



The ectoparasites of hybrid ducks in New Zealand (Mallard x Grey Duck)

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ABSTRACT

We studied the population genetics of one population sample of hybrid Mallard x Grey Ducks and their lice in New Zealand. We aimed to document the relationship between ectoparasite load and host phenotype, and test for an association between the mtDNA diversity of the lice and their hosts, which is predicted based on maternal care. We found three feather lice species previously described for these hosts: *Anaticola crassicornis* (wing louse), *Anatoecus dentatus* (head louse), and *Trinoton querquedulae* (body louse). No new or rare lice species were uncovered. Most ducks in our sample were more Mallard-like than Grey Duck-like hybrids for the five colour and plumage traits examined. We confirm that based solely on phenotypic characters it is difficult to distinguish between Mallards, hybrids and Grey Ducks. We detected no association between the number of lice and host phenotype for two of the three louse species (while controlling for bird size). However, the Grey Duck-like hybrids had fewer head lice (*A. dentatus*) than their Mallard-like counterparts. Only three of the 40 hosts had mtDNA haplotypes that characterise Grey Ducks. We present the first genetic data of *Anaticola crassicornis*, *Anatoecus dentatus* and *Trinoton querquedulae* from New Zealand waterfowl. We found that the lice mtDNA had greater sequence diversity than the homologous gene for the ducks. A mitochondrial phylogeny for *A. crassicornis* collected from hosts worldwide has been previously published, and we added our novel data to infer evolutionary relationships among worldwide populations of this louse. None of the three lice species showed a close association of parasite and host mtDNA lineage despite lack of paternal care in these duck species.

1. Introduction

Hybridisation between host species has the potential to bring into contact parasites that have diverged in isolation (Detwiler and Criscione, 2010). Different populations of a given parasite species are engaged in slightly different coevolutionary associations with their local hosts (Thompson, 2005). The outcome of secondary contact for the parasites is expected to be as complex as their host interactions; competition, selection, extinction, interbreeding and merging are all possible. And at the same time, the interaction between parasites and new hybrid host genotypes will provide a selective force that might determine the final outcome (Baird et al., 2012). Host specificity is determined by opportunities for host switching or colonization, availability of suitable hosts, and how host switching affects parasite fitness (Poulin, 2007). Although the host range of a parasite is constrained by its history, it is known to vary in accordance to the presence and relative abundances of local host species (Krasnov et al., 2004).

Lice (Insecta: Phthiraptera) are permanent parasites of their hosts (i.e. they spend their whole life cycle on one host) and usually exhibit

high host specificity (Clayton et al., 2004). In birds, feather lice predominantly show vertical transmission from parents to offspring, during brooding and feeding of chicks (Clayton et al., 2016). However, the chewing lice parasitising ducks, geese and swans (Aves: Anseriformes) around the world are among the least specific of all avian lice (Escalante et al., 2016). Whether these parasites are generalists because of the recent radiation of their hosts, because of their hosts' behaviour and ecology or because of the biology of the lice (i.e., increased dispersal capabilities) is still unknown. The diversification of modern ducks is estimated to have occurred by rapid radiation sometime during the Miocene (10–5 Myr ago; Sun et al., 2017), which would probably provide enough time for their lice to diverge (Clayton et al., 2016). An alternative explanation for the broad host range exploited by these lice invokes their host ecology, i.e. many waterfowl species migrate to regions where they form mixed-species flocks allowing parasite transmission, while other species co-occur in bodies of water providing additional opportunities for host transfer (Escalante et al., 2016). In addition, hybridisation between waterfowl species is relatively common (Tubaro and Lijmaer, 2002) providing further opportunities for lice transfer between host species.

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Some of the best documented examples of hybridisation in ducks are between the sexually dimorphic Mallard (*Anas platyrhynchos*) and several non-dimorphic related species (Rhymer et al., 1994). Cases include the extensive hybridisation between Mallards and Mexican Ducks (*A. platyrhynchos diazi*) that have caused the two species to be declared conspecific (AOU, 1983). The Hawaiian Duck (*A. wyvilliana*) is currently classified as Endangered by the IUCN Red List (BirdLife International, 2017) mainly due to cross-breeding with introduced Mallards. American Black Duck (*A. rubripes*) numbers have been greatly reduced due to hybridisation with Mallards (Kirby et al., 2004). In New Zealand and Lord Howe Island, hybridisation of the native Grey Duck (*A. superciliosa*) with Mallards has greatly reduced the population size of pure Grey Ducks (Williams, 2017) to the point where the species is on the brink of local extinction (Tracey et al., 2008; Guay et al., 2015). In New Zealand, the Mallard phenotype is also declining as the number of ducks with hybrid phenotype increases (Gillespie, 1985). Currently, wild Mallards and Mallard x Grey Duck hybrids are the most common and widespread species, with approximately 500,000 individuals being hunted each year (McDougall and Amundson, 2017). Thus, implementing hunting regulations, censusing and conducting field work is problematical because of the difficulty distinguishing between pure-Mallard, hybrids and pure-Grey Ducks (Muller, 2008; Williams, 2017). The hybridisation of Mallard and Grey Ducks will have provided an opportunity for their parasites to come into contact and may have resulted in a similar mixing of genotypes in lice as seen in their hosts and/or the opportunity for competitive exclusion of lineages. However, in both these species female ducks provide maternal care (Johnson et al., 1999), while the males desert the female and offspring (Kear, 1970), therefore, transmission of lice might be expected to be primarily from mother to offspring as happens with mitochondrial DNA (mtDNA). Therefore, we hypothesize that although the New Zealand population of Grey and Mallard Ducks are dominated by hosts with intermediate phenotype, their lice populations might reveal less mixing.

In our study we focus on three species of lice that have been recorded on Grey Ducks and Mallards, each from a different genus: *Anaticola crassicornis*, *Anatoecus dentatus*, and *Trinoton querquedulae* (Pilgrim and Palma, 1982; Aksin, 2011; Grossi et al., 2014; Escalante et al., 2016). A fourth louse genus has also been recorded from New Zealand Mallards, *Holomenopon* (Pilgrim and Palma, 1982) but this was not found in our survey, so is not discussed further. These lice are all members of the insect order Phthiraptera. The three species differ in their host microhabitat (wing, head, body), dispersal abilities (DiBlasi et al., 2018), and possess widespread geographic distributions providing excellent examples of ‘ecological replicates’ (Clayton et al., 2016). *Anaticola crassicornis* is a feather wing louse (Johnson et al., 2012). DNA sequence variation suggests that this species could be a complex of cryptic, geographically isolated species (Escalante et al., 2016). *Anaticola crassicornis* collected from Grey Ducks in Australia were genetically similar to lice collected from other Australian ducks but differentiated from both the lineage living on Mallards in Japan and Sweden and the lineage on USA Mallards (Escalante et al., 2016). However, the molecular phylogeny of *A. crassicornis* collected from waterfowl hosts worldwide did not include lice from New Zealand. The head louse, *Anatoecus dentatus*, lives and feeds on the head and neck of its host (Clayton et al., 2016). The species has recently been synonymised with *A. icterodes*. All *A. dentatus* collected from a number of different waterfowl species in Canada were genetically identical, suggesting little host-parasite specialisation (Grossi et al., 2014). The body louse, *Trinoton querquedulae*, is also a generalist and found on Mallard, Grey and many other duck species; however little is known of its genetic diversity worldwide (Singh, 1970; Pilgrim and Palma, 1982).

Most parasite surveys sample fewer than 10 host individuals therefore the detection of new or rare parasite species is unlikely (Clayton et al., 2016). By sampling a large number of hosts, we aimed to avoid this bias.

The objectives of this study were to examine a population sample of hybrid Mallard x Grey Ducks from New Zealand in order to: (1) document the relationship between ectoparasite load and phenotype. Although hybrids are often predicted to have increased numbers of lice compared to parental phenotypes (Fritz et al., 1994), the abundance of lice and mixing of genotypes might not create a stable association and therefore we aimed to provide data as a snapshot that can be used to study changes over time (Wolinska et al., 2008); and (2) test for an association between the mtDNA diversity of the lice and their hosts, which is predicted based on lack of paternal care. Maternal care would result in ectoparasite transmission predominantly by mother-offspring contact with lower rates of horizontal transmission. Although unique species of lice have not been described from the New Zealand Grey Duck, distinct mtDNA lineages might have evolved within the New Zealand region, as seen for Australian *Anaticola crassicornis* (Escalante et al., 2016). If lice lineages had differentiated prior to introduction of Northern Hemisphere ducks (and their parasites) we might detect maternal transmission of Grey Duck mtDNA and maternal transmission of distinct lice mtDNA. Thus, we present the first genetic data for *A. crassicornis*, *A. dentatus* and *T. querquedulae* from New Zealand waterfowl. We also compare *A. crassicornis* mtDNA diversity from New Zealand with that found worldwide.

2. Material and methods

2.1. Duck and lice samples

Duck specimens from Opiki, Manawatu, New Zealand (40.444505 °S, 175.379740 °E) were provided by a local hunter. Forty Mallard-Grey Duck hybrids were shot on 1 May 2015. The carcasses were put in individual plastic Zip Lock® bags and sealed to avoid lice straggling and frozen until use.

To remove and collect as many lice as possible from each duck, we used the Lipovsky (1951) body washing method. Briefly, a frozen bird carcass is placed inside a bucket with 15 L of fresh, warm water with 20 ml of dishwashing liquid. The detergent acts as a wetting agent. Each bird is washed three times, ruffled under water so that the wetting agent penetrates the plumage and loosens the lice. Each bucket of soapy water was then put through a series of sieves (8 mm, 600 µm, 500 µm, and 212 µm). Subsequently, the lice from the three washes of the same individual duck were collected together in a 50 ml vial and stored in 99% ethanol. Thirty-one ducks were washed, and their lice collected using this method (Suppl. Table S1). The body washing method proved an extremely accurate predictor of total abundance for wing and body lice in an evaluation of five different methods to quantify chewing lice in birds (Clayton and Drown, 2001).

Lice were identified using published keys (Price et al., 2003) by visual inspection of their morphology under a microscope (Leica S6D). The total lice number and the number of individuals of each species were recorded for each of the 31 duck specimens washed.

Infestation parameters were estimated following Rózsa et al. (2000). Prevalence was defined as the proportion of birds with lice, with 95% confidence intervals estimated using Sterne's exact method (Reiczigel, 2003). Mean intensity was defined as the mean number of lice per host in the total sample of infested hosts. The mean abundance of lice was calculated by multiplying prevalence and mean intensity. To set 95% confidence intervals of mean intensity and mean abundance we used a bootstrap procedure with 20000 replications (Rózsa et al., 2000). We used the software Quantitative Parasitology v.3 (Reiczigel and Rózsa, 2005) to estimate these parameters.

2.2. Host morphological measurements

Six morphological measurements (± 0.1 mm, unless otherwise specified) were taken from each thawed bird ($n = 37$): wing chord length (WC, carpal joint to longest primary feather unflattened), bill

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