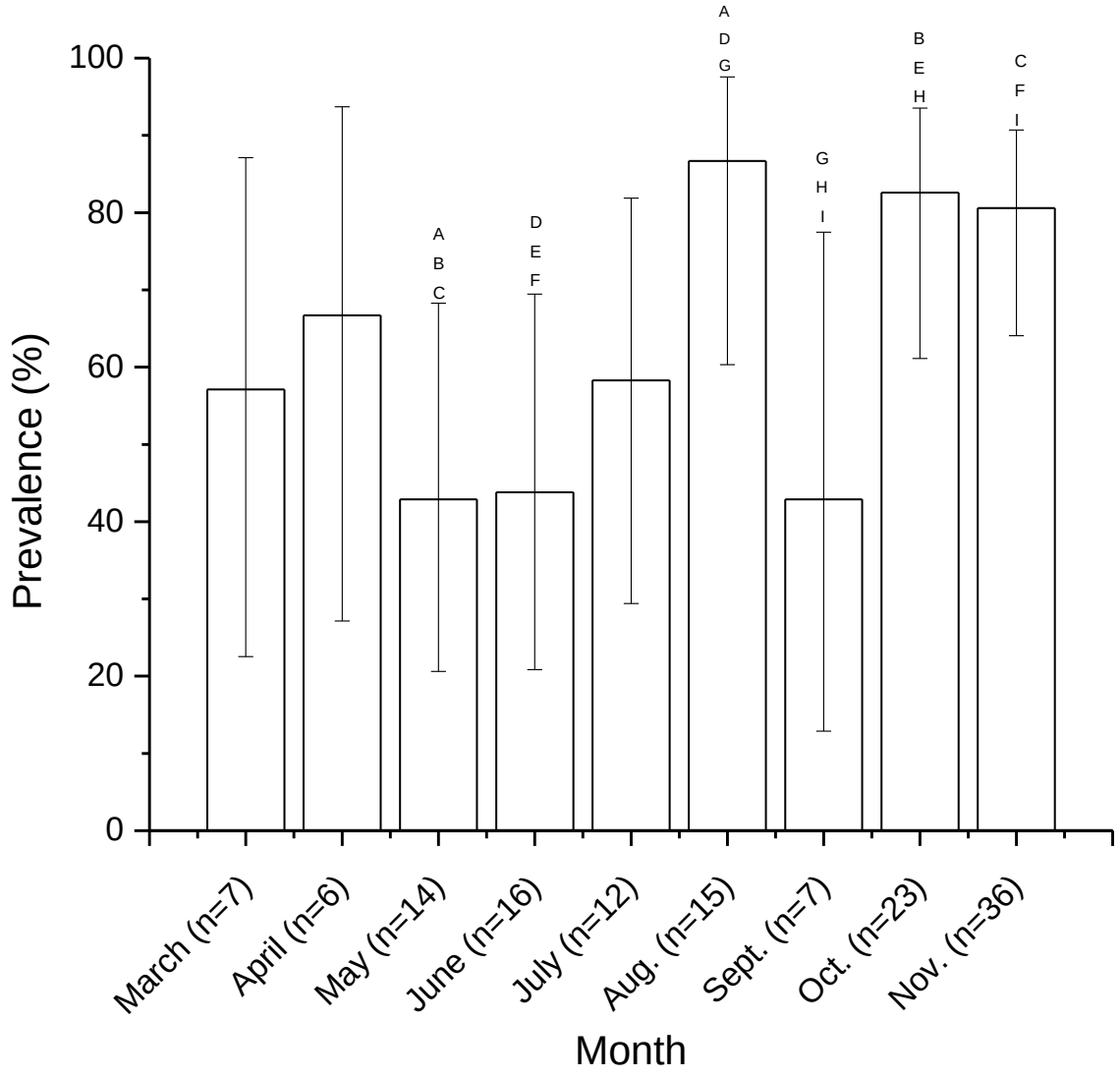

Fig. 5-5. Prevalence by month of *Anatoecus* spp. (*A. dentatus* and *A. penicillatus*) collected from adult Canada geese (>2520g) (n=136) examined from 1994 to 2012 in Manitoba, Canada, with 95% confidence intervals. Matching letters indicate significant differences between pair-wise comparisons ($P<0.05$).

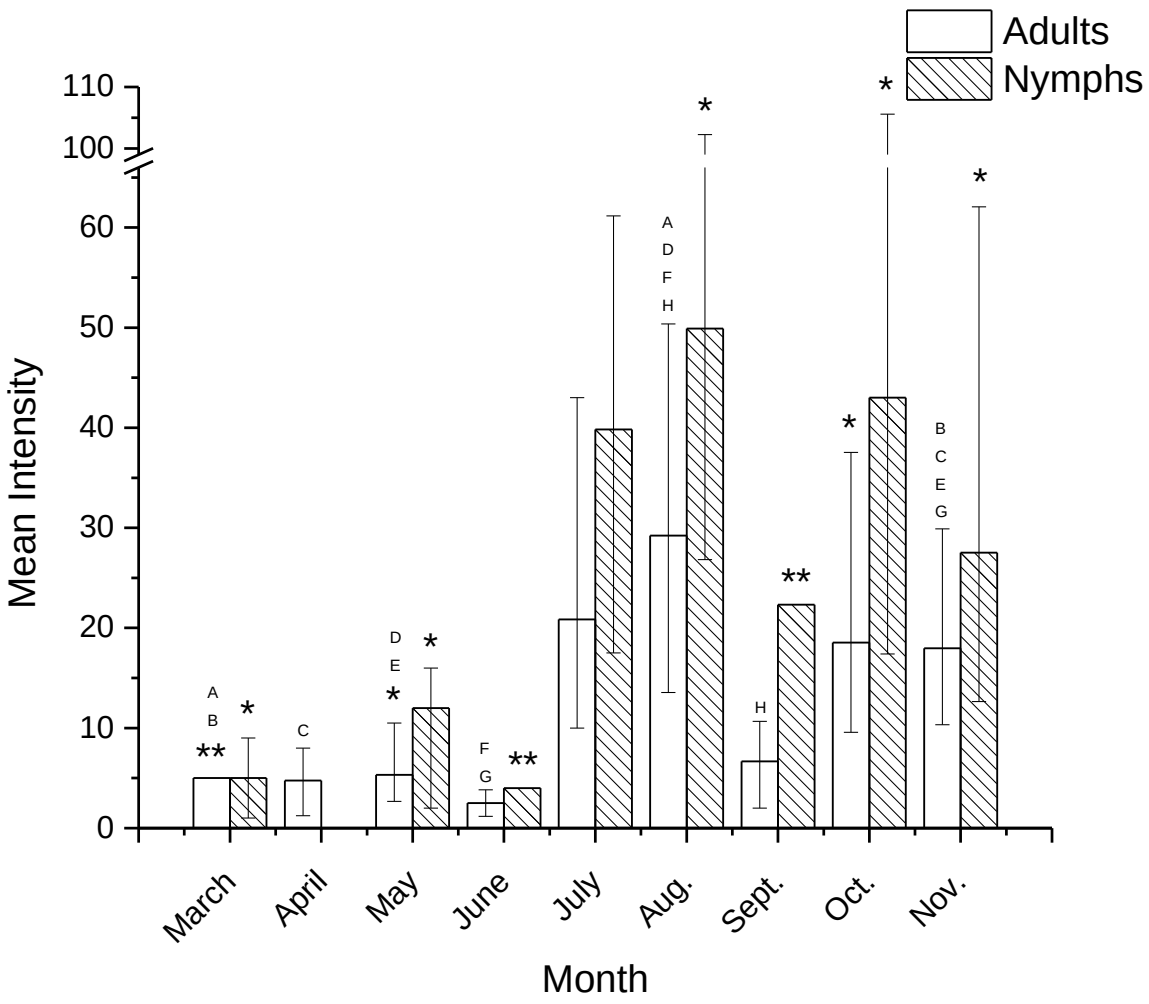

Fig. 5-6. Mean intensity by month of *Anatoecus* spp. (*A. dentatus* and *A. penicillatus*) collected from Canada geese (>2520g) (n=136) examined from 1994 to 2012 in Manitoba, Canada, with 95% confidence intervals. Matching letters indicate significant differences between pair-wise comparisons (P<0.05). * 90% confidence interval, ** Confidence limits are uncertain.

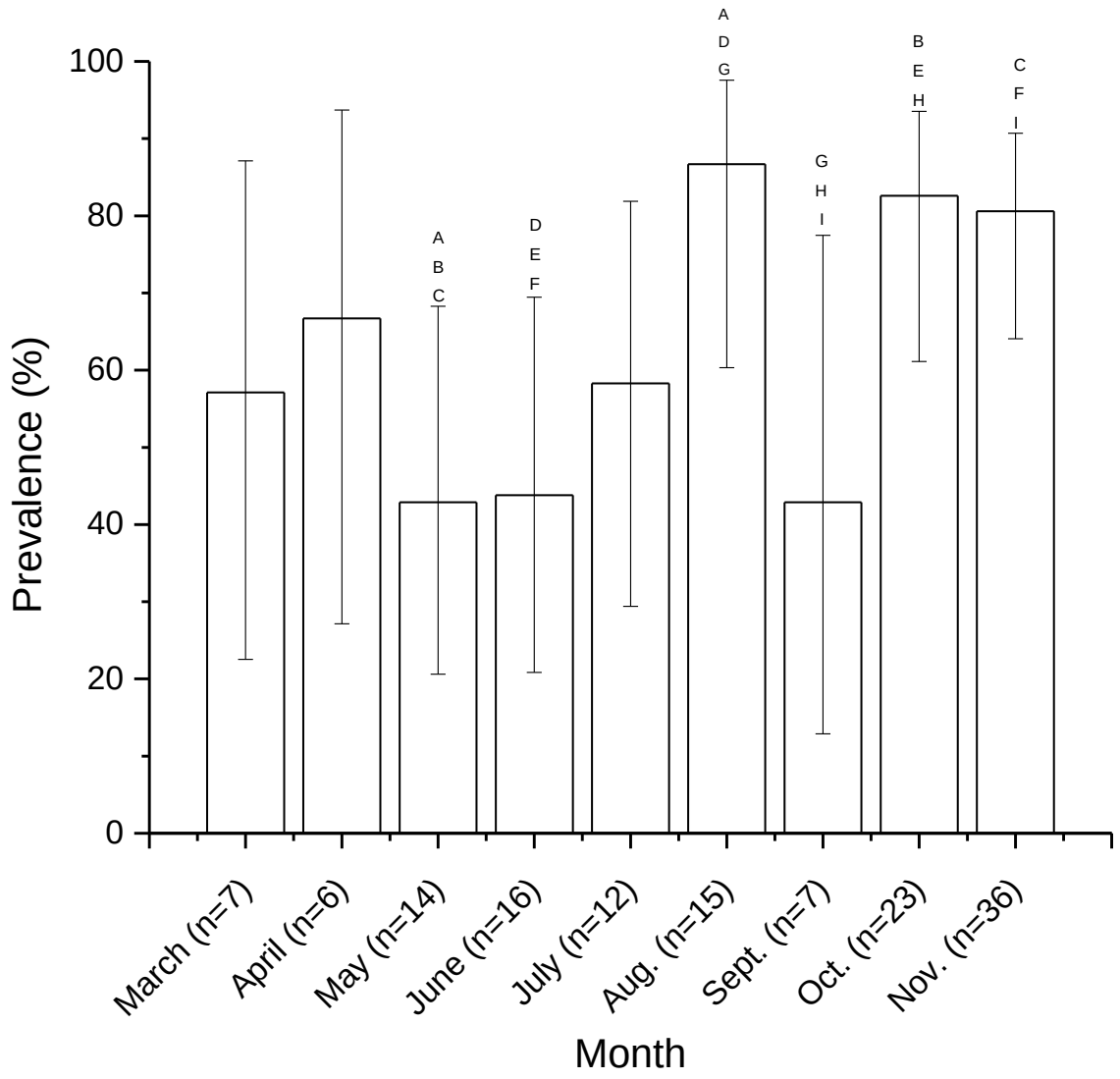

Fig. 5-7. Prevalence by month of *Anatoecus* spp. (*A. dentatus* and *A. penicillatus*) collected from adult Canada geese (>2520g) (n=136) examined from 1994 to 2012 in Manitoba, Canada, with 95% confidence intervals. Matching letters indicate significant differences between pair-wise comparisons ($P<0.05$).

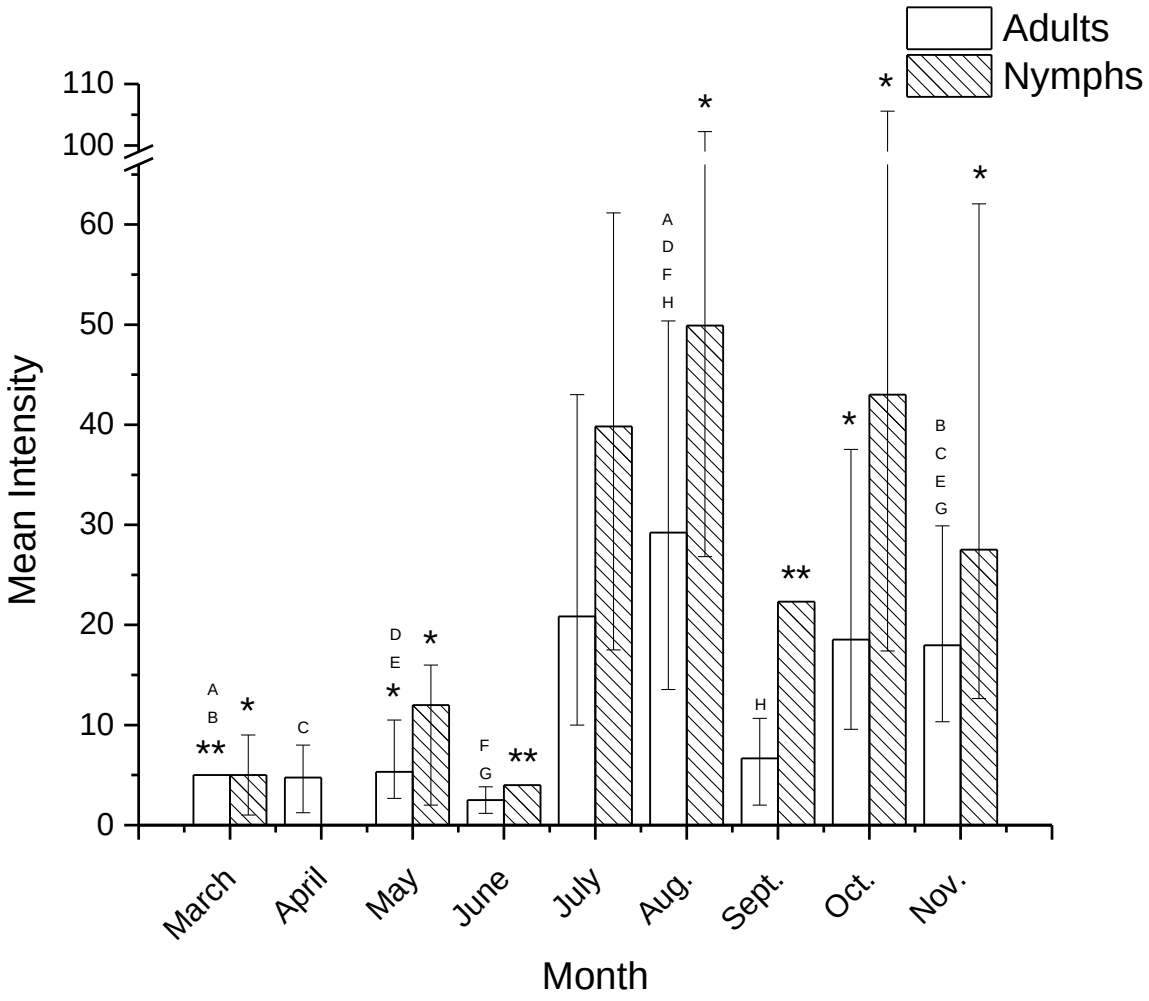

Fig. 5-8. Mean intensity by month of *Anatoecus* spp. (*A. dentatus* and *A. penicillatus*) collected from Canada geese (>2520g) (n=136) examined from 1994 to 2012 in Manitoba, Canada, with 95% confidence intervals. Matching letters indicate significant differences between pair-wise comparisons (P<0.05). * 90% confidence interval, ** Confidence limits are uncertain.

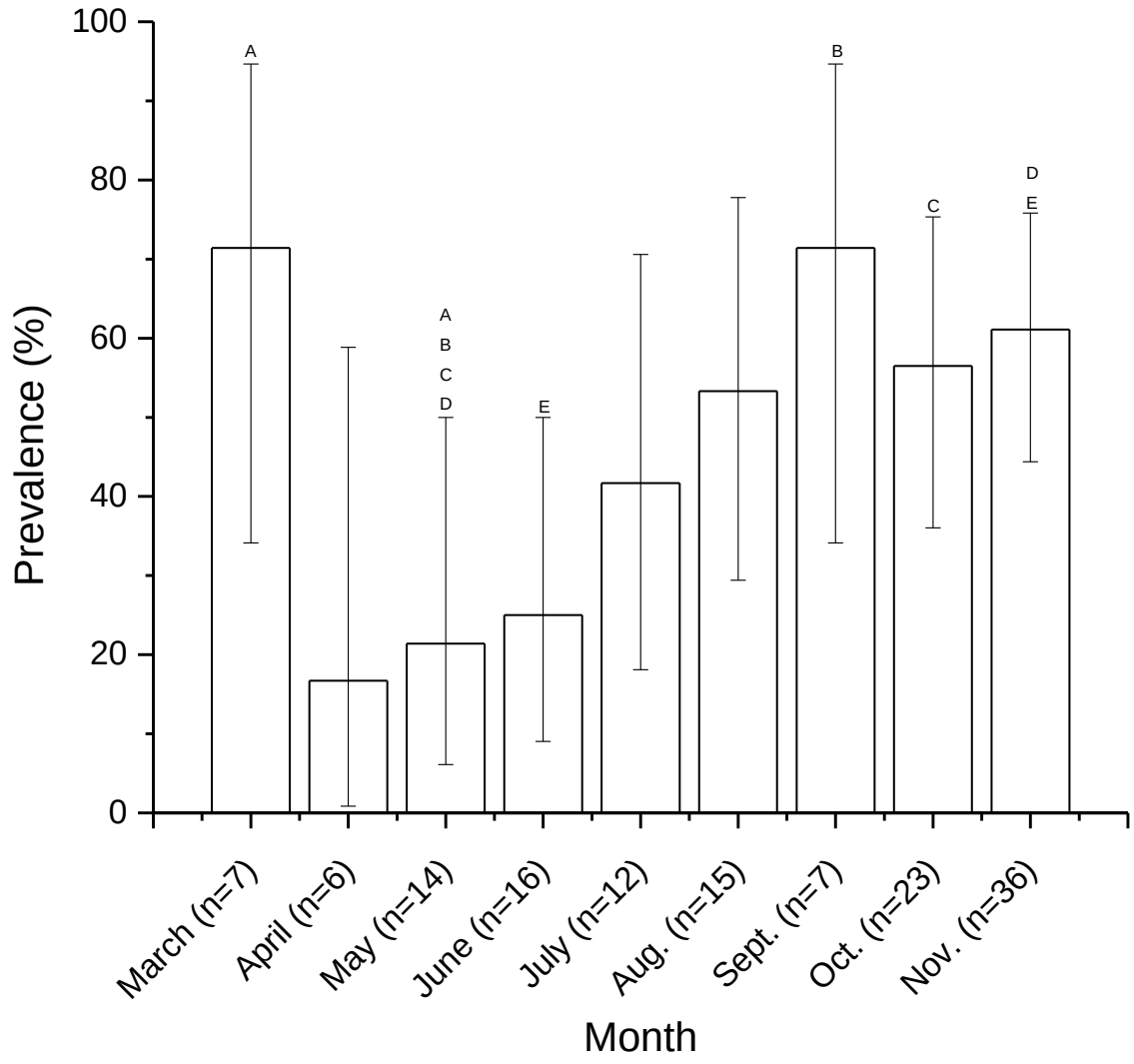

Fig. 5-9. Prevalence by month of *Ciconiphilus pectiniventris* collected from adult Canada geese (>2520g) (n=136) examined from 1994 to 2012 in Manitoba, Canada, with 95% confidence intervals. Matching letters indicate significant differences between pair-wise comparisons ($P<0.05$).

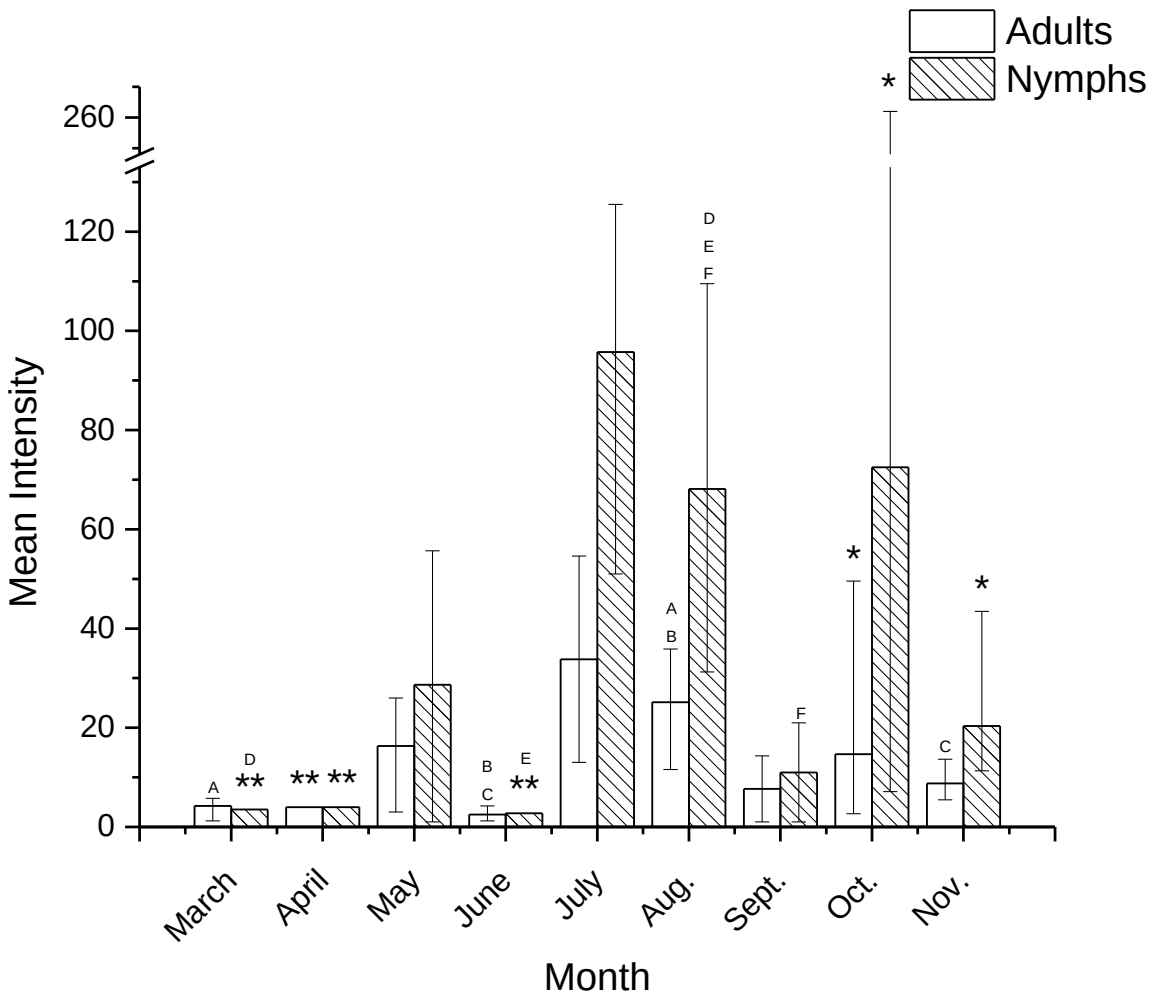

Fig. 5-10. Mean intensity by month of *Ciconiphilus pectiniventris* collected from Canada geese (>2520g) (n=136) examined from 1994 to 2012 in Manitoba, Canada, with 95% confidence intervals. Matching letters indicate significant differences between pair-wise comparisons (P<0.05). * 90% confidence interval, ** Confidence limits are uncertain.

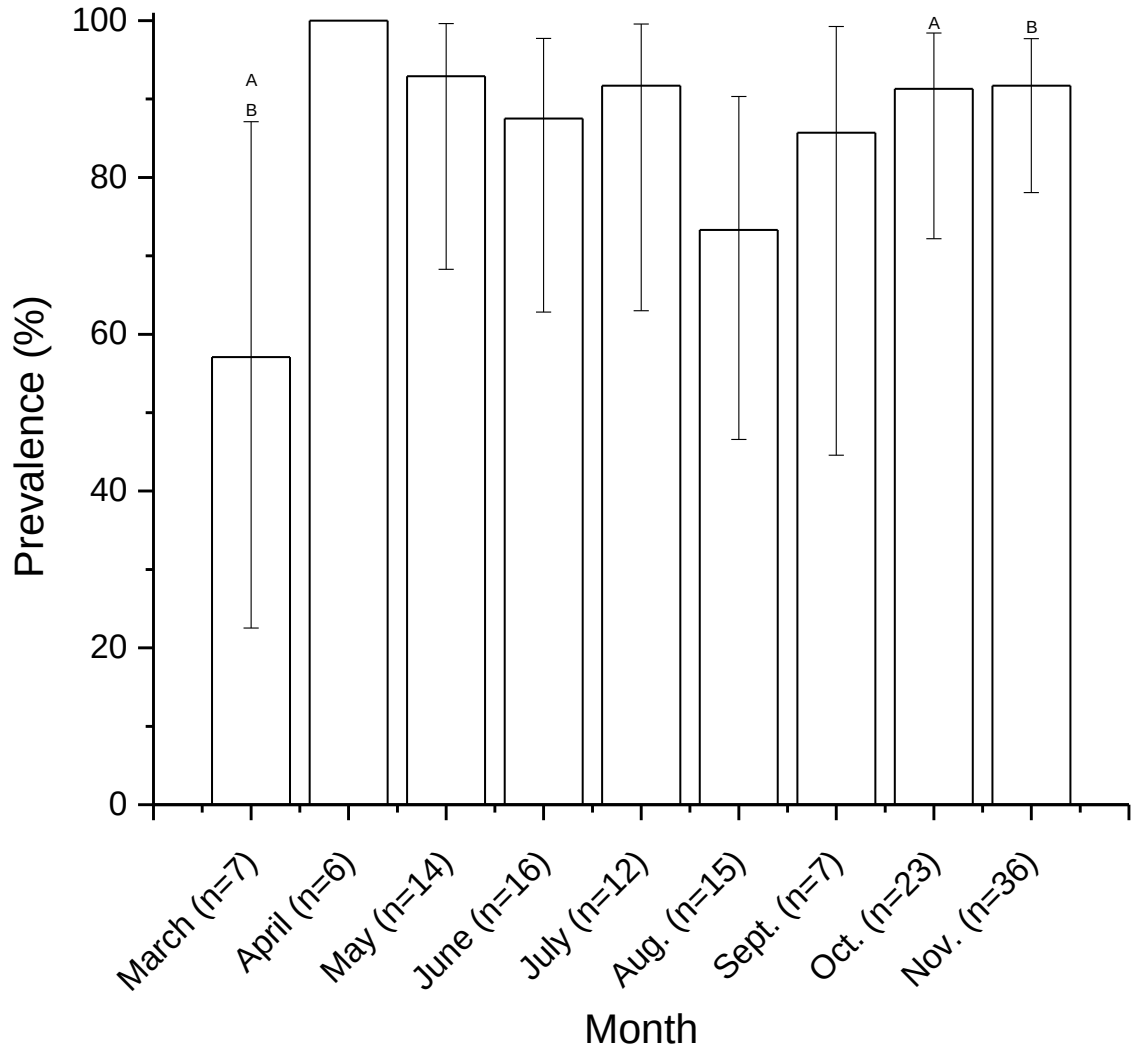

Fig. 5-11. Prevalence by month of *Ornithobius goniopleurus* collected from adult Canada geese (>2520g) (n=136) examined from 1994 to 2012 in Manitoba, Canada, with 95% confidence intervals. Matching letters indicate significant differences between pair-wise comparisons ($P<0.05$).

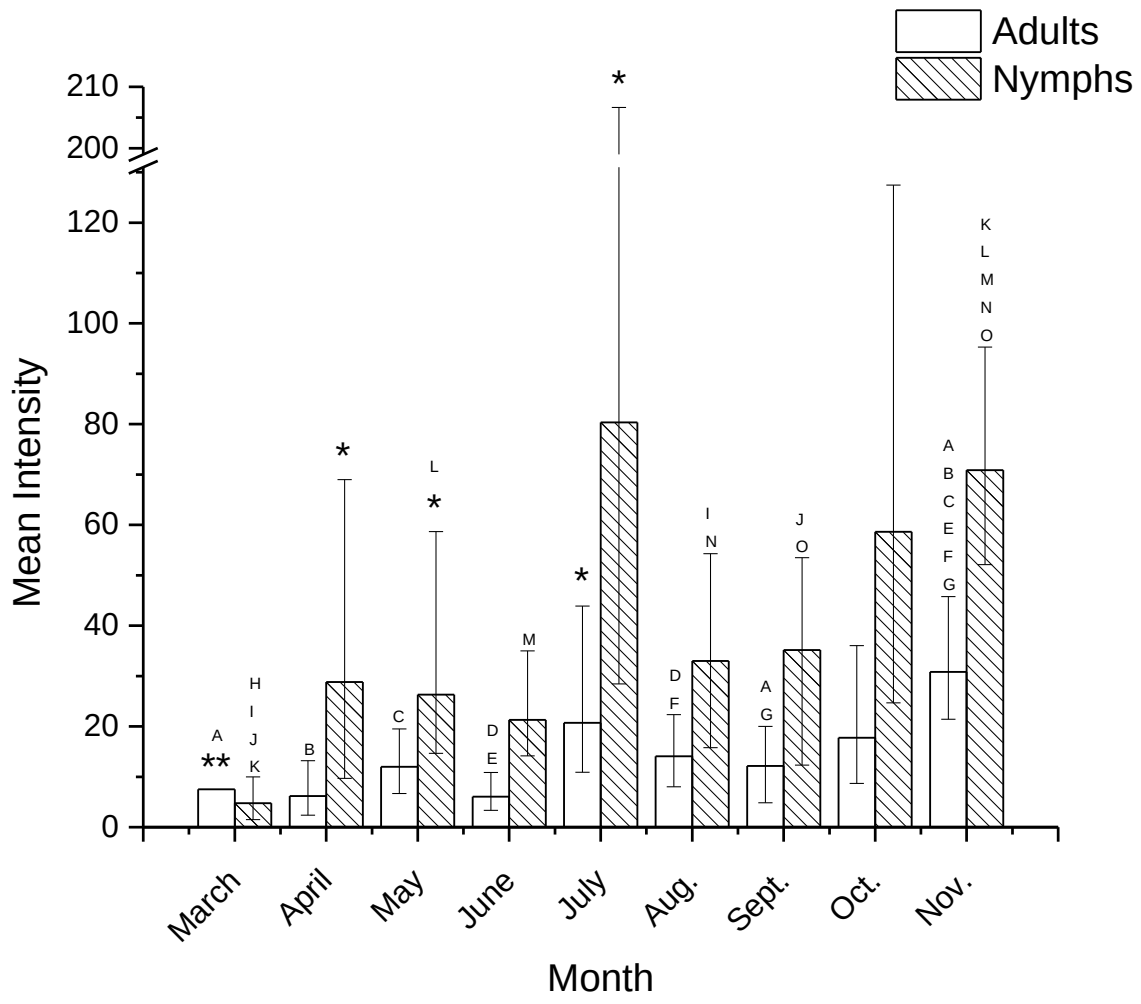

Fig. 5-12. Mean intensity by month of *Ornithobius goniopleurus* collected from Canada geese (>2520g) (n=136) examined from 1994 to 2012 in Manitoba, Canada, with 95% confidence intervals. Matching letters indicate significant differences between pair-wise comparisons ($P<0.05$). * 90% confidence interval, ** Confidence limits are uncertain.

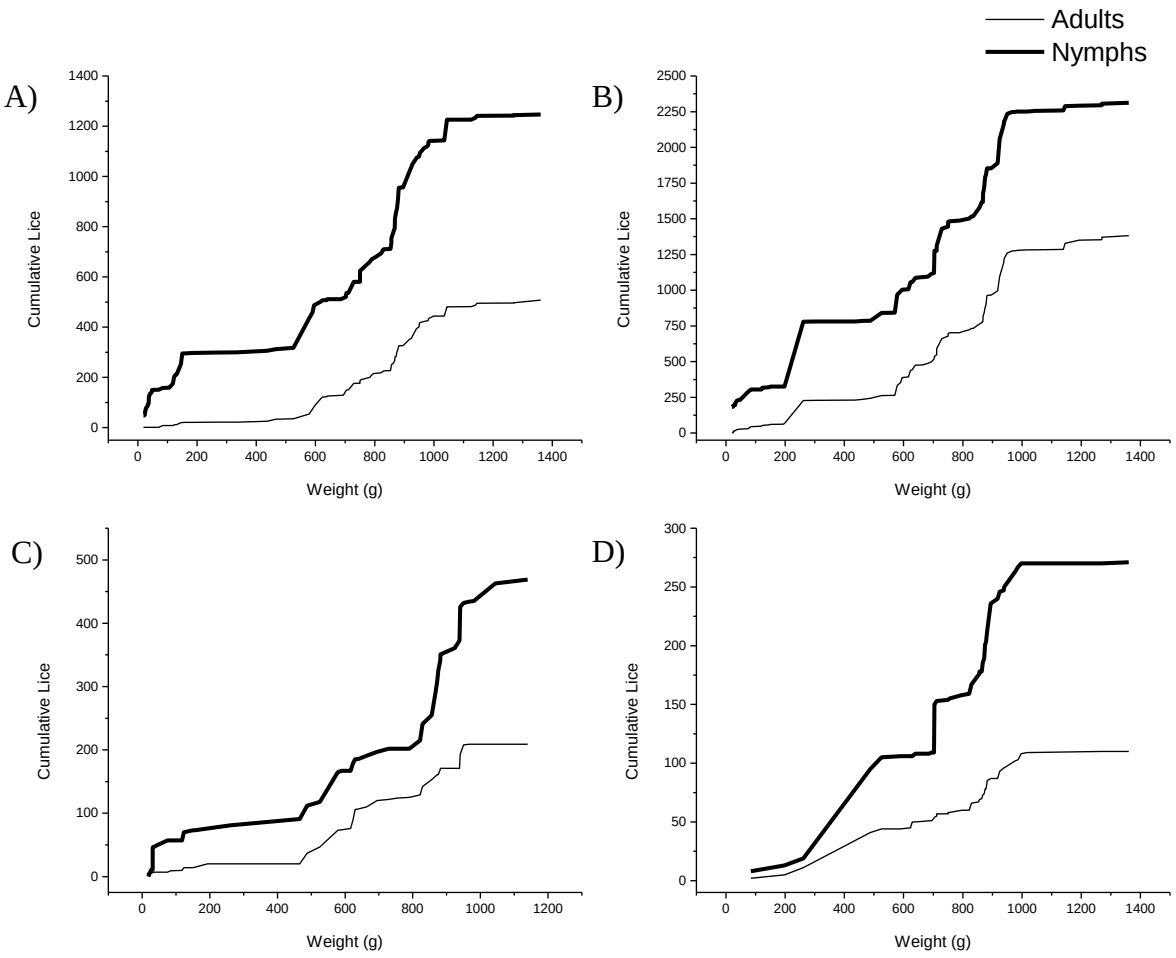

Fig. 5-13**.** Cumulative number of adults and nymphs for each species of chewing lice as weight of mallards (n=104) increases. A) *Anaticola crassicornis*, B) *Anatoecus dentatus*, C) *Holomenopon maxbeieri* and *H. leucoxanthum* D) *Trinoton querquedulae*.

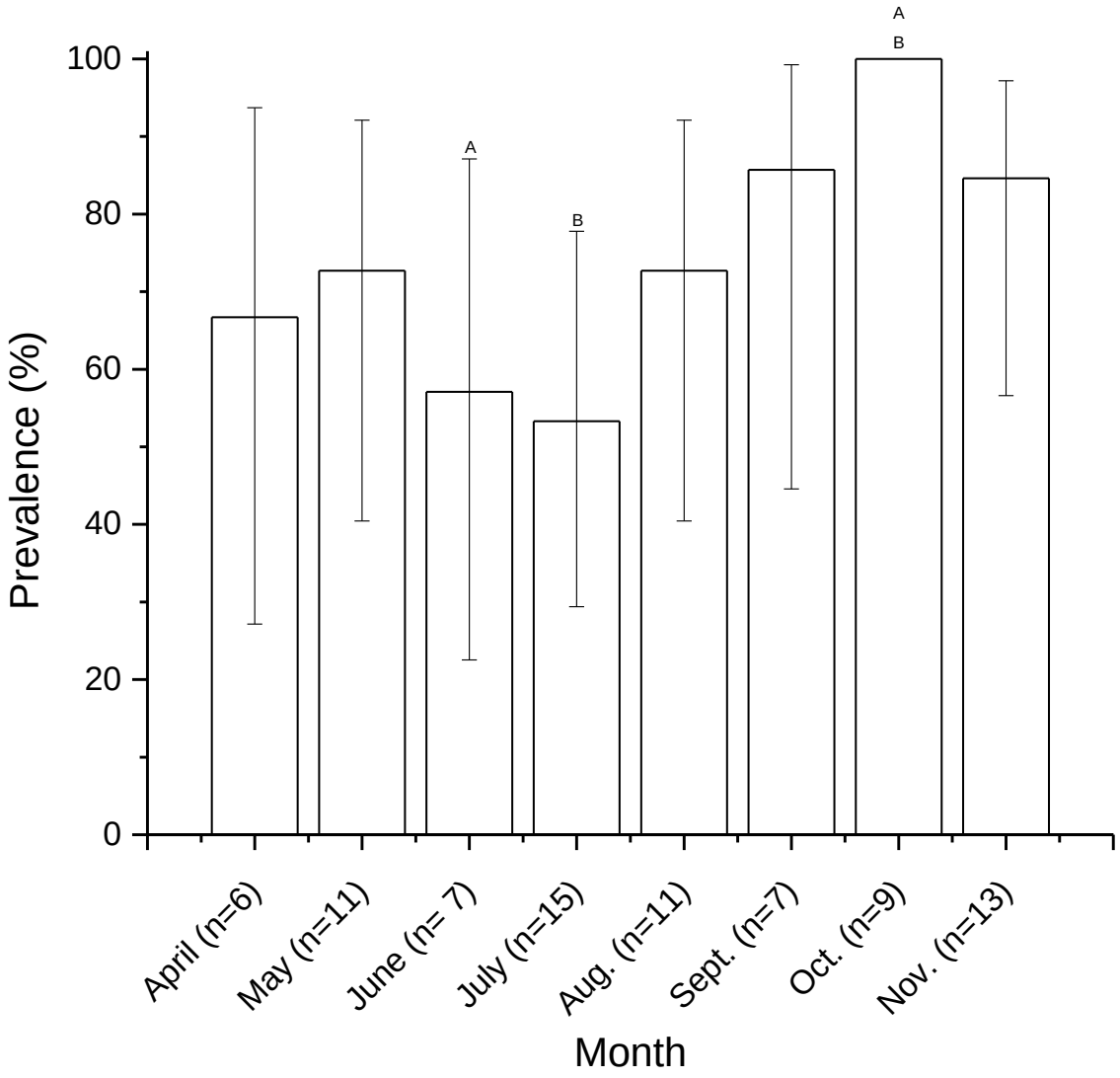

Fig. 5-14. Prevalence by month of all lice collected from adult mallards (>800g) (n= 79) examined from 1994 to 2012 in Manitoba, Canada, with 95% confidence intervals. Matching letters indicate significant differences between pair-wise comparisons ($P<0.05$).

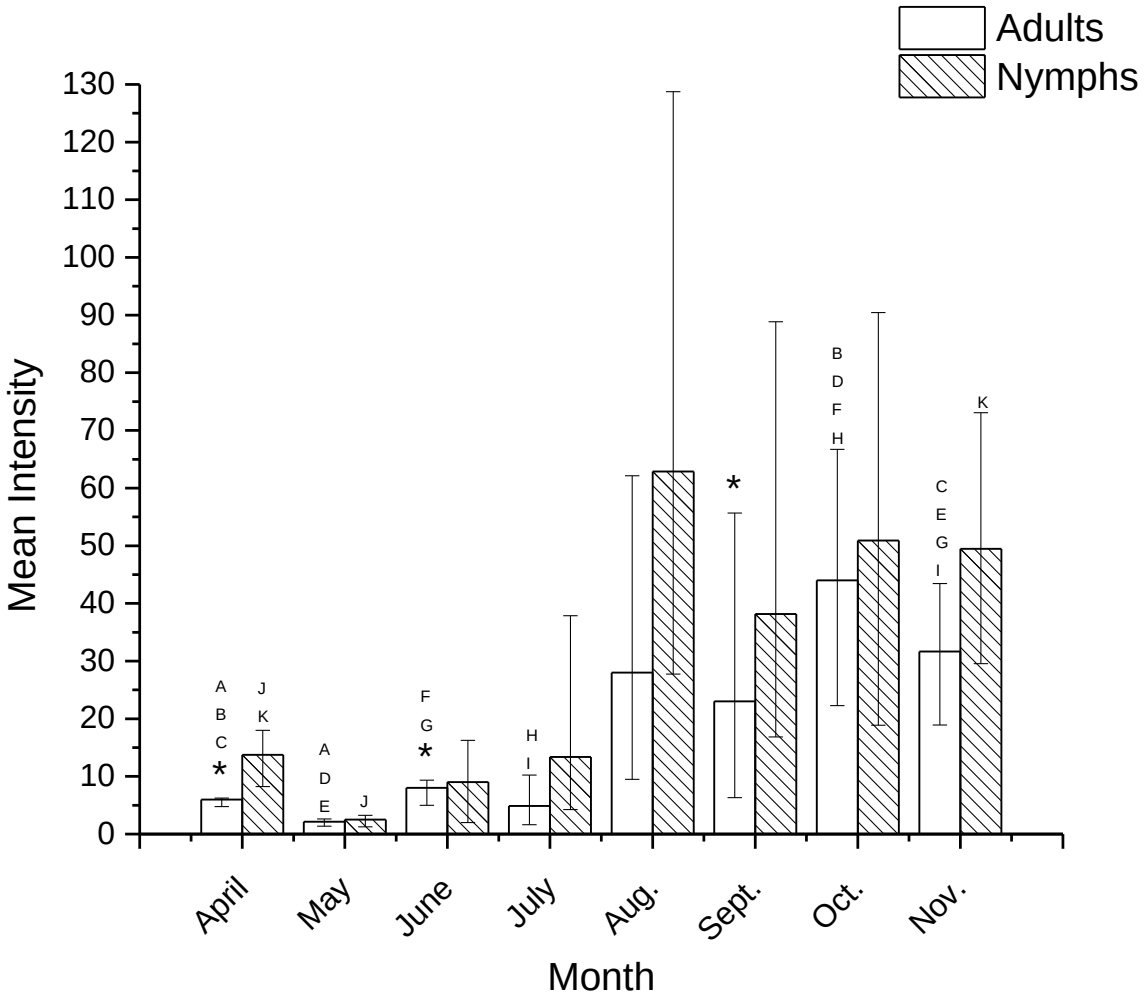

Fig. 5-15. Mean intensity by month of all lice collected from adult mallards (>800g) (n=79) examined from 1994 to 2012 in Manitoba, Canada, with 95% confidence intervals. Matching letters indicate significant differences between pair-wise comparisons ($P<0.05$). * 90% confidence interval.

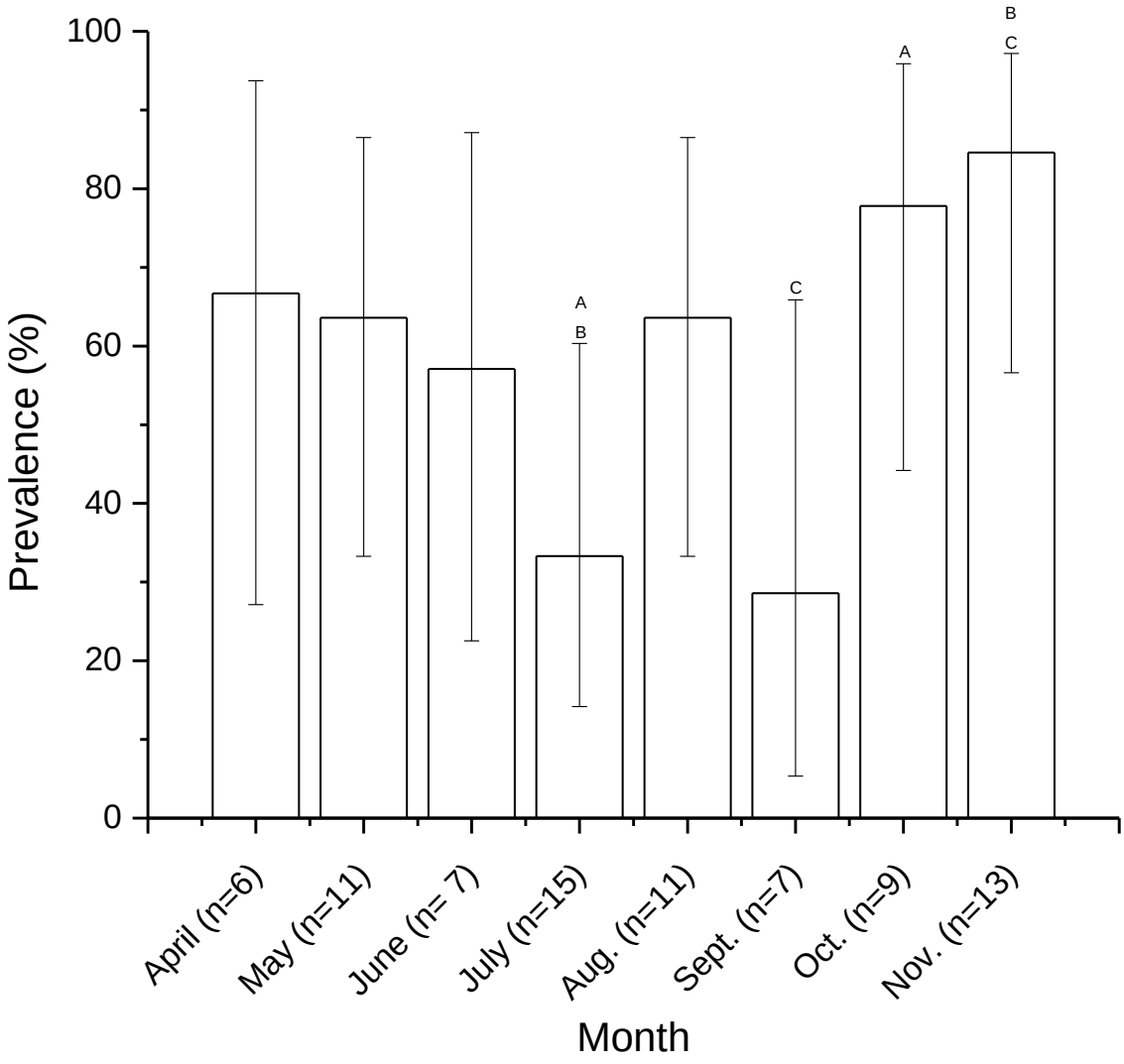

Fig. 5-16. Prevalence by month of *Anaticola crassicornis* collected from adult mallards (>800g) (n=79) examined from 1994 to 2012 in Manitoba, Canada, with 95% confidence intervals. Matching letters indicate significant differences between pair-wise comparisons ($P<0.05$).

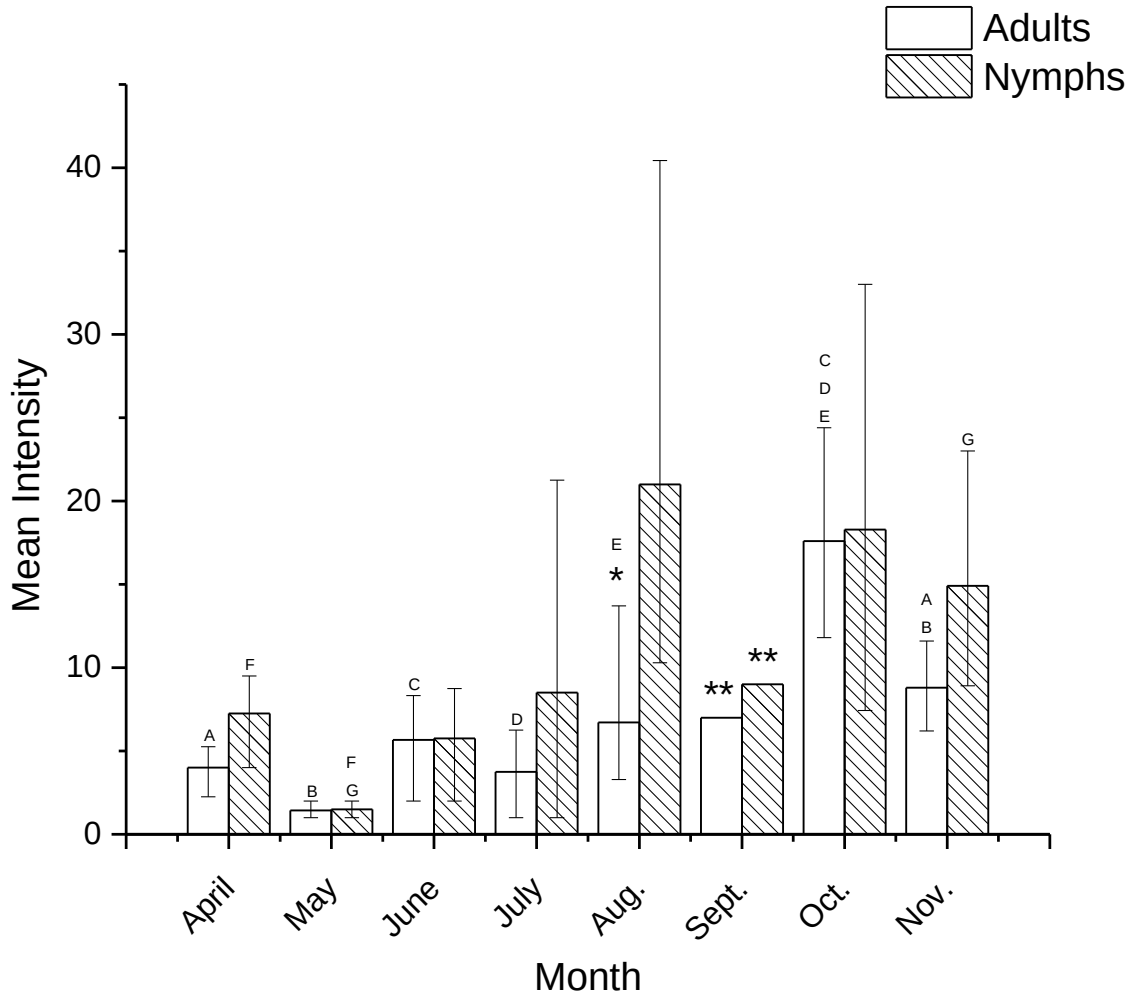

Fig. 5-17. Mean intensity by month of *Anaticola crassicornis* collected from adult mallards (>800g) (n=79) examined from 1994 to 2012 in Manitoba, Canada, with 95% confidence intervals. Matching letters indicate significant differences between pair-wise comparisons (P<0.05). * 90% confidence interval, ** Confidence limits are uncertain.

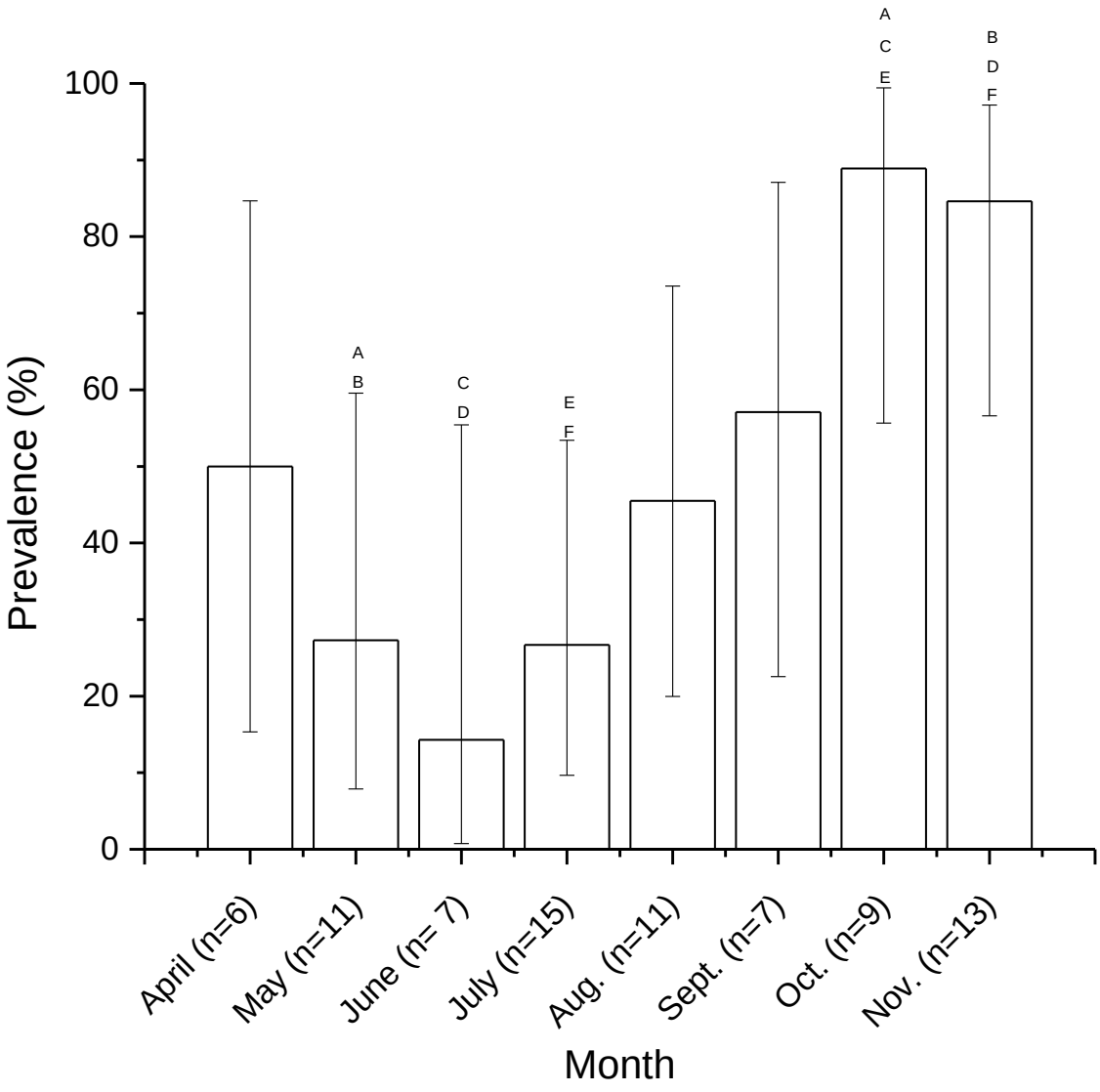

Fig. 5-18. Prevalence by month of *Anatoecus dentatus* collected from adult mallards (>800g) (n=79) examined from 1994 to 2012 in Manitoba, Canada, with 95% confidence intervals. Matching letters indicate significant differences between pair-wise comparisons ($P<0.05$).

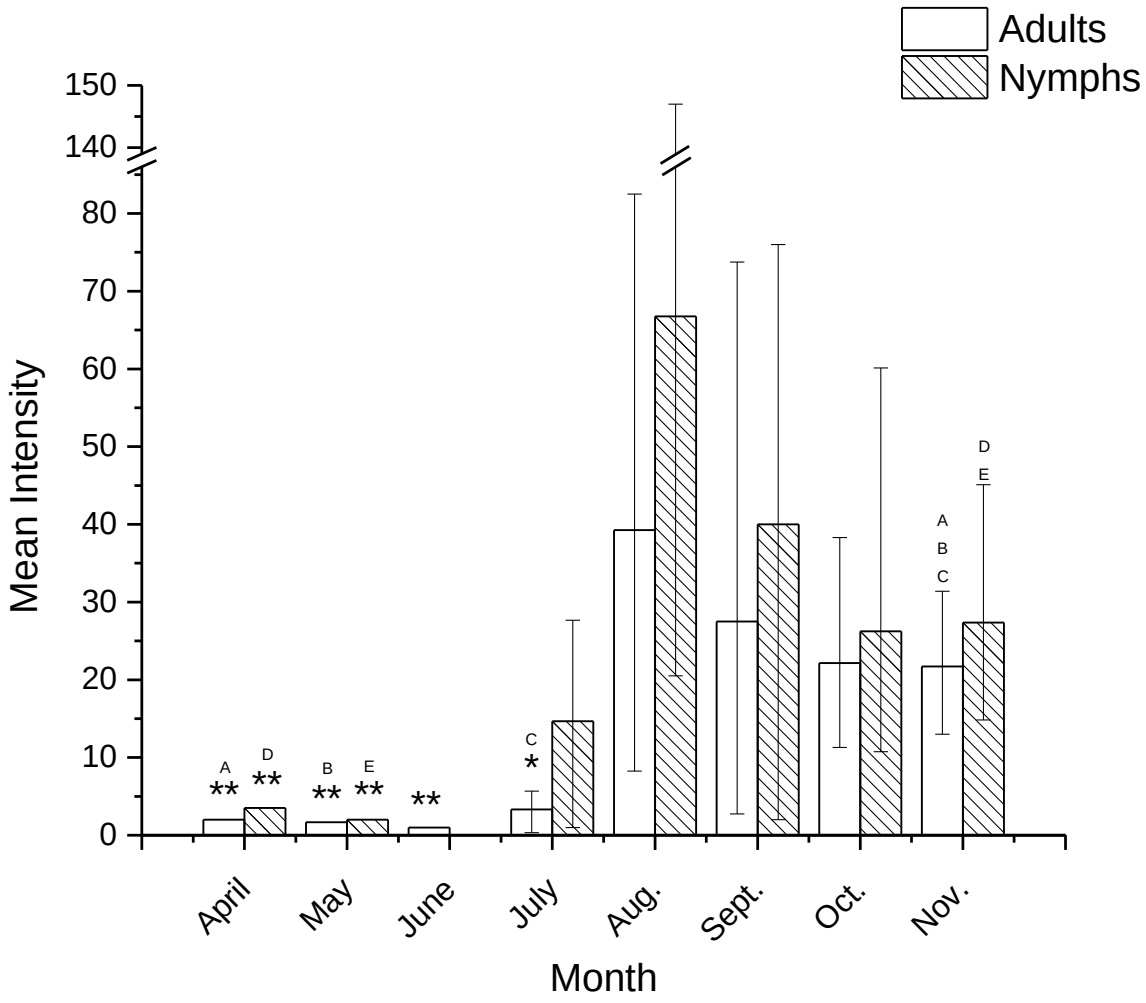

Fig. 5-19. Mean intensity by month of *Anatoecus dentatus* collected from adult mallards (>800g) (n=79) examined from 1994 to 2012 in Manitoba, Canada, with 95% confidence intervals. Matching letters indicate significant differences between pair-wise comparisons ($P<0.05$). * 90% confidence interval, ** Confidence limits are uncertain.

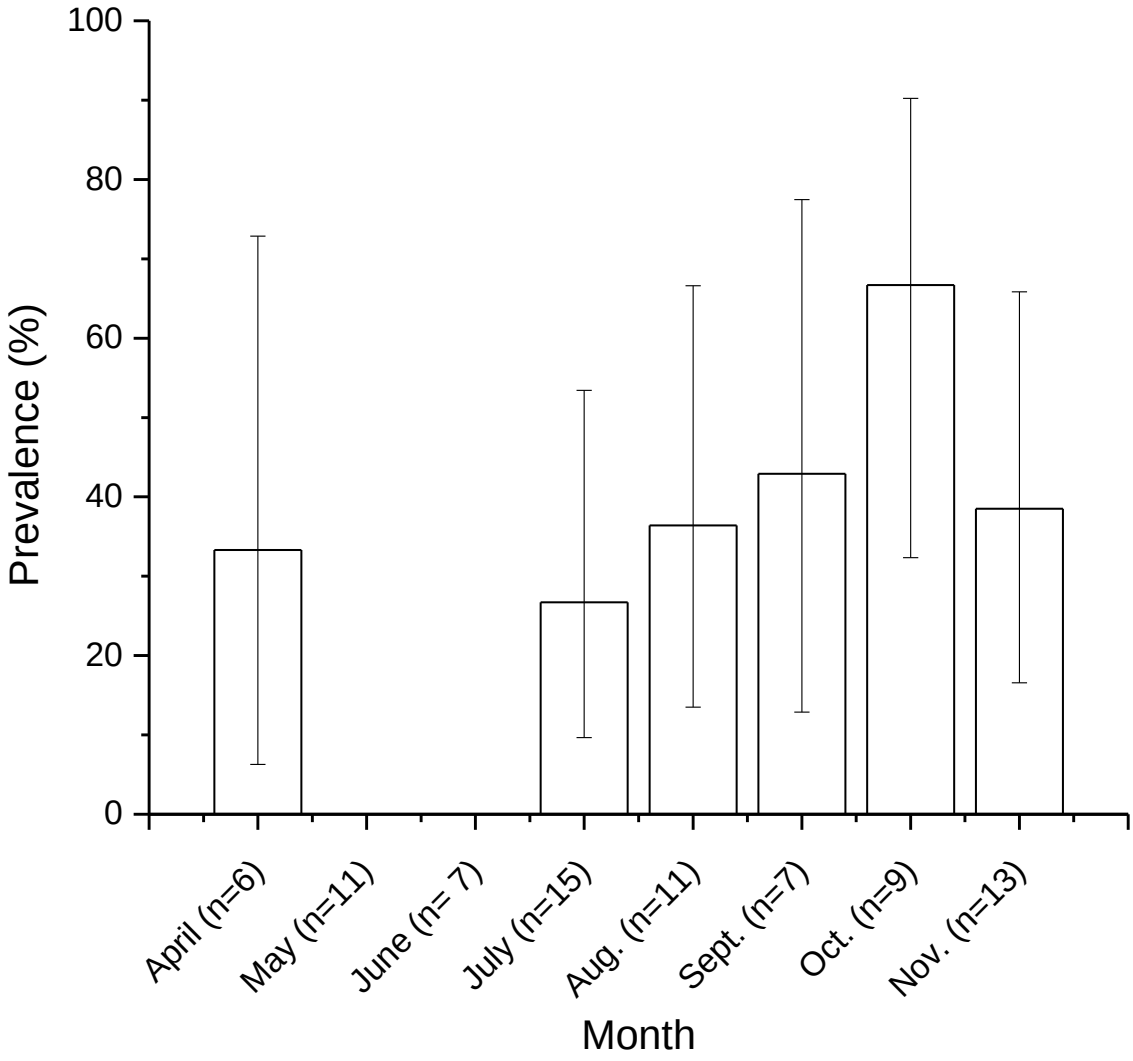

Fig. 5-20. Prevalence by month of *Holomenopon* spp. (*Holomenopon leucoxanthum* and *Holomenopon maxbeieri*) collected from adult mallards (>800g) (n=79) examined from 1994 to 2012 in Manitoba Canada, with 95% confidence intervals.

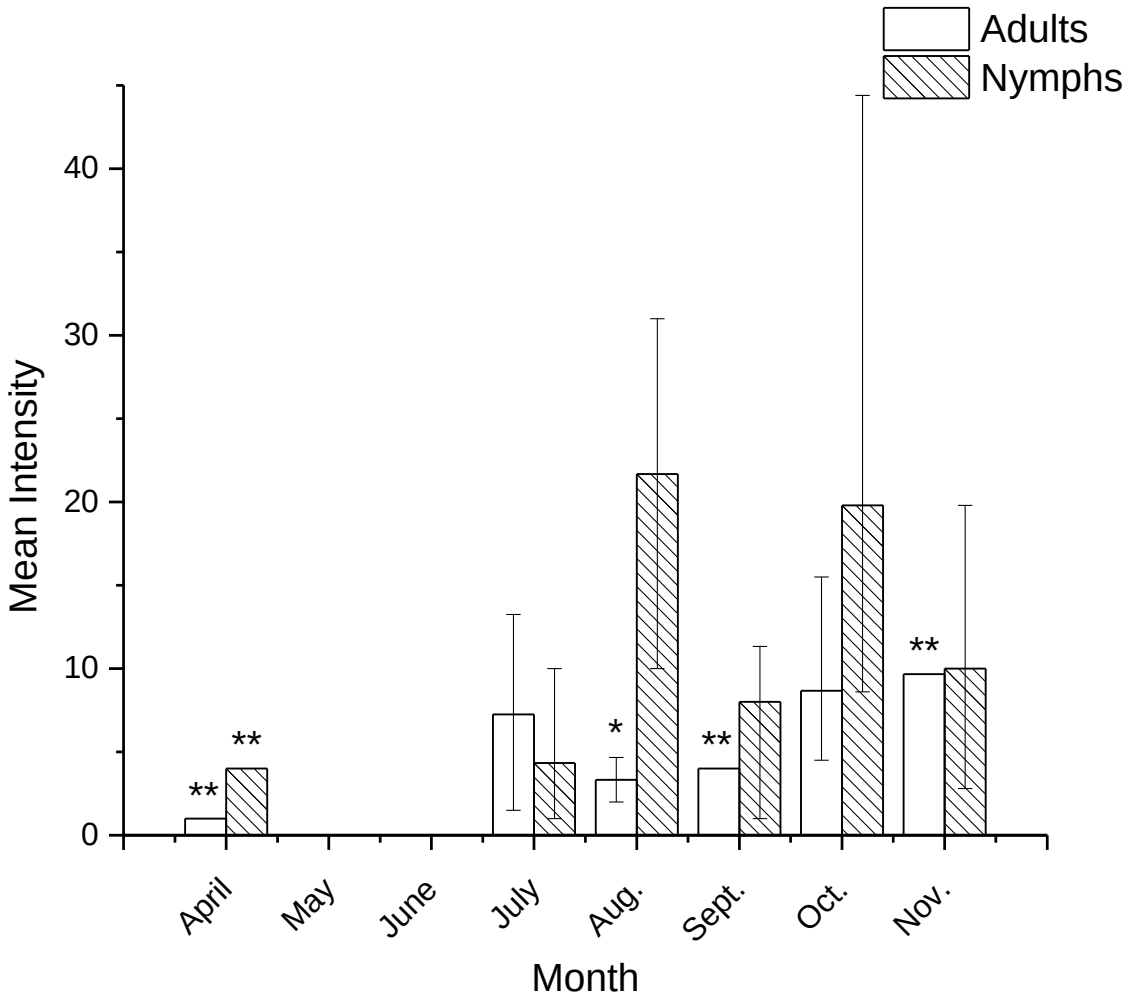

Fig. 5-21. Mean intensity by month of *Holomenopon* spp. (*Holomenopon leucoxanthum* and *Holomenopon maxbeieri*) collected from adult mallards (>800g) (n=79) examined from 1994 to 2012 in Manitoba, Canada, with 95% confidence intervals. * 90% confidence interval, ** Confidence limits are uncertain.

CHAPTER 6: General Discussion

This is the first in-depth, quantitative study in which the chewing lice on Canada geese and mallards have been studied. The genus *Anatoecus* received a lot of attention; subsequently *Anatoecus icterodes* and *Anatoecus dentatus* were synonomized; this resulted in recognition of two male morphotypes: one with an effractor and reticular comb and one without. Male *A. dentatus* is not the only *Anatoecus* species with an effractor. Males of *Anatoecus penicillatus* and *Anatoecus keymeri*, which is a louse found on flamingoes, also have effractors (Clay 1974; Kéler 1960). However, *A. dentatus* is the only species to possess a reticular comb. The function of this structure is unknown; however, their location surrounding the genitalia leads one to believe it may play a role in reproduction or copulation. The effractor is an interesting structure in and of itself; it is even more fascinating that approximately half of the known species of *Anatoecus* possess it. This raises the question, is the effractor an acquired trait or, is it an ancestral trait that was lost? A phylogeny of *Anatoecus* species may be able to answer this.

Anatoecus dentatus infests at least 82 species of Anseriformes and therefore is not a host specific louse. Since chewing lice disperse mainly through direct contact, how often does *A. dentatus* disperse from one host to a different species of host? I have observed several species of ducks and Canada geese sharing the same pond, therefore the opportunity for interaction between different host species does exist. It would be interesting to compare the gene flow of *A. dentatus* on the same species of host to *A. dentatus* infesting different host species, in order to infer the level of dispersal.

Anatoecus pygaspis and *Anatoecus keleri* both infest American flamingoes (*Phenicopterus ruber*). There is no description of female *A. keleri* and the males of *A.*

keleri are distinguishable from *A. pygaspis* by characteristics of the genital sac (Clay 1974). This distinction by the male genitalia is similar to how *A. icterodes* and *A. dentatus* were previously separated. Therefore *A. pygaspis* and *A. keleri* are good candidates for another molecular study.

Canada geese and mallards share three of the same genera: *Anaticola, Anatoecus* and *Trinoton.* When the prevalence for each genus on Canada geese was compared to that on mallards, they were all significantly different (p-value <0.05). However, the most noticeable difference in prevalence was between *Trinoton* on Canada geese (0.02%) and on mallards (37.9%). *Trinoton anserinum* infests Canada geese while *Trinoton querquedulae* infests mallards; perhaps these different species have different life cycles and *T. anserinum* lives longer and has a lower reproductive output. *Trinoton anserinum* could also be experiencing interspecific competition on Canada geese, most likely with *Ornithobius goniopleurus*. *Ornithobius goniopleurus* is the only species of louse that does not have an ecological equivalent on mallards, and is found on all regions of the host body. Interspecific competition has been shown to exist between *Columbicola baculoides* (Paine) and *Columbicola macrourae* (Wilson) on mourning doves (*Zenaida macroura*) (Malenke *et al.* 2011). *Columbicola baculoides* populations were significantly smaller when in the presence of *C. macrourae*, than they were alone. Conversely, *C. macrourae* populations were unaffected by the presence of *C. baculoides.* To determine the life cycle and longevity as well as whether interspecific competition is taking place, louse populations on Canada geese and mallards could be experimentally manipulated.

Ducks and geese are commercially raised, and some domesticated species, such as the rouen clair duck (*Anas platyrhynchos rouen clair*), are related to mallards. Therefore,

it is possible to raise Canada geese and mallards successfully in captivity. In order to manipulate louse populations effectively, hosts would have to be de-loused. Lice are commonly removed from Columbiformes by lowering the humidity to <25% relative humidity for 10 weeks, this kills 100% of lice and eggs (Moyer *et al.* 2002). The same method could be applied to Canada geese and mallards. Once hosts are louse free, they can be experimentally infested with different combinations of lice, collected from birds that were not dried. Some species, such as *T. anserinum*, may be difficult to integrate into such experiments because of its low prevalence and intensity. Experimental manipulation would help answer many basic questions about louse life histories, such as do larger louse species live longer, what is the reproductive rate of each louse species and how long does each species of louse live. Spatial distribution of each louse species when it is the only species present on a host could also be determined; distributions could then be compared to determine whether a species of louse alters it spatial distribution when other lice are also present on the same host. Rock pigeons (*Columba livia*) are host to *Columbicola columbae* and *Campanulotes compar*. When experimentally infested with both species, *C. columbae* changed its spatial distribution and was found significantly less often on abdominal feathers, compared to when *C. compar* was not present. In contrast, *C. compar* did not significantly change its spatial distribution in the presence of *C. columbae* (Bush and Malenke 2008). Along the same lines as this, you could also examine whether the presence of certain louse species suppresses the population of others, in experiments similar to what was described above on mourning doves. In the presence of *C. macrourae, C. baculoides* populations were significantly smaller than when found alone (Malenke *et al.* 2011).

When studying horizontal dispersal in lice, the interaction between parents and chicks is often overlooked. Authors are usually trying to show that vertical transmission is taking place and that chicks are only coming into contact with their parents (Lee and Clayton 1995). In addition, measurements such as chick weight and feather development are usually taken into account. However the differences in louse dispersal between precocial chicks, which leave the nest shortly after hatching, and altricial chicks, which are born naked and rely on their parents for food and warmth, have not been compared. Each type of development has a different level of parental interaction. The studies in which louse dispersal has been examined have all involved altricial species (Brooke 2010; Darolova *et al.* 2001; Lee and Clayton 1995). Vertical transmission in altricial species is straight forward, *i.e.*, chicks are not able to leave the nest until they can fly, by which time they have come into contact with their parents numerous times, and lice could easily be transferred. Since precocial species, such as those in Anseriformes, leave the nest soon after hatching, they have the potential to come into contact with individuals other than their parents and perhaps even other species of hosts. It is common to see several species of ducks and geese occupying the same ponds. Different species of anseriform lice are usually found on multiple Anseriformes hosts (Price *et al.* 2003). The avian social system has been shown to impact ecological characteristics of chewing lice on territorial versus colonial birds. The hooded crow (*Corvus corone cornix* Linnaeus) is a territorial species while, the rook (*Corvus frugilegus* Linnaeus) is a colonial species; however, each is host to five of the same genera of lice. The prevalence on hooded crows was 53% compared to 92% on rooks (Rózsa *et al.* 1996). In addition, louse populations infesting rooks were more species-rich, and less aggregated than hooded crows.

Therefore colonial species of hosts seem to harbour more parasites that are less isolated then territorial hosts. This is probably due to an increase in direct contact between colonial hosts (Rózsa *et al.* 1996). The levels of host interaction appear to influence louse population structure.

Hosts examined in this study mainly came from rehabilitation centres. This raises concerns that data on lice collected from these birds are biased, and that infestation parameters may be artificially elevated because of the disproportionate number of sick and injured hosts in the sample. Some birds are sick when they are brought in; most of these suffer from dehydration. However, the majority of birds are brought in because of broken wings, usually acquired by be collisions with vehicles, flying into power lines or having been mauled by a cat. There are no studies to examine the effects of having a broken wing on louse populations; however, theoretically a bird should still be able to preen with a broken wing, though survival time following an accident may be limited. Hosts at the rehabilitation centres are kept in individual cages and after hosts are euthanized they are individually bagged; this keeps cross contamination and accidental loss of lice to a minimum. The index of discrepancy for both adult Canada geese and mallards was 0.72; therefore both populations show a high level of aggregation, and there are more individuals with fewer lice than more. One of the major benefits of dealing with rehabilitation centres is that birds are dead at the time of examination. Therefore body washing, the collection method that accounts for greatest efficiency of collection can be used (Clayton and Drown 2001). In addition, working with rehabilitation centres allows you to examine threatened species for which permits to collect in the wild would not be issued. If birds have to be kept alive, techniques such as mist netting and walk-in traps

combined with either visual inspection or fumigation would have to be used to assess louse populations. These techniques are useful for qualitative studies, but they make quantitative comparisons between studies difficult.

From the literature, many of the experimental examples as well as observational data about louse ecology come from lice infesting Columbiformes (pigeons and doves). Columbiformes have become the model hosts for chewing louse studies because they are found on every continent with the exception of Antarctica, and they are small and easy to raise in captivity. Important aspects of louse biology, such as wing lice feeding on the downy portion of the body feathers (Nelson and Murray 1971), chewing lice reducing feather mass (Booth *et al.* 1993), efficiency of louse attachment during flight (Clayton *et al.* 2003) and louse/host size correlations (Bush and Clayton 2006) all come from lice infesting Columbiformes. However, columbiform lice make up only a small fraction of the chewing lice known. The work being done with columbiform lice is very important and ground breaking in the louse world; however, there is a risk of conclusions being over generalized. Repeated studies on unrelated hosts infested with different louse species need to be done in order to evaluate the universality of these observations.

In this thesis, I have provided a baseline of information on anseriform lice and presented the first quantitative information about lice on Canada geese. Hopefully it will inspire others to work with this group of lice and conduct comparative studies so more is known about the ecology, biology and infestation parameters of these fascinating parasites.

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