University of Auckland

Doctoral Thesis

Breeding Ecology and Productivity of Mallards and Mallard-grey Duck Hybrids in New Zealand

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A thesis submitted in fulfilment of the requirements
for the Degree of Doctorate of Philosophy
in the School of Biological Sciences,
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ABSTRACT

Introduced primarily for sport hunting, mallards (*Anas platyrhynchos*) became widely established in New Zealand (NZ) following the release of 25,000 individuals during 1940–1960. Hybridisation and introgression between mallards and the native grey duck (*A. superciliosa*) has been extensive, and today, mallards and mallard-grey duck hybrids (hereafter mallards) are the predominant game bird in NZ. Perceived declines in mallard abundance in some regions have prompted NZ Fish and Game Council to initiate research to better understand causes of population change. During 2014–2015, I collected data from 304 radiomarked female mallards, 491 nests, and 190 broods from 2 study sites in NZ (Southland and Waikato) to answer essential questions about breeding season vital rates and habitat requirements, and to determine factors important in affecting population growth rates. Breeding incidence averaged 0.91 (SE = 0.03), renesting propensity following failure of nests or broods was 0.50 (SE = 0.03), egg hatchability of successful nests was 0.93 (SE = 0.01), partial depredation occurred in 0.16 of nests (SE = 0.16), and daily nest survival was 0.9789 (SE = 0.17). Cumulative nest survival ranged from 0.22 for nests along drainage ditches in Waikato to 0.61 when they were located along roadsides in Southland. Mean daily brood survival was 0.9816 (SE = 0.003) and cumulative survival ranged from 0.16 for second-year (SY) females in Waikato to 0.30 for after-second year females (ASY) in Southland. Female breeding season survival averaged 0.79 (SE = 0.06) and post-fledging survival was 0.51 (SE = 0.008). Older females had higher breeding effort and reproductive success; they nested earlier, laid larger clutches, hatched more eggs per nest, and fledged more ducklings. Predicted fecundity suggested ASY and SY females recruited 0.25 and 0.36 female offspring into the breeding population, respectively. Model-predicted population growth rates suggested an annual decrease of 0.16 per year. Sensitivity analyses indicated that duckling survival, particularly of older females, was the most influential factor regulating growth of mallard populations, followed by breeding survival of ASY females and duckling survival of SY females. Management initiatives that focus on improving survival of ducklings and females will have the greatest potential to increase duck production.

DEDICATION

An influential professor once told me that wildlife management is people management. Some of the simplest ways that people can manage waterfowl populations is to abstain from harvesting females, purchase hunting licenses to aid in conservation initiatives, and abide by the regulations. As such, I would like to dedicate this thesis to all the keen duck hunters of New Zealand who ‘go for green’ and remain within the limit.

ACKNOWLEDGEMENTS

In 2005, a young, enthusiastic person who had recently discovered her love for birds, ducks, and scientific research said “I want to research mallards and obtain a PhD!” At the time, I had a 2-year technical degree with little work or academic experience, so the ensuing 8-year journey to become eligible to apply for a PhD position saw me: attend 2 universities, obtain a BSc and MSc degree, work 9 field research positions and numerous part-time jobs, volunteer for several organisations, and live in 3 states and 4 provinces. Along the way I met amazing people and gained some wonderful friends, including my best-friend and husband, Simon. Then, at the end of that journey, the stars aligned and I found myself en route to New Zealand to research mallard duck productivity for my PhD project.

It is without a doubt that I owe thanks to many people and organisations. First and foremost, I would like to thank my co-supervisor Courtney Amundson (U.S. Geological Survey) and advisor Todd Arnold (University of Minnesota); your guidance, advice, feedback, and continued patience was always appreciated. Courtney – you first inspired me in 2005 to begin a career in academia and wildlife research. During the past 12 years, in one way or another, you’ve supported me through this journey. Whether it was giving advice on R codes, double checking my results, providing feedback on manuscripts, recommending me for graduate school or future employment, flying 2000 km on a days’ notice to stand at my impromptu wedding, or simply just being a friend. Thank you so much for sharing this journey with me. Todd – I’m sure I drove you crazy with questions, but you always responded, never failing to provide much needed advice and feedback. Your visit to NZ was perfectly timed and I only wish that you could have stayed longer. I’ve learned so much about data analysis and interpretation during this project and you have been integral to that. Thank you for always sharing your knowledge and R codes.

I would also like to thank my academic supervisor, Rochelle Constantine (University of Auckland) – you took me under your wing after I was abandoned, even though mallards are a tad different than the cetaceans you study. You provided the perfect amount of support to help me finish my dissertation. The logistics of the University were overwhelming, especially as I was based off-campus. But you always knew how to push the right buttons to get the paperwork done and always provided me with immediate feedback and support whenever it was required.

This project was made possible by various Fish and Game Councils and numerous staff members. Firstly, this project would never have existed without the demand from local duck hunters, which promoted Fish and Game to research mallards and offer a fully-funded PhD position; I thank New Zealand Fish and Game Council and Southland Fish and Game Council for the financial support. I also thank Auckland/Waikato and Eastern Fish and Game Councils for their logistical support. I especially thank David Klee, not only for this opportunity and for selecting me as the PhD student to spear-head the 'mallard telemetry project' but also for your patience and hard-work (especially throughout the first year), support, excessive amount of help with field logistics, and of course the various fishing trips and necessary lessons on kiwi-isms and ways. To the other employees of the Auckland/Waikato Fish and Game Region, thank you for providing me with an office space and making me feel welcomed: Adam – for your help with the truck-set up and all the equipment malfunctions; Robyn – for all the administrative help and organisation; John – to you and Oscar for nest-searching and cannon-net training; Ben – for allowing David to work so hard on this project and for always remembering to put some honey aside for me. To Zane and the staff at Southland Fish and Game, thank you for helping with field work and logistics, for supporting the crew and taking care of them, and for working during the holidays once the crew had departed. To Andy and the staff at Eastern Fish and Game, thank you for providing me with an office space to write and finish my thesis, and special thanks to Matt McDougall for all of his help with the many aspects of this project.

The support and enthusiasm I received from local landowners and the hunting community (most notably the Te Awamutu Fish and Game Club) frequently reminded me of why I was doing this research and inspired me to continue to work hard and strive for the best possible results. I sincerely hope that the results I present here will provide the information needed to ensure that there will continue to be 'a duck in your sight' for many years to come. I especially thank: Rex Murray for the beef that fed us during the 2nd year of the project and for the opportunity to shoot my first green-head – I do apologize for making your dog work so hard; Pete and Jill Shaw for your hospitality and for watching our broods when we weren't there; Grant Annan for all the help nest-searching, for taking the crew hunting and fishing, and for your offerings of wild game and produce; Judy Fentress for teaching the crew how to properly candle eggs and always taking the time to show us your plethora of birds; and, Alby Cooper for allowing us to rent such a wonderful house for our field season. Bill Jarvis (Southland Fish and Game), Dave Stack, Dave Shelley, Mitch O'Brien, as well as several

other dedicated hunters and their respective dogs – thank you for all your hard work and time. As nearly all of our field research was conducted on private land, I would like to thank the numerous landowners in the Waikato and Southland study areas for permitting us to access your land to track the ducks.

I acknowledge Ducks Unlimited Canada, notably Bob Emery and Jim Devries, for loaning me a large portion of the equipment required for this project and for providing numerous recommendations and feedback on field procedures. I thank Dr. Karen Machin (University of Saskatchewan) and Dr. Martin Wild (University of Auckland) for training me to perform abdominal-implant surgery. Aside from the scholarship provided by New Zealand Fish and Game Council, I also received financial support through a Postgraduate Scholarship from the Natural Science and Engineering Research Council of Canada.

I would also like to thank Jillian Cosgrove and Simon Allard for their contributions toward the digitisation of the study areas, which greatly aided in the analysis of Chapter 3. In regards to Chapter 6; I would like to thank Joshua Stafford (Associate editor of Wildlife Society Bulletin), Erin Roche (U.S. Geological Survey)[1] and two anonymous reviewers for their constructive reviews of the manuscript.

This project involved a copious amount of data collection that would have been impossible without the hard-work and dedication of many field technicians and volunteers. I would like to express my gratitude and acknowledge the hard work of: Julie Unfried, Taylor Davis, Jillian Cosgrove, John Walker Price, Evan Shields, Nathan Cross, Nicole Benson, Riley Bartel, and Taylor Parker, all of whom travelled from America or Canada to help research mallards during winter and spring in New Zealand. I hope you all took away fond memories of your time here. Jules – I have no idea how I would have survived that first year without you, thank you for keeping my head above water, for your friendship, and for your dedication to the project – I will never forget that. I also thank Erin Garrick, Simon Allard, Jane Reeves, Katie Gibbs, Shae Vickers, and Jess Earnshaw, for their time and assistance with this project. I wish you all the best in your future endeavours.

I have saved the bulk of my thanks for last and would like to sincerely thank my husband, parents, brother, and friends for their support during this project – I apologize for missing important birthdays, wedding, births, and for moving to the other side of the globe.

[1] Current affiliation: Idaho Fish and Game

But thank you for always inviting met to every event even though we both knew I couldn't make it. Thank you especially for the Skype dates when it most mattered. Owen & Isla – I am so sorry I missed the first few years of your life, but I will make this up to you when we finally live in the same country. I hope that you develop a passion for nature and wildlife and I hope mallards (and waterfowl in general) will continue to be a sustainable resource wherever you, your children, and grand-children end up in this world. To my dog Squid, once again, I dragged you to a new home and often neglected to give you the walks and attention you so deserved while I stressed over field work or writing, yet you were always happy to sleep under my desk, keep my feet warm, and to provide doggie-kisses when I most needed them. Finally, my deepest thanks goes to my husband Simon. You entered my life just as I embarked on my MSc. journey and have only seen me wear the hat of a graduate student, overly stressed researcher, or a slightly crazed writing-machine. But you have been a trooper, despite my stressful outbursts, distractions, and necessary overseas work trips. You have selflessly taken care of me and Squid these past 7 years. Thank you for following me around the world, for supporting my dreams, encouraging me when things were hard, for being my rock, for your patience, your guidance, and your love – it's your turn to lead the way for a while and my turn to make your dreams come true.

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Appendix 1

GLOSSARY

ASY – After-second year. One of two designated age classes. After-second year females are ≥1.5 years of age and, at the time of marking, were entering (or had entered) their second breeding season or more.

Beat-outs – A technique used to locate nests (by beating vegetation with sticks) or flush hidden broods from tall or emergent vegetation or in other concealed areas (i.e., culverts, bank edges).

Candled – A technique used to measure the incubation stage of an egg based on the comparative size of the air sac. Typically, a small tube (radiation tube or toilet paper roll) is used to view the egg against a lit background (i.e., sun).

Fish and Game – New Zealand Fish and Game Council, a non-government organisation that is mandated with the protection and conservation of game birds and freshwater sport fish. Fish and Game initiated the study and financially supported the research. The organisation is divided into 12 regional councils, of which Auckland/Waikato, Southland, and Eastern Regions are frequently referred to throughout the thesis.

Fledged – Stage at which ducklings (55–83 days post-hatch) are capable of flight, but not necessarily independent of the female.

IDATE – Nest initiation date (day when the first egg was laid in a given nest). This term is widely used when presenting statistical results.

Implant – Abdominally implanted radiotransmitter. One of two techniques used to mark females in this study.

MCMC – Markov chain Monte Carlo. An algorithm which repeatedly draws a set of random samples from a probability distribution.

Pest-fish – Invasive or introduced fish which compete with native species for invertebrates and greatly reduce populations of native fish, invertebrates, and aquatic plants. In NZ, koi carp (*Cyprinus carpio*), gambusia/mosquitofish (*Gambusia affinis*), goldfish (*Carassius auratus*), rudd (*Scardinius erythrophtalmus*) and catfish (*Ameiurus nebulosus*) are the biggest conservation threats to aquatic systems.

Pipping – In reference to eggs or the age of eggs. Pipping is indicated when small, star-like, cracks appear on the egg shell, caused by the duckling trying to break away the egg cap once it is ready to hatch (i.e., fully incubated and developed). For mallards in this study, pipping typically occurred around 24–27 days post incubation.

P&S – Prong-and-suture back-mounted radiotransmitter. One of two techniques used to mark females in this study.

SOU – Southland study site. One of two study areas where female mallards were monitored. Represents the Southland Plains Unit of the Southland Region.

SY – Second-year. One of two designated age classes. Second year females are < 1.5 years of age and, at the time of marking, were entering (or had entered) their first breeding season.

Unmarked (nest or female) – A term used to describe females that were not equipped with a radiotransmitter or in reference to a nest attended by such a female.

VHF – Very high frequency. The type of radio-frequency of the transmitters used in this study.

WAI – Waikato study site. One of two study areas were female mallards were monitored. Represents the Waipa and Waikato District of the Waikato Region.

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Chapter 3: Effects of Surgically Implanted Transmitters on Reproduction and Survival in Mallards

Nature of contribution by PhD candidate	Original research idea; study design; collection of data; compilation and organization of data; statistical data analyses; preparation of the manuscript, tables, and figures.
Extent of contribution by PhD candidate (%)	90%

CO-AUTHORS

Name	Nature of Contribution
Todd Arnold	Advice and guidance on study design; assistance with stastical analyses; editing and proofing the manuscript; providing feedback which improved the overall quality of the final paper.
Courtney Amundson	Advice and guidance on study design; assistance with stastical analyses; editing and proofing the manuscript; providing feedback which improved the overall quality of the final paper.
David Klee	Advice and guidance on study design; assistance with data collection; editing and proofing the manuscirpt.

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Courtney Amundson	Advice and guidance on study design; assistance with stastical analysis; editing and proofing the manuscirpt; providing feedback which improved the overall quality of the final paper.
David Klee	Advice and guidance in the study design; assistance with data collection; editing and proofing the manuscirpt.

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Chapter 5: Factors Affecting the Survival and Detection of Mallard Broods and Ducklings in New Zealand

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Courtney Amundson	Advice and guidance in the study design; assistance with stastical analysis and code modification; editing and proofing the manuscirpt; providing feedback which improved the overall quality of the final paper.
David Klee	Advice and guidance in the study design; assistance with data collection; editing and proofing the manuscirpt.

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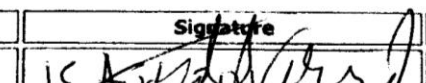
Todd Arnold		15 Aug 2017
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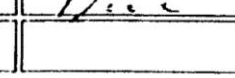
David Klee		11/8/17

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Chapter 6: Productivity of Mallards in New Zealand

Nature of contribution by PhD candidate	Original research idea; study design; collection of data; compilation and organization of data; statistical data analyses; preparation of the manuscript, tables, and figures.
Extent of contribution by PhD candidate (%)	80%

CO-AUTHORS

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Todd Arnold	Advice and guidance in the study design; recommendations on model parameters; editing and proofing the manuscirpt; providing feedback which improved the overall quality of the final paper.
David Klee	Advice and guidance in the study design; assistance with data collection; editing and proofing the manusclrpt.

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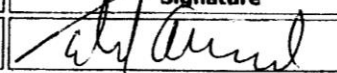
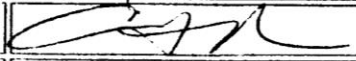
Todd Arnold		15 Aug 2017
Courtney Amundson		14 Aug 2017
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Chapter 1

1. General Introduction

1.1 Mallard Biology

The mallard (*Anas platyrhynchos*) is the most abundant, well-studied, and widely recognised duck in the world (Baldassarre 2014). Mallards are ubiquitous throughout their native range in North America, Eurasia, and Greenland, and have been introduced to Africa, Australia, New Zealand (NZ), and the Hawaiian Islands where there are well-established breeding populations (Baldassarre 2014, Cumming et al. 2016). Mallards are highly adaptable and are habitat generalists; in their native range, they use agricultural fields more often than any other duck, consume a wide range of food (although aquatic invertebrates remain the main food source), tolerate urban environments, use all types of freshwater and brackish habitats, and nest in an innumerable number of habitat types (Bellrose and Kortright 1976, Baldassarre 2014). Similar patterns of adaptability have been observed in NZ (Williams 1981).

Mallards are notorious for mating with closely-related duck species (Baldassarre 2014). The grey duck (*A. superciliosa*), also referred to as the Pacific black duck, is a non-dimorphic dabbling duck that is native to NZ, Australia, eastern Indonesia, New Guinea, Micronesia, and Polynesia (Williams 1981). It is closely related to the mallard, but is smaller, less fecund, and possibly has lower survival rates (Williams and Basse 2006). New Zealand grey ducks (*A. superciliosa superciliosa*) are one of three known subspecies in the South Pacific, and were once widespread throughout NZ, inhabiting mountainous areas, estuaries, inlets, and all types of freshwater habitats (Johnsgard 1978). Hybridisation and displacement by mallards, habitat depletion, and over-exploitation are responsible for the demise of the grey duck (Williams and Basse 2006). Today, genetically pure grey ducks are rare in NZ and they are classified as Nationally Critical (Williams 2013). Instead, a hybrid form of mallard × grey duck (*A. platyrhynchos* × *superciliosa*) dominates the population (Dyer and Williams 2010).

Male mallards characteristically have a bright green head and neck, white neck-collar, chestnut-coloured breast, yellow bill, and a grey-coloured body, whereas females are a drab brown colour (Baldassarre 2014). Both sexes have a purple-blue speculum that has anterior and posterior white borders (Baldassarre 2014). In NZ, plumage characteristics have become less pronounced due to introgression with the grey duck and males may lack a green head and/or neck, have a faded-brown breast, a grey-coloured bill, and both sexes may have reduced white bordering of the speculum (Gillespie 1985). Males are larger and heavier than females; in NZ, mean body mass during summer banding is 1160 g and 1025 g, respectively.

Mallards are a preferred game bird; they have become widely domesticated for food and game farming and are the most heavily hunted duck in North America (Baldassarre 2014) and NZ (Williams 1981). The average life-span of a mallard is approximately 3 years, but birds may live up to 20 years (Schekkerman and Slaterus 2008). In NZ, the maximum age recorded for a banded/recaptured bird was 16 years (M. McDougall, Eastern Fish and Game Council, pers. comm.). Within their native range, mallards are migratory; they typically breed in northern latitudes and over-winter in warmer, southern climates. But in NZ, mallards tend to be sedentary (Balham and Miers 1959), and recent recovery data suggests that approximately 85% of band returns occur within 50 km from banding sites (Balham and Miers 1959, McDougall 2012). Further, there is little genetic exchange between the North and South Island populations (Guay et al. 2015b).

Mallards are seasonally monogamous and females will breed as yearlings (e.g, will nest during the first breeding season following hatch; Sowls 1955). Mallards have a tendency to nest on the ground in tall dense grass, but will select a wide range of nesting habitats in both upland and marsh areas (Baldassarre 2014). On average, mallards in North America will lay 9 eggs per clutch (range = 8.6–9.8; Ackerman et al. 2003, Coluccy et al. 2008, Howerter et al. 2014) and will incubate eggs for approximately 26 days (Howerter et al. 2014). Females persistently renest following nest failure, and in North America, may nest up to 6 times in a single breeding season (Arnold et al. 2010). Males assist in selecting the nest-site, but they do not provide any nest defence, nor do they participate in incubation or brood-rearing (McKinney 1985). Males break the pair-bond and leave the female before ducklings hatch, usually following the onset of incubation, but females will remain with the ducklings for approximately 50 days post-hatch (Baldassarre 2014). Ducklings are precocial and typically leave the nest within 12 hours following hatch but may remain in the nest for up to 30 hours and survive $\geq$ 2 days without food (Kear 1965, Bjärvall 1967). Broods are dependent on

wetlands with abundant invertebrate populations for food and emergent vegetation for cover (Baldassarre 2014).

1.2 Introduction and Establishment to New Zealand

The introduction of mallards to NZ was thoroughly researched by Dyer and Williams (2010), who reported that:

> "Initial introduction began in the 1860's, during which time a handful of individual ducks were translocated from London, the Melbourne Zoo, and the Acclimatisation Society of Victoria and initially placed within a few Botanical Gardens located throughout the country. Following this, local Acclimatisation Societies and other individuals began distributing mallards throughout NZ via game farming and release programs, whereby ducks were raised from eggs laid by breeding stock and released into the wild. By 1910, a minimum of 115 birds had been imported to NZ but despite breeding and release programs, mallards had failed to disperse widely and only small, urban populations had successfully established. An additional 400 or more birds were imported over the next 2 decades and by 1920 wild populations consisting of imported and farm-reared birds had become large enough to sustain harvest in some regions. However, concerns over hybridisation between mallards and grey ducks and the tame quality of the released mallards temporarily diminished most interest in continuous release programs. But, the widespread decline of the native grey duck, which became apparent in the early 1930's, motivated Acclimatisation Societies to vigorously increase efforts in an attempt to create a sustainable breeding population capable of supporting sport-hunting and harvest. Resultantly, during 1940–1960 over 25,000 individual mallards were reared and released throughout the country."

While importations, game-farming, and releasing of mallards into NZ were on-going, intensive land-use changes were also occurring. The modification of lowlands and forests had begun with human (i.e., Polynesian) settlement, but European settlement (circa 1840) led to dramatic modifications, including the removal of indigenous grasslands and forests, the drainage of swamps, wetlands, and alluvial flatlands, and increased agricultural and pastoral expansion (Molloy 1980). Agricultural productivity intensified from 1920 onward and with the application of new soil science, fertilisers, and improvements to plant and animal breeding, the number of stocking units increased around 150%, meat and dairy productivity doubled, and wool production tripled (Molloy 1980, MacLeod and Moller 2006). By 1970,

nearly 90% of wetlands had been converted to farmland (Ausseil et al. 2011) and recently, at least 60% of NZ land cover had been converted to agricultural or pastoral land (Molloy 1980, MacLeod and Moller 2006).

Concurrently, grey ducks were hunted extensively (Balham 1952). Despite early reports of declining numbers, high hunting mortality was recorded until the mid-1970's (Balham 1952, Barker et al. 1991), at which time harvest of mallards began to exceed that of grey ducks (McDougall 2012). Over-hunting and depletion of habitats significantly impacted grey duck populations. Although their historic habitats had been removed, grey ducks reportedly used disturbed areas and were often seen in urban parks and agricultural fields (Williams and Basse 2006). But their nesting requirements excluded the use of grassy strips of vegetation that survived along drainage ditches or other modified habitats (e.g., roadsides, hedgerows), and they possibly struggled to adapt to the altered environments, which were easily exploited by opportunist mallards (Williams 1981, Williams and Basse 2006). During 1963–1970 in the Waikato region, grey duck pairs declined by 70% while mallard pairs increased 145% (Williams and Basse 2006). Similar degrees of displacement were likely occurring simultaneously throughout the country, and by 1980, it was estimated that approximately 5,000,000 mallards inhabited NZ (Williams 1981).

Hybridisation between mallard and grey ducks was reported as early as 1922 (Thomson 1922) but it wasn't until 1985 that researchers expressed concerns that ongoing hybridisation presented a conservation issue to the continued persistence of grey ducks (Gillespie 1985). Yet, introgression has not been unidirectional, and grey duck characteristics are expressed in both the genotype and phenotype of hybrids (Rhymer et al. 1994, Guay et al. 2015b). Often, first generation hybrids are easy to distinguish as they present traits of both parents, but after a few generations of back-crossing, hybrids (especially females) are nearly indistinguishable from parent species (Guay et al. 2014). In instances of extreme introgression, hybrid swarms, whereby the individual gene pool of both parents no longer exist, may become commonplace and researchers suspect this may have occurred already in NZ (Rhymer et al. 1994, Guay et al. 2014, Guay et al. 2015b). Today, it is difficult to discriminate between variably-plumaged mallards, hybrids, and grey ducks without the aid of genetic analyses. As such, the species are combined for management and monitoring purposes. Further, because 'grey-like ducks' are genetically introgressed with mallards, the Department of Conservation has recently recognised hybrids as a unique taxonomic entity, which is classified as non-threatened (Robertson et al. 2017).

Here, I determined all females as phenotypically mallard before marking. Preliminary genetic work on a subset of these females suggested that 23% and 32% of birds in Southland (N = 52) and Waikato (N = 50), respectively, were genetically hybrid (i.e., having ≥ 5% genetic contribution from both mallard and NZ grey duck; P. Lavretsky, University of Texas El Paso, unpublished data). In addition, these birds displayed unique genetic assignments by site, with 62% of females from Southland and 32% of samples from Waikato, having ≥ 95% genetic assignment to the South and North Island mallard cluster, respectively (P. Lavretsky, University of Texas El Paso, unpublished data). These molecular results suggest that females likely have a relatively high degree of island-based philopatry and rarely move or breed between the 2 main islands. Genetically pure grey ducks were not detected within the subsample. Thus, I do recognize that a portion of the birds studied here were mallard × grey duck hybrids but feel certain that grey ducks were excluded from marking. For clarity and simplification, I refer to the birds studied here as mallards, however these data, results, and inferences apply to both mallards and mallard × grey duck hybrids.

1.4 Project Rationale

New Zealand is heavily burdened with introduced and invasive species, especially meso-carnivores, which threatened much of the endemic wildlife and has already resulted in high rates of extinction (Atkinson 1989). Understandably, most government-led conservation initiatives have focused on preserving the remaining indigenous forested habitats and associated endemic avifauna, yet nearly 60% of the land coverage in NZ is comprised of low-lying agroecosystems (MacLeod et al. 2008). While national agencies and regional councils direct their focus on the protection of areas outside of low-lying agriculturally dominated landscapes, individual landowners implement their own conservation efforts as they deem appropriate (MacLeod et al. 2008). These efforts are further supported and reinforced by New Zealand Fish and Game Council (hereafter Fish and Game), a non-government organization that is mandated, by the Wildlife Act 1953 and Conservation Act 1987, to promote the sustainable management of natural and physical resources in NZ and to protect and manage game species (e.g., game birds and freshwater sport fish).

Government funding is not available to Fish and Game, instead revenue is solely obtained from game bird and angling license sales. Mallards are the primary driver of game bird license sales (D. Klee, Auckland/Waikato Fish and Game, pers. comm.). In the past 3 years, game bird license sales generated nearly 25% of the yearly revenue (~$2.6 million; R.

Sowman, NZ Fish and Game, pers. comm.) and proceeds are used to maintain, protect, and enhance sport fish and game birds and their associated habitats (i.e., rivers, streams, and wetlands). Although some of this land is owned and managed by various Fish and Game regional councils, much of the focus is on habitat restoration within privately owned farmland. Over the past 3 years, Fish and Game regional councils throughout NZ spent a mean combined annual amount of $1.3 million and $1.7 million on habitat protection and species management, respectively (NZ Fish and Game, unpubl. data). Efforts and initiatives directed by Fish and Game benefit mallards as well as numerous native species that are currently designated as nationally critical, at risk, or recovering. Furthermore, native species that are naturally uncommon or not threatened also use habitats that are protected and restored by Fish and Game. For example, within the study areas, I frequently observed royal spoonbill (*Platalea regia)*, grey teal (*Anas gracilis*), Australasian shoveler (*A. rhynchotis*), Australasian harrier (*Circus approximans)*, black swan (*Cygnus atratus*), white-faced heron (*Egretta novaehollandiae*), pied stilt (*Himantopus himantopus*), pukeko (*Porphyrio melanotus*), paradise shelduck (*Tadorna variegata*), spur-winged plover (*Vanellus miles novaehollandiae*), and eels (*Angulla sp.*). Ultimately, management programs are directed at conserving and protecting mallards and freshwater sport fish, but the benefits of these initiatives are integral to the protection of native and endemic species which also reside in the low-lying agricultural areas of NZ.

Recent analyses on hunting dynamics in NZ concluded that from 1997–2012, hunter effort in the Eastern Fish and Game Region had declined over time (McDougall and Amundson 2017). Over the last 35 years, the annual number of license sales has decreased from 50,000 (Caithness 1982) to an average 38,200 in the past 3 years (R. Sowman, NZFG, pers. comm.). Further, waterfowl populations have appeared to decrease in several regions over the past decade. Decreasing license sales may result from changing societal values, perceived declines in waterfowl populations, increased costs associated with licenses and hunting equipment, or lack of access to private lands and preferred hunting areas (Ringelman 1997, Vrtiska et al. 2013). Reductions in hunter numbers not only limit the ability of waterfowl managers to obtain sufficient knowledge required to effectively manage populations, but also decreases revenue from game bird license sales and associated funds that are available for habitat and wetland conservation (Enck et al. 2000, Anderson et al. 2007, Vrtiska et al. 2013). Thus, in response to perceived reductions in game bird numbers,

Fish and Game initiated a 2 year research project aimed at understanding breeding season vital rates, habitat use and selection, and population growth rates.

1.5 Research Objectives

Previous research on mallards in NZ has evaluated dispersal distance (Balham and Miers 1959, Williams 1981), survival and harvest rates (Balham and Miers 1959, Barker et al. 1991, McDougall and Amundson 2017), and the degree of hybridisation with the grey duck (Rhymer et al. 1994, Guay et al. 2015a), but knowledge about reproductive ecology and population growth rates are lacking. Effective management of wildlife populations requires that managers have a thorough understanding of population growth and the underlying vital rates (e.g., breeding incidence, nest and offspring survival) that affect population growth rates. Given the economic importance of mallards to Fish and Game, and the association between gamebird license sales and habitat and wetland restoration and management, it is essential that waterfowl managers implement sustainable harvest strategies and protect important breeding habitats.

Thus, understanding population demographics and habitat use of mallards in NZ warranted further investigation and led to 4 main research goals:

i) Determine the incidence of non-breeding among adult female mallards.
ii) Assess survival of nests and broods.
iii) Determine habitat selection patterns during specific life-history phases (e.g., nesting and brood-rearing) and determine if choices are adaptive.
iv) Develop and implement a population model and identify influential vital rates that affect population change.

1.6 Thesis Organisation

I have organised this thesis as 4 independent manuscripts intended for publication in peer-reviewed journals. To maintain the independence of individual chapters, there may be some redundancy in the introductions, description of study sites, and methods. However, to reduce this repetition within the methods sections of each chapter, I have provided a detailed description of study sites and field methods in Chapter 2, and use chapter-specific methods sections to discuss methods that are relevant to the statistical analysis or overall understanding of the respective chapter. I have created a single reference list at the end of the thesis to minimise repetition in each chapter.

The overall aim of this study was to quantify breeding-season vital rates and habitat use patterns of female mallards in NZ, and to relate these vital rates to overall productivity and population growth rates. All manuscripts derived from this study (Chapters 3–6) are co-authored by Todd Arnold (University of Minnesota), Courtney Amundson (US Geological Survey) and David Klee (Auckland/Waikato Fish and Game Council). The thesis chapters are arranged as follows:

- Chapter 2 provides detailed information of the study sites and field methods.

- In Chapter 3, I examine the nesting ecology of mallards in NZ and address key hypotheses about adaptive nest-site selection. This chapter will be broken down into two manuscripts intended for publication: i) Nesting Ecology of Female Mallards in NZ, which will focus predominately on the effects of site, year, and female attributes (currently in review in Ibis); and ii) A Spatial Analysis of Factors Affecting Nest Success and Selection of Female Mallards in NZ, which will incorporate results from a co-authored technical report on nest survival in response to multiple spatial scales (target journal: Journal of Wildlife Management). This manuscript is also co-authored by Jillian Cosgrove (Auckland/Waikato Fish and Game Council)[2].

- In Chapter 4, I investigate the survival of broods and ducklings and identify key components that affect duckling survival rates while accounting for imperfect detection of broods and ducklings.

- In Chapter 5, I synthesise results from Chapters 3 and 4 with regional banding data and conduct a sensitivity analysis to investigate factors that affect the population growth rate.

- In Chapter 6, I evaluate how marking and capture techniques affected subsequent survival and reproductive effort. This chapter has been published in *Wildlife Society Bulletin* (DOI: 10.1002/wsb.809), and whilst I have changed the format to remain consistent throughout this thesis, the text is the same as the published article.

- Finally, in Chapter 7, I discuss the overall conclusions of this study.

[2] Current affiliation: Oregon State University, Department of Fisheries and Wildlife

Chapter 2

2. Study Areas and Methods

2.1 Study Areas

This study took place in two study areas in NZ (Figure 2.1), selected because of their contrasting population size and perceived population trends, historically abundant waterfowl numbers, and high importance to hunters and license sales. The first study area was in the Southland Plains Unit of the Southland Region, southern South Island (SOU; 46.2000°S, 168.3219°E), and was chosen because mallard populations appeared stable. The area was once abundantly inundated with swamps and peatlands and densely forested by matai (*Prumnopitys taxifolia*), kahikatea (*Dacrycarpus dacrydioides*), kōwhai (*Sophora sp.*), and ribbonwood (*Plagianthus regius*; Ledgard 2013). Today, much of the indigenous forests have been removed and it is now defined by flat or gently undulating landscapes, widespread agriculture and pastoral production (mainly sheep), and the channelisation of rivers and streams such that every watercourse has been modified (Miskell 1993). Aside from pastoral landscapes that predominately consist of ryegrass (*Lolium perenne*), cocksfoot (*Dactylis glomerata*), and clover (*Trifolium* sp.), the study area included part of the Oreti River which flowed through the western section, woodlots of planted pine that were sparsely located throughout, and cultivated hedgerows or shelterbelts of planted trees such as Monterey cypress (*Cupressus macrocarpa*), blue gum (*Eucalyptus saligna*), radiata pine (*Pinus radiata*), gorse (*Ulex europaeus*), or giant tussock grasses such as toetoe or pampas (*Cortaderia* sp.), that delineated the numerous pasture boundaries.

The second area was located mainly within the Waipa District of the Waikato Region, central North Island (WAI; 37.9167°'S, 175.3000°'E) and was chosen because mallard populations appear to be decreasing although the area was once renowned as having high duck populations. Historically, this area was dominated by large peat-swamps, bogs, alluvial flats, and vast tracks of indigenous forests consisting of kahikatea, tawa (*Beilschmiedia tawa*), tītoki (*Alectryon excelsus*), and puketea (*Laurelia novae-zelandiae*) trees (Buckland

2008). Today, the landscape is highly-modified and predominately characterised by rolling farmland and intensive agriculture (mainly dairy), but includes remnant lowland indigenous forest fragments, 2 steep-sided river valleys that are lined with rural residential development, and 14 peat lakes that are within the catchment areas of the dairy pastures (Buckland 2008). The Waikato and Waipa Rivers outline the eastern and western boundaries of the study area, respectively. The landscape vegetation is dominated by similar exotic pasture grasses as the Southland site, but planted and cultivated hedgerows such as hawthorn (*Crataegus monogyna*) and English holly (*Ilex aquifolium*) outline the various pastures and land boundaries, and invasive weeds and shrubs such as blackberry (*Rubus fruticosus*) or gorse thrive in unmanaged landscapes.

Specifically, the study areas were comprised of: i) actively grazed pasture, which included a complex system of drainage ditches, stock ponds, hedgerows, treelines, and shelterbelts; ii) settlements, including urban parkland and open spaces; iii) dense cover (including deciduous hardwoods, exotic, indigenous, and harvested forests, and gorse stands); iv) short-rotation cropland; v) river, lakes, or ponds; vi) surface mines and landfills; vii) and, orchard and vineyards (Table 2.1; Land Resource Information Systems Portal: © Landcare Research. 2011–2013. Landcover Database v.4.0). Due to heavy grazing in both study areas, nesting habitat is generally constrained to linear areas comprised of rank grass along roadways, drainage ditches, railways, hedgerows, treelines or shelterbelts, and the riparian margins of ponds, lakes, streams, or rivers. Expansive areas of dense nesting cover were not present in either study area, but unmanaged and ungrazed areas of gorse, blackberry, or other shrubs occurred erratically. Brood-rearing typically occurred in drainage ditches, lakes, ponds (including natural, man-made rural, residential ornamental, or dairy effluent), or in upland habitats within the grazed pasturelands (Garrick et al. 2017; J. Sheppard, unpubl. data). Birds began nesting during July–August and raised broods throughout September–January, although nests and broods have been reported during March–May. Moulting of flight feathers generally occurred during November–January. Nest predators included introduced and invasive mammals such as ship rats (*Rattus rattus*), Norway rats (*R. norvegicus*), stoats (*Mustela nivalis*), weasels (*M. erminea*), ferrets (*M. furo*), feral cats (*Felis catus*), as well as one native raptor, the Australasian harrier (Williams 2001). Introduced brush-tail possums (*Trichosurus vulpecula*), European hedgehogs (*Erinaceus europaeus*), dogs (*Canis domesticus*), and Australian magpies (*Gymnorhina tibicen*) also reportedly destroy nests or cause abandonment of nesting birds (Williams 2001, Morgan et al. 2006, Innes et al. 2015).

Duckling predators included Australasian harriers, pukekos, short-fin and long-fin eels (*Angulla australis* and *A. dieffenbachii*, respectively), mustelids, and cats.

Figure 2.1 – Map of study areas in New Zealand where female mallards were studied, 2014–2015. Bathymetry data were extracted from NIWA (Mitchell et al. 2012) and terrestrial data were extracted from the Landcover Database v.4.0 © Landcare Research and Land Information New Zealand © LINZ Data Service.

Table 2.1 – Landscape composition of each study area where female mallards were studied during 2014–2015. Habitat composition was derived from the Landcover Database v.4.0 © Landcare Research.

Habitat type	Southland	Waikato
Actively grazed pasture	0.927	0.883
Settlements, urban parkland	0.023	0.070
Dense cover	0.019	0.027
Short-rotation cropland	0.014	0.006
River, lakes, ponds	0.009	0.008
Surface mine, landfill	0.007	0.0004
Orchard and vineyards	0.000	0.008

2.2 Capture and Monitoring Procedures

During 2014–2015, pre-breeding female mallards were captured at both sites using baited funnel traps (Bub 1991) that were placed on the edge of refuge ponds (i.e., ponds that were not hunted during the most recent hunting season) on private rural land. Trapping began in early July in Southland and early June in Waikato. Due to annual variations in land-owner permissions, trap locations, and bird movements, study areas (defined by a 100% minimum convex polygon of nests from radiomarked birds) differed in size (SOU_{2014} = 2,365 ha; SOU_{2015} = 9,224 ha; WAI_{2014} = 26,638 ha; WAI_{2015} = 18,256 ha; Figure 2.2). Each year, 60 female mallards per study area were captured and equipped with a 22 g intra-abdominal radiotransmitter (hereafter implant; Model IMP/150, Telonics, Mesa, Arizona, Rotella et al. 1993, Paquette et al. 1997). Transmitters were fully encapsulated (i.e., no percutaneous antenna), equipped with mortality sensors that were activated after 8 hours of inactivity, and programmed with a 12 hour on, 12 hour off (in 2014) or 14 hour on, 10 hour off (in 2015) duty cycle (procedures of abdominal implantation are described in detail in Chapter 6 – section 6.4.1).

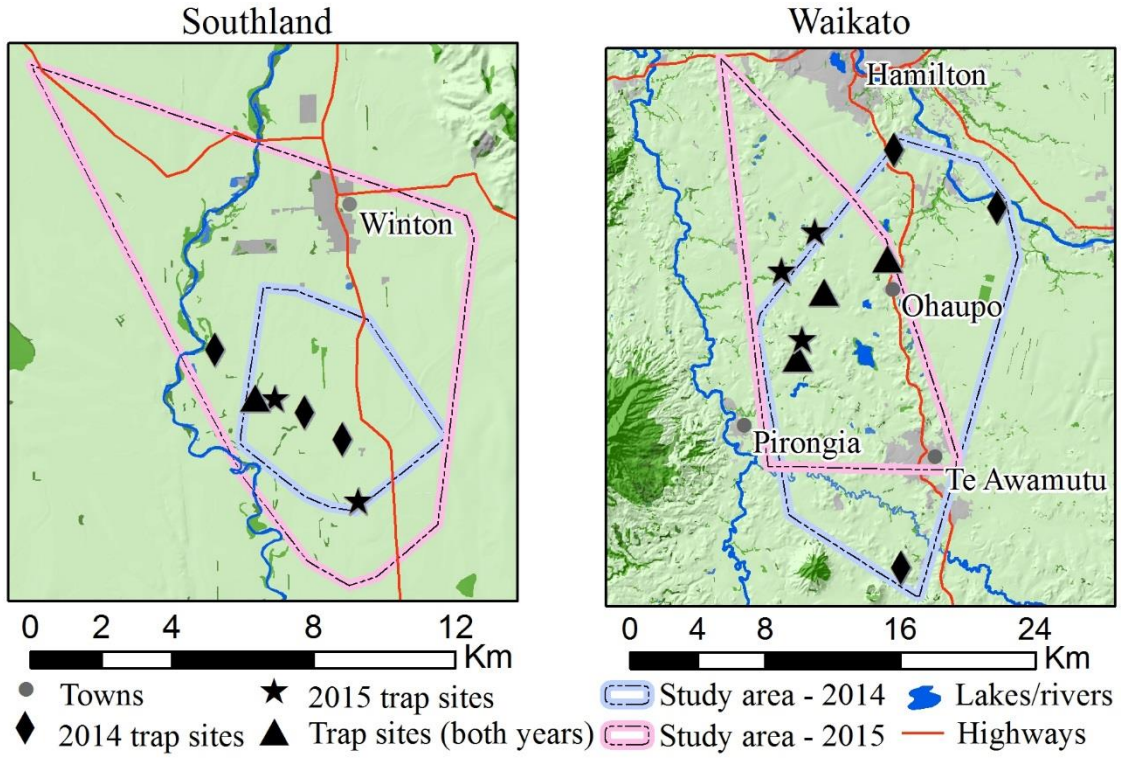

Figure 2.2 – Map of year-specific study areas (2014 = blue outline; 2015 = pink outline) and trap sites (2014 = diamond; 2015 = star; both years = triangle) for Southland (left map) and Waikato (right map) study areas, illustrating nearby towns, motorways, and major lakes and rivers. Map data were extracted from LINZ and Landcare Research.

All trapped females were equipped with a NZ Department of Conservation steel leg band and a coloured-auxiliary wrap-around band (in 2015 only) and weighed with electronic (± 1 g) or Pesola scales (± 10 g). A ruler was used to measure wing chord (± 1 mm) from the end of the carpo-metacarpus to the tip of the longest primary feather, and electronic calipers (± 0.1 mm) were used to measured: (i) head length from the back of the head to the tip of the bill, (ii) culmen length (i.e. total length of the upper part of the bill), (iii) tarsus length of the tarsometatarsal bone, excluding joints, and (iv) keel length from the tracheal pit to the hind margin of the sternum. Females were aged as either after-second year (ASY) or second-year (SY) based on the perceived depth of the bursa of Fabricus from cloacal examination (Hochbaum 1942) and characteristics of the greater secondary coverts, primaries, and general wing plumage (Carney 1992). The second greater-secondary covert feather was collected for additional verification of age assignments (Krapu et al. 1979), and 5–7 flank feathers and < 3 mL of blood (from the jugular vein) were also collected from each bird for related studies.

Radiotracking began the day following transmitter deployment to monitor survival and nesting behaviour. Females were tracked every 1–3 days using hand-held telemetry or locations were triangulated using truck-mounted, null-array antenna systems (Kenward 1987) and Location of a Signal Software, version 1.03 (LOAS; Ecological Software Solutions, Hegymagas, Hungary). If females went missing during ground tracking, they were searched for extensively during road searches throughout the study area and beyond until they were relocated or the nesting period had nearly completed (end of November). Additionally, during the peak breeding season, 1–3 aerial telemetry flights were conducted at each site by searching parallel transects up to 10 km outside of the study area boundary at an average height of 300 m above ground (Gilmer et al. 1981). During aerial flights some missing females were relocated (approximately 8 each year).

Whenever a female was triangulated to the same location between consecutive tracking attempts, the female was approached on foot in anticipation that she would be nesting. To minimise disturbance and investigator-induced nest abandonment, investigators attempted to locate the nest without flushing the female, checked nests remotely every 1–7 days via telemetry, and visited nests directly only if the female was absent or if a week or more had passed since the last visit. When nests were located, they were marked with flagging 1 m from the nest and eggs were counted, candled to determine development stage (Weller 1956), and measured (length and breadth, to nearest 0.1 mm using electronic or Vernier calipers) to calculate egg volume (Hoyt 1979). Nests were subsequently checked every 7–10 days until fate (e.g., hatched, depredated, abandoned) was determined.

From late August to early November, roadsides, riparian edges of drainage ditches, lakes, ponds, and other suitable nesting habitats were searched to find nests of unmarked mallards using a combination of techniques including beat-outs, foot searches, and well-trained pointing dogs. Unmarked nests were monitored similarly to nests of marked females. To increase the sample size of brood-rearing females, nesting females were captured on their nest during late incubation ($\bar{x}$ = 33 days post-initiation; SD = 3.8; range = 19–40) using a mist-net (Bacon and Evrard 1990; n = 32), automatic nest trap (Weller 1957; n = 9), a long-handled dip net (Loos and Rohwer 2002; n = 11), net-gun (n = 7), walk-in trap (Dietz et al. 1994; n = 2), or by hand (n = 4). Nest trapped birds were equipped with a 9 g back-mounted (prong-and-suture) radiotransmitter (hereafter P&S; Model LB-66, Telonics, Mesa, Arizona; Rotella et al. 1993, Paquette et al. 1997). The P&S transmitter was rectangular-shaped (44 mm long, 14 mm wide on posterior end, 17 mm wide on anterior end, and 8 mm high), with a

150 mm external whip antenna, 3 suture-tubes located ventrally at the anterior, centre, and posterior ends of the transmitter, and a stainless steel 2-prong anchor (15 mm wide x 17 mm long) at the anterior end of the transmitter.

Protocols for back-mounted attachment followed Mauser and Jarvis (1991). One investigator firmly held the bird, while the other investigator attached the P&S transmitter. Feathers were gently removed from a 3–5 cm area around the incision site and 0.2–0.4 mL of a local anaesthetic (Marcain; 0.5% bupivacaine hydrochloride; AstraZeneca Ltd, Auckland, NZ) was subcutaneously injected around the incision site, on the dorsal side of the body between the mid-line of the scapula and slightly adjacent to the spine. While waiting for the anaesthetic to take effect, mass, morphometric measurements, blood, and feathers were collected. The incision site was then soaked with 70% isopropyl alcohol and Betadine® (7.5% w/v povidone – iodine) and a 3–5 mm incision was made in the skin perpendicular to the body axis. The anchor of the transmitter was inserted into the incision one prong at a time, and a suture was then threaded through each suture-tube and the subcutaneous skin layer directly below the transmitter to hold it in place. If required, a double-suture pattern was used to close the incision site around the prong. Once the transmitter was securely attached, the female was immediately released away from the nest toward the closest source of water. On average, the attachment process took 22 mins (SD = 7 mins) and birds were held for 44 mins (SD = 9 mins) from capture to release. Instruments and transmitters were cold-sterilised with CIDEX® OPA (0.55% Ortho-phthalaldehyde; Advanced Sterilization Products, Irvine, CA, USA.). All P&S females were tracked using the same protocol as females marked with implant transmitters.

Nests were passively checked using telemetry on the estimated day of hatch and every day thereafter until the female and ducklings had left the nest. Investigators then approached the nest to confirm hatch, counted the remaining eggs and hatched membranes to determine initial brood size, and recorded nest vegetation characteristics (methods used to collect nest vegetation are described in Chapter 3 – section 3.2.2). Following hatch, brood-rearing females were tracked every 1–3 days until the brood was 10 days of age, and then every 5–7 days thereafter until the female: died; re-paired or flocked once ducklings were 45 days old or more; lost all the ducklings (e.g., complete brood mortality); successfully fledged at least 1 duckling (55–83 days post-hatch); went missing; or radio-loss or failure occurred. During brood observations, investigators used binoculars or spotting scopes to obtain a full count of the surviving ducklings without disturbing the female and brood, but due to the secretive

nature of broods and the landscape of the study areas, this was not always possible. At approximately 10, 30, 45, and 60 days of age, or whenever total brood failure was suspected, more invasive techniques (i.e., double observer methods or pushing/flushing broods towards hidden observers or cameras, closely approaching and flushing broods, or beat-outs) were used to obtain full counts of the surviving ducklings.

Peak nest initiation occurred in early September and most ducklings fledged by mid-December; yet, some renesting birds nested in late November. Following fledging or nest failure, investigators continued to track females weekly to monitor post-breeding survival and to detect potential late renesting attempts. Females were tracked until they died, were not located within 10 km of the study area, or the transmitter no longer emitted a detectable signal following a weakening pulse rate, up to 270 days post-marking ($\bar{x}$ = 223.8 days; SD = 20.0; range = 183–270). The total number of females marked and the associated number of nests and broods monitored in each site varied annually due to: i) renesting behaviour; ii) the number of unmarked nests that were located in each site, each year; and, iii) the proportion of females attending unmarked nests that were trapped and marked with P&S transmitters (Table 2.2).

Aside from females that died during the study (n = 62), known fates were recorded for 38 females; 7 females that were marked in 2014 were recaptured in 2015 in bait-traps during marking (n = 3) or on the nest (n = 4); 10 females were recaptured during subsequent summer banding programs in 2016 (n = 2) and 2017 (n = 8); and 21 birds were reported via hunters during harvest in 2015 (n = 13), 2016 (n = 5), and 2017 (n = 3). Recaptured females were not remarked, but recapture information was used to better inform female survival rates and where applicable, nest survival information was collected.

Table 2.2 – Number of females that were radiomarked wtih abdominal-implant and prong-and-suture transmitters, and the number of nests and broods that were monitored in each site, each year.

	Southland		Waikato		
Transmitter type	**2014**	**2015**	**2014**	**2015**	**Total**
Females marked					
Implant	62	61	60	60	243
Prong-and-Suture	22	12	10	17	61
Nests monitored					
Implant	65	67	63	75	270
Prong-and-Suture	36	15	14	18	83
Unmarked	42	58	21	15	136
Broods monitored					
Implant	33	35	32	33	133
Prong-and-Suture	20	10	11	16	57

2.3 Ethics Approval

Research and procedures were approved under University of Auckland Animal Ethics Permit 001331.

Chapter 3

3. Nesting Ecology of Female Mallards in New Zealand

3.1 Introduction

New Zealand has faced many conservation issues due to introductions of exotic species, most notably mammalian predators (Atkinson 1989). But, some naturalisations were desirable to many, such as mallard, ring-necked pheasant (*Phasianus colchicus*), and brown trout (*Salmo trutta*). During 1867–1940, small numbers of mallards were hand-reared and released by acclimatisation societies throughout NZ for sport and game hunting (Dyer and Williams 2010). The eventual widespread establishment of mallards in NZ resulted from the combined release of approximately 25,000 individuals during 1940–1960 and the genetic introgression between mallards and the native grey duck (Balham and Miers 1959, Dyer and Williams 2010, Guay et al. 2015b). Today, mallards and their hybrids (hereafter mallards) are combined for management and monitoring purposes (McDougall and Amundson 2017), and are the most numerous and widely harvested game bird in the country (Williams 1981, Caithness 1982, Robertson 2007).

Perceived declines in mallard abundance in some regions have prompted Fish and Game to initiate research to better understand causes of population change. Breeding incidence and reproductive performance are important life history events that have profound influences on the population dynamics of many waterfowl species (Johnson et al. 1992). Specifically, nesting ecology incorporates the portion of the reproductive cycle from the probability of a female laying an egg, to the rate at which clutches hatch or are destroyed. Several vital rates fall under its umbrella including: breeding incidence, renesting propensity, nest survival, egg hatchability, and partial clutch depredation. Breeding incidence, or the probability that a female initiates a clutch in a given breeding season, is high for most studies

of mallards in North America (e.g., Hoekman et al. 2002, Coluccy et al. 2008), but may be lower for species that are non-migratory, subject to different selective pressures in dissimilar ecosystems (Rigby and Haukos 2012, Dugger et al. 2016), or vary with age and condition (Dufour and Clark 2002, Coluccy et al. 2008). Renesting propensity, or the probability that a female will initiate another nest after failure of a nest or brood, is another important reproductive strategy for enhancing reproductive success (Cowardin and Johnson 1979, Guyn and Clark 2000). Finally, nest survival is often the most influential parameter affecting population growth rates of mallards in North America (Cowardin et al. 1985, Howerter et al. 2014), but the overall reproductive success of a nest is also dependent on clutch size, egg hatchability, and partial depredation events (Ackerman et al. 2003). In NZ, partial depredation may be especially important because introduced nest predators (i.e., rats, stoats, and cats) may be too small to consume the entire clutch at once (Dowding and Murphy 2001). Further, egg hatchability (i.e., the proportion of eggs that hatched out of those that were incubated to term) can be influenced by pre-incubation delays, laying date, female age, or clutch size (Koenig 1982, Arnold et al. 1987, Arnold 1993, Ackerman et al. 2003).

Nesting characteristics such as the timing and duration of breeding or clutch and egg size influence various vital rates and overall productivity. Some studies suggest female mallards that nest later within a season have lower nest and brood survival, which may be related to seasonal patterns of wetland density or food abundance (Rotella and Ratti 1992, Dzus and Clark 1998, but see Howerter et al. 2014). Similarly, Krapu et al. (2004b) found that clutch size declined throughout the nesting season, thus highest reproductive outputs occurred earlier in the season in response to larger clutches. Other researchers found that bigger eggs yielded larger ducklings that had greater survival and recruitment (Dawson and Clark 2000, Anderson and Alisauskas 2001, Pelayo and Clark 2003). Shorter incubation periods reduce predator exposure making nests and nesting females less vulnerable to depredation (Arnold et al. 1987, Feldheim 1997), however longer breeding seasons allow more time for renesting (Arnold et al. 2010). To understand productivity, researchers must also understand how nest characteristics are affected by ecological variation.

Nesting habitat may also confer advantages to nest survival and may benefit subsequent reproductive stages (e.g., brood survival; Sheppard 2013, Gibson et al. 2016a). Presumably, birds select high-quality habitats that confer greater reproductive success, as expected if habitat selection is adaptive (Clark and Shutler 1999). However, maladaptive habitat choices may result if: i) recent anthropogenic landscape changes have decoupled

formerly-reliable cues that evolved to select appropriate nesting habitats (Schlaepfer et al. 2002, Chalfoun and Martin 2007, Howerter et al. 2008, Chalfoun and Schmidt 2012); ii) organisms have evolved strategies to reduce risks and enhance fitness by valuing one breeding season vital rate over another (Levin et al. 1984, Nichols 1996, Paasivaara and Pöysä 2008, Streby et al. 2014); iii) organisms are translocated and introduced to non-native environments or hand-reared and released to environments that differ from their natal origins (Armstrong and Seddon 2008, Tavecchia et al. 2009); or, iv) hybridisation between captive stocks and wild populations result in disruption of local adaptations (Allendorf et al. 2001). Disparity between habitat quality and fitness benefits result in perceptual or ecological traps, which may have negative consequences on individual fitness and population growth rates (Schlaepfer et al. 2002, Battin 2004). Therefore, in addition to vital rate estimation, identifying and improving nesting habitat, understanding when optimal timing of reproduction occurs, and ensuring habitat management programs are active during this critical time of the birds' annual cycle, are equally important for conservation initiatives (Kentie et al. 2015, Cumming et al. 2016).

Mallards have been widely studied throughout their native, Holarctic distribution (Drilling et al. 2002) and knowledge of nesting ecology and breeding season vital rates have been paramount in conservation and management programs, especially in North America (e.g., Johnson et al. 1987, Greenwood et al. 1995, Emery et al. 2005, Howerter et al. 2014). Yet, previous research of mallard nesting ecology in NZ has been sparse and existing studies were conducted over 50 years ago before reliable methods (i.e., Mayfield method) for estimating nest survival were widely in place (Balham 1952, Williams 1981). Since then, agricultural intensification, urbanisation, and hybridisation between mallards and grey ducks have increased, and while predator control programs have been implemented throughout native forests, many predator communities in low-lying wetland habitats have flourished (O'Donnell et al. 2015). In 2014–2015, I investigated nesting ecology and nest-site selection of mallards at 2 study sites in NZ. Specifically, I examined effects of study site, year, and female attributes (e.g., age, body condition, and body size) on several vital rates including: i) breeding incidence; ii) renesting propensity following failure of nests and broods; iii) egg hatchability; vi) partial clutch depredation (i.e., the reduction of clutch size between investigator visits with at least one egg left intact in the nest bowl; hereafter partial depredation); and, v) daily nest survival, which I used to calculate cumulative nest success. Further, I investigated nest characteristics including initiation date of the first detected nest

attempt, incubation and season lengths, clutch size, and mean egg volume. Finally, I analysed the composition of nesting habitats in a 1 m^2 quadrant centred on the nest and within a 200 m radius buffer of the nest-site. I evaluated nest-site selection between nests and non-nest locations or random points and related measures of selection to nest survival.

3.2 Methods

3.2.1 Study Areas and Field Methods

This study took place in two study sites in NZ (Chapter 2 – Figures 2.1, 2.2), from June 2014 – January 2016. The first study site was located in the Southland Plains Unit of the Southland Region, southern South Island (SOU; 46.2000°S, 168.3219°E) and the second site was located mainly within the Waipa District of the Waikato Region, central North Island (WAI; 37.9167°'S, 175.3000°'E). Study sites are described in detail in Chapter 2 – section 2.1.

Pre-breeding mallards were captured at both sites using baited funnel traps (Bub 1991). Trapping began in early July in Southland and early June in Waikato. Each year, 60 female mallards per study site were equipped with a 22 g intra-abdominal radiotransmitter (hereafter implant; Model IMP/150, Telonics, Mesa, Arizona, Rotella et al. 1993, Paquette et al. 1997). From late August – early November, roadsides, riparian edges of drainage ditches, lakes, ponds, and other suitable nesting habitats were searched to find nests of unmarked mallards using a combination of techniques including beat-outs, foot searches, and well-trained pointing dogs. To increase sample size of brood-rearing females for concurrent studies, nesting females were captured on their nest during late incubation using a mist-net (Bacon and Evrard 1990; n = 32), automatic nest trap (Weller 1957; n = 9), a long-handled dip net (Loos and Rohwer 2002; n = 11), net-gun (n = 7), walk-in trap (Dietz et al. 1994; n = 2), or by hand picking the bird up off the nest (n = 4), and equipped with a 9 g back-mounted prong-and-suture radiotransmitter (hereafter P&S; Model LB-66, Telonics, Mesa, Arizona; Rotella et al. 1993, Paquette et al. 1997). On average, nesting birds were trapped and radiomarked with P&S transmitters at 33 days post-initiation (SD = 3.8; range = 19–40). During capture, mass and morphometric measurements were collected for each female and they were aged as either after-second year (ASY) or second-year (SY) based on the perceived depth of the bursa of Fabricus from cloaca examination (Hochbaum 1942) and characteristics of the greater secondary coverts, primaries, and general wing plumage (Carney 1992). Capture, marking, and measuring techniques are described in detail in Chapter 2 – section 2.2 and Chapter 6 – section 6.4.1.

Following transmitter deployment, implant females were radiotracked every 2–3 days using hand-held and truck-mounted radio-telemetry systems (Kenward 1987) to determine the onset of nesting and to monitor nesting behaviour. When nests were located, eggs were counted and candled to determine development stage (Weller 1956), and measured (length and breadth to nearest 0.1 mm using electronic or Vernier calipers) to calculate egg volume (Hoyt 1979). Nests were subsequently checked every 7–10 days until fate was determined and the number of eggs were recorded during each visit to evaluate partial depredation and egg hatchability. Nest fate was classified as: i) successful if $\geq$ 1 egg hatched; ii) abandoned if the nest was deserted following investigator disturbance or partial depredation of less than half of the clutch (Ackerman et al. 2003); iii) destroyed if at least half of the clutch was removed or eaten, or the female was killed while nesting; iv) non-viable if all eggs were addled (e.g., no sign of embryo development); v) or, unknown (e.g., nests could not be relocated, investigators were unable to revisit nest due to land access). In instances where females may have been prone to investigator-induced nest abandonment (i.e., based on previous nesting histories), the female was not disturbed until the nest was in late incubation (> 28 days post-initiation). Following failure of nests or broods, females were tracked weekly to detect renesting attempts. All females were tracked until they died, left the study area, or the transmitter no longer emitted a detectable signal following a weakening pulse rate. Females equipped with P&S transmitters were tracked using the same protocol as implant females and unmarked nests were monitored similarly to nests of marked females.

3.2.2 Nest Habitat Classification

To better understand which habitat types confer reproductive advantages, I simultaneously evaluated nest survival and nest-site selection (Clark and Shutler 1999). Habitat selection is an hierarchal process (Johnson 1980) so I measured nest-site characteristics within a 200 m radius buffer around the nest to identify larger-scale habitat components which may influence selection of nesting areas within the home range (i.e., second-order selection), and within 1 m^2 of the nest site to identify important microhabitat components such as nest vegetation structure and composition immediately surrounding the nest (fourth-order selection). I used a 200 m radius buffer to characterise second-order selection because analyses of nesting data in Waikato illustrated that nest survival was most strongly associated with this spatial scale (J. Cosgrove, Auckland/Waikato Fish and Game, unpubl. data).

Following nest success or failure, visual obstruction measurements (Veg_Density; dm) were collected at the nest site by placing a Robel pole (Robel et al. 1970) in the centre of

the nest and reading visual obstruction as the maximum height (in decimetres) at which the pole was completely obscured by vegetation. Readings were recorded at each cardinal direction 4 m away from an observer height of 1 m (i.e., crouching), and the mean of the 4 measurements was used as an index of vegetation density (Varner et al. 2013). A modified (50 cm^2) Daubenmire frame (Daubenmire 1959) was used to record the proportion of 6 nest-vegetation types in a 1 m^2 quadrant-frame centered on the nest (Tables 3.1, A1.1). To measure fourth-order selection, 1–4 "non-nest" points per nest were systematically collected 10 m away from the nest in each cardinal direction. Vegetation measurements of non-nest points were not collected if locations fell within a pasture (unless the nest itself was in a pasture or within a structure surrounded by pasture such as tree, stump, or silage bale; n = 20), in water, on a road, or on other non-nestable surfaces (e.g., mud, farmyard). Approximately 90% of all nest-sites were comprised predominately of grass, sedge/rush, or shrub/tree habitat (Appendix 1 – Section A1.1), so only the composition of these habitat variables were considered when evaluating nest survival and selection at the 1 m^2 scale. Nest vegetation was recorded following nest fate as opposed to predicted hatch date, which may lead to bias due to temporal variation in vegetation height and cover because, on average, vegetation measures of successful nests were recorded later in the growing season than for nests that failed (Gibson et al. 2016b, McConnell et al. 2017). To control for this and to avoid confounding survival with vegetation covariates, I regressed vegetation measures of density, grass, sedge, and shrub by the date of vegetation measurements and used the residuals to create relative vegetation density and composition variables (Gibson et al. 2016b).

During vegetation measurements of nests and non-nest locations, the type of habitat the nest was located in (HAB_TYPE) was classified and grouped into 1 of 5 main categories (Table 3.2). The patch width of the various habitat types differed such that habitat patches were widest along waterbodies, fields, and roadsides, but narrowest along drains and hedgerows (Appendix 1 – Section A1.2). If a nest was located in more than 1 habitat type (i.e. along a drain but next to a road), it was classified based on the nearest habitat type.

Table 3.1 – Description of nest-site vegetation used by female mallards in Southland and Waikato, 2014–2015.

Vegetation Composition	Definition
Grass	Species belonging to the Poaceae family, including rank grass and pasture grass such as ryegrass, cocksfoot, and giant tussock grasses.
Sedge	Includes species within the Cyperaceae, Juncaceae, Typhaceae family such as raupō (*Typha orientalis*), *Carex secta*, and *C. geminate*. Also includes other Poales outside the Poaceae family, as well as flax[1] (*Phomium* sp.).
Forb	Herbaceous flowering plants (non-woody dicots) such as clover and other legumes, chicory (*Cichorium intybus*), plantains (*Plantago* sp.), and other non-woody angiosperms excluding grasses, sedges, and rushes.
Shrub	Shrubs, trees (wood-stemmed dicots), and tree ferns such as: planted hedgerows, invasive woody species such as blackberry and gorse, and planted and cultivated tree rows or stands.
Ground	Bare ground, lichen, moss and other Bryophytes, leaf litter, or dead branches.
Emergent	Emergent vegetation along the edges of drainage ditches, ponds, lakes, streams, creeks, and ephemeral wetlands, or surface water within paddocks.

[1] Taxonomically, flax is neither a grass, sedge, nor rush, but it was grouped within the 'sedge' category because it is a monocot, whereas species within the forb and shrub category are typically dicots.

Table 3.2 – Description of habitat types where nests of female mallards were located in Southland and Waikato, 2014–2015.

Habitat type	Definition
Roadside	The margins of paved and unpaved roads, dairy tracks, and railways.
Drain	The riparian margin or edge of a drainage ditch or modified creek or stream which functions primarily as a drainage ditch.
Waterbody	The riparian margin of effluent, natural or man-made stock ponds, lakes, rivers, natural streams or creeks, and nests located on floating islands of vegetation.
Hedgerow	Shelterbelts and treelines, defined as a linear strip of vegetation typically used to delineate two pasture fields or other habitat types.
Non-linear	Non-linear habitat types such as pastureland (or substrate within a pastureland such as a brush pile or stump), farmyards, rural backyards, areas around agricultural-related buildings, non-linear areas of scrub/wood-shrub fields, woodlots, and forest stands.

3.2.3 Geospatial Habitat Classification

I imported aerial imagery with a resolution of 0.75 m (SOU) and 0.50 m (WAI) and data layers for roads and highways, lakes, and major rivers from Land Information New Zealand Data Service (© Waikato Regional Aerial Photograph Service 2012; The Southland Consortium 2014; Land Information New Zealand and Landcare Research, 2015), and thematic classification of land cover from Land Resource Information Systems Portal (© Landcare Research. 2011–2013. Landcover Database v.4.0) into ArcGIS (v. 10.3, Esri Inc., Redlands, CA, USA) to aid in the digitisation of each study area (1:5,000 scale). I digitised road area by assuming that all primary roads were 7.5 m wide (3.25 m lane + 0.5 m shoulder) and that motorways were 12 m wide (DTR 2016). Using aerial imagery, I determined the respective width of non-digitised waterways including streams, creeks and drainage ditches (range = 2–20 m wide) and their associated riparian margins (range = 0.5–20.0 m wide), and independently digitised these using the *buffer* tool in ArcGIS. I identified and digitised artificial ponds (including effluent and stock ponds), drainage ditches, and other water bodies

from aerial imagery or during the course of field work. I then digitised dense habitat from the Landcover Database, which I defined as: broadleaved or deciduous hardwoods, gorse, manuaka (*Leptospermun scoparium*) and/or kānuaka (*Kunzea ericoides*) stands, flax-dominated swamp, herbaceous freshwater vegetation, and indigenous, exotic, and harvested forests. I also included the riparian habitats of drains, streams, creeks, rivers, ponds, and lakes, roadside habitat (buffered at 2.5 m in accordance with aerial imagery), and other dense cover (e.g., hedgerows, treelines, shelterbelts), scrub/shrublands, or grass habitats, identified from aerial imagery or during the course of field work. I did not consider actively grazed pastureland as potential nesting habitat because of the frequent rotation of livestock within these areas which generally deterred nesting birds (e.g., only 2 birds nested directly in pasture in this study, both nests failed within 1 week). No nests were located within short-rotation crop, orchards, vineyards, urban parklands or open spaces, settlements, gravel pits, or landfills; thus, I excluded these habitat types from the representative layer of potential nesting habitat. A subset of imagery within the study sites was ground-truthed during fieldwork.

To evaluate second-order habitat selection, I generated 1000 random points within the digitised study area boundaries (which were derived from a minimum convex polygon of all radioed females in each site), but did not include points located in waterbodies, roads, or urban areas (e.g., cities or towns). Random points were a minimum of 1 m apart (i.e. closest distance of any 2 recorded nests in this study). Using the *buffer* and *intersect* tool in ArcGIS, I assigned map features to 1 of 3 habitat types to determine the proportion of: i) waterbodies (water), including lakes, ponds, effluent ponds, rivers, streams, creeks, drains and ditches; ii) dense habitat (Dense_Veg); and, iii) roads (paved/primary roads only), within a 200 m radius of each nest location and random point (Figure A1.2). I only considered paved roads in the analysis of nest survival and selection because Cosgrove et al. (2015) found that nest survival was positively related to this habitat type, but found no relationship between survival and other road types (e.g., non-paved roads, cattle chutes/races, rural lanes). I used the *near* tool in ArcGIS to determine the distance from each nest or random point to the nearest road (Dist_Road) and water (Dist_Water) habitat.

3.2.4 Statistical Methods

I used generalised linear models (glm) in R*3.3.0 (R Development Core Team 2015) to examine breeding incidence, renesting propensity, egg hatchability (range = 0.33–1.0), partial depredation (range = 0.0–0.89), daily nest survival, relative nest initiation date of the first nest attempt (range = 1–110, 15 July–1 November, respectively), clutch size (range = 4–17),

egg volume (range = 37.7–67.9 cm^3), incubation length of successful nests that were found during laying (range = 22–31 days), and nest-site selection. I modelled response variables using a binomial distribution with a logit link (breeding incidence, renesting propensity, egg hatchability, partial depredation, nest-site selection, and nest survival), or Gaussian distribution with an identity link (nest initiation date, clutch size, egg volume, incubation length). I used the 'lme4' package (Bates et al. 2015) to incorporate random effects of: i) female identity (i.e., band number) into the analysis of renesting propensity because some females renested multiple times; and ii) nest identity (i.e., nest ID) in the analysis of nest-site selection at the local scale because non-nest sites were constrained within a 10 m radius of the nest-site and there were multiple non-nest sites for each nest. I used the logistic-exposure method (Shaffer 2004) and 'nestsurvival' package (M. Herzog, U.S. Geological Survey, unpubl.) to model daily nest survival based on nest visitation intervals, whereby exposure days equalled the number of days between nest observations. This type of model provides reliable estimates of daily nest survival when nest visitation intervals vary between nests and accounts for biases associated with variations in the age of nest discovery (Shaffer 2004, Stien and Ims 2016). Of the marked females, ages of 10 birds, wing lengths of 2 birds, initiation date of 19 nests, clutch size of 48 nests, or egg volume of 17 nests were unknown, but I estimated or imputed values for these missing variables as described in Appendix 2.1 (otherwise sample size would have varied from model to model based on missing values).

I evaluated vital rates and nest characteristics separately, whereby I independently selected models to include biologically plausible covariates that were important in similar studies of nesting ecology. I treated highly correlated variables as competing models but otherwise examined all possible subsets of the identified covariates (Table A2.1; Doherty et al. 2012). To assess model fit, I visually inspected bivariate relationships between the fitted and residual values of the global model to verify homogeneity of the variance and linearity and to examine potential outliers. Further, I visually assessed that residuals were normally distributed using quantile-quantile plots and fitted a linear regression model to the actual and predicted responses and examined R^2. I compared models using Akaike's Information Criterion, corrected for small sample size (AIC_c) and considered competitive models that were ≤ 2 AIC_c units of the best model (Burnham and Anderson 2002), but eliminated models which contained uninformative parameters from the candidate set (i.e., AIC_c values were lower for a higher-ranking, but simpler, model that contained a subset of the parameters under consideration; Arnold 2010). I present results of the top model rather than model

average parameter estimates because even minimal amounts of multicolinearity among predictor variables can result in bias and unreliable estimates (Cade 2015). Results and descriptions of full model sets are provided in Tables A2.2–A2.14.

For abdominal-implant females only, the proportion of nests that failed before they could be discovered can be determined from the average daily survival rate (DSR) of nests for each site-year, raised to the average age of nests when first discovered (Appendix 2 – section A2.1) in each site-year (d): proportion of nests found = DSR^d (McPherson et al. 2003, Arnold et al. 2007). Using this information and despite an intensive tracking effort, only 78% of nests in Southland in 2014, 85% of nests in Southland in 2015, and approximately 76% of nests in Waikato each year, were found prior to nest failure. Thus, my estimates of breeding incidence, renesting propensity, and season length are biased low because some nests were destroyed before they were discovered.

3.2.5 Data Considerations and Censoring

These data contained nest records of marked and unmarked birds, thus when considering effects of female attributes, I was only able to use information from marked individuals. Further, females with implants were captured pre-breeding following supplemental feeding and P&S birds were trapped during late incubation. Due to temporal differences in breeding stages at time of marking, I was unable to readily compare body condition indices between implant and P&S females. While I incorporated effects of female age in all analyses, I only evaluated effects of female body condition and size in analyses which focused on the larger sample of implant females (e.g., breeding incidence, renesting propensity, and nest initiation date), but I included a transmitter effect in analyses that combined females of both transmitter types (e.g., nest survival, clutch size, egg hatchability). However, given that P&S females were trapped during nesting, as opposed to pre-breeding as were implant females, transmitter effects could also indicate a time/stage of trapping effect. I defined body size (SIZE) as the first eigenvalue of a Principal Component Analysis (PCA) using wing, head, and keel length measurements (Alisauskas and Ankney 1987); all variables had positive loading factors (wing = 0.54; keel = 0.56; head = 0.62) and PC1 explained 57% (SD = 1.30) of the variation among the 3 measurements. I regressed log body mass on PC1 and used residuals from the resulting equation (predicted mass = 7.00 + 0.045*PC1; $R^2 = 0.43$) as an index of body condition (Devries et al. 2008, Arnold et al. 2010). I standardised condition and size indices to aid interpretability (i.e., 1 unit represents a bird that was 1 SD larger or in better condition than other nesting females).

Implant females that were older weighed 44 g more and had 4.3 mm longer wing chord than did SY females (Mass: t = -3.51, df = 223, $p < 0.001$; Wing: t = -4.84, df = 233, $p < 0.001$). Further, implant females from Southland weighed 22 g more than females in Waikato (t = -1.70, df = 232, $p = 0.09$). As such, implant females were in better body condition if they were older or if they were from Southland (Age: t = -3.40, df = 224, $p < 0.001$; Site: t = -2.11, df = 231, $p < 0.04$); so, I considered interactions between condition and site and condition and age in subsequent analyses. Four birds died from capture-related mortality, 2 others were depredated within 9 days of marking, and 1 was shot 14 days post-marking during the ongoing hunting season in Southland in 2014. I included these 7 birds in the calculations of body size and condition indices, but excluded them from all analyses of nesting ecology.

Breeding incidence. I defined breeding incidence as the probability that a female initiated $\geq$ 1 nest during the study year and only considered implant females because all P&S females were captured while nesting. I censored 3 females which could not be tracked due to restrictions to private land, 27 females that went missing before I could assign breeding status, and 5 birds that died during the nesting season for which I was unable to confirm nesting status.

Renesting propensity. In the analysis of renesting propensity, I additionally investigated covariates that have been shown previously to influence renesting in waterfowl (Fondell et al. 2006, Arnold et al. 2010), including: age of the previous nest when failed (Pre-Nestage; age = days since nest initiation), initiation date of previous nest attempt (Pre.IDATE), clutch size of previous nest (Pre.Clutch), fate of the previous nest (Pre-Fate), and the number of previous nest attempts (Pre-Attempt). I only considered abdominal implant birds in this analysis because the number of previous nest attempts of P&S females was unknown. Of 154 implant females that experienced nest or brood failure, I excluded females that: i) were unable to renest because they died during nesting ($n = 19$) or brood-rearing ($n = 7$); ii) had unknown nest ($n = 1$) or brood fate (e.g., female went missing, unable to track due to land restrictions, transmitter no longer emitted a detectable signal following a weakening pulse rate; $n = 10$); iii) or, previous nest failed due to non-viable eggs ($n = 2$). I included birds that nested after brood failure because this accounted for over one-quarter of all renesting attempts, but renesting following fledging was uncommon in this study ($n = 3$) and is atypical of mallards (Stafford et al. 2001, Arnold et al. 2010).

Egg hatchability. In the analysis of egg hatchability, I only considered eggs that survived to the end of incubation (i.e., excluded eggs that were partially depredated), and defined hatchability as: $eggs\ hatched/(eggs\ hatched + eggs\ unhatched)$. I summarised egg hatchability of all successful nests (e.g., marked and unmarked females) and only considered marked females to evaluate effects of female age and transmitter type.

Partial depredation. I defined partial depredation as the proportion of nests that experienced at least 1 partial depredation event (removal of $\geq$ 1 egg), which did not result in nest failure. To quantify partial depredation of eggs, I only considered nests that failed due to depredation or were successful (i.e. did not consider nests with unknown fates or those that were abandoned due to investigator disturbance). I considered only marked females to evaluate effects of female age and transmitter type.

Daily nest survival. I defined nests as successful if more than one egg hatched. I did not consider nests that failed or were abandoned due to investigator disturbance (n = 44) or nests that had unknown fates (n = 10). Because I evaluated survival based on nest visitation intervals rather than each nest, I right-censored the final nest visits of 5 nests which were destroyed or abandoned following investigator disturbance immediately prior to hatch, and considered them successful to the date before the disturbance event. I also included an interval-specific variable for nest age (calculated as the number of days since initiation to the start of the interval) because nest survival is often positively related to nest age (Klett and Johnson 1982, Pieron and Rohwer 2010). Proportion of road habitat was negatively correlated with distance to nearest road (r = -0.75, p < 0.001, n = 435) so I treated these variables in competing models (Tables A2.6–A2.8).

Sample size between nests with available local and landscape scale habitat information differed (i.e., local-scale habitat information was not collected for 60 nests). Thus, I conducted the analysis of nest survival at multiple stages; the top model with the lowest AIC_c value, and competitive models within 2 AIC_c units of the top model, were brought forth to the subsequent stage of analysis and the process was repeated. The first modelling stage incorporated all nests and evaluated effects of landscape scale habitat and transmitter effects (e.g., whether bird was marked with implant transmitter, or unmarked, upon initial nest discovery). The second modelling stage incorporated both landscape and local scale habitats, and the third modelling stage evaluated only implant females and considered effects of habitat (brought forth from stage 2) and female attributes.

Timing and duration of breeding. To understand when breeding occurred, I analysed the onset of nesting (initiation of the first detected nest attempt of abdominal implant females only) and incubation length (time from when the last egg was laid and clutch was completed until the first egg hatched). I calculated nest initiation date as the date the first egg was laid in the initial nesting attempt based on the number of eggs and stage of incubation upon discovery, assuming a laying interval of 1 egg per day (Bellrose and Kortright 1976) and that partial nest depredation had not occurred before nests were located, unless there was evidence to the contrary (e.g., egg shells or fragments outside the nest bowl). I only considered first detected nests in the evaluation of nest initiation date because I was mainly interested in understanding when the initial onset of nesting occurred. I censored 14 records of first nest attempts for which nest initiation date was unknown (i.e., nest failed before clutch size and incubation status could be assessed).

Preliminary field work suggested that incubation lengths differed among sites, so instead of assuming an average incubation period of 25 (Weller 1956, Caldwell and Cornwell 1975), 26 (Howerter et al. 2014), or 28 days (Palmer 1976), I evaluated the observed incubation length of all successful nests (including marked and unmarked birds) that were found during laying (i.e., the number of fresh eggs increased between initial and subsequent visits) for which hatch dates were confirmed. I assumed birds laid 1 egg per day, including the day the nest was found. Hatch dates were confirmed by: i) noting pipping eggs the day prior to suspected hatch; ii) counting $\geq$1 wet duckling(s) at the nest on the day of hatch; iii) or, recording eggs in the nest bowl 2 days prior to the presence of dry ducklings. I included additional covariates of initiation date and clutch size because incubation length may decrease with seasonal progression but increase with clutch size (Arnold 1993, Feldheim 1997). I also explored nesting season duration (the time from the discovery of the first detected nest attempt to the initiation date of the last detected nest during each field season). I assumed that the first nest of the season was successfully located and representative of season start date. In both years of the study, the earliest initiation date of the first detected nest was the 15th of July. Thus, I assigned the 15th of July as day 1 of the nesting season and scaled all initiation dates relative to this date.

Clutch size and egg volume. I summarised clutch size of all nests monitored throughout the study, but only considered marked females (i.e., implant and P&S females) to evaluate effects of site, year, initiation date, female age, nest attempt number, and transmitter type. I excluded nest records from the analysis of clutch size if: partial depredation (i.e., egg

fragments were found around nests) was evident upon nest discovery (n = 2) or between revisits during laying (n = 2); females were killed on the nest during laying (n = 9); females abandoned the nest before clutch completion (n = 21); or, if investigators were unable to obtain a count before the nest was destroyed (n = 14).

I determined mean egg volume of each nest by averaging the volume of eggs in each clutch. I included nests of marked and unmarked birds in my evaluation of site, year, initiation date, clutch size, and transmitter effects. Egg measurements of 5 nests were taken following partial depredation events, so I assumed the remaining eggs were representative of the mean clutch volume. Egg measurements were not obtained at 197 nests that were terminated before eggs could be measured.

Nest habitat and nest-site selection. Measures of non-nest sites (local-scale selection) were independent of randomly generated points for which landscape-scale habitat information was extracted, thus I was unable to combine the spatial extents into the same analysis. Instead, I evaluated nest-selection in 2 separate stages: i) evaluation of local-scale habitat only, using nest records and measures of associated non-nest locations; and, ii) evaluation of landscape-scale habitat only, using all nest records and randomly generated points from GIS. Local scale habitat was not collected for 60 nests, so these were excluded from the analysis of nest-site selection.

3.3 Results

I radiomarked 304 female mallards (Implant = 243; P&S = 61), including 143 after-second-year, 151 second-year, and 10 unknown-aged females. A total of 489 nests (Implant = 271; P&S = 83; unmarked female = 135) were monitored, including 181 first detected nest attempts, 90 known renest attempts of implant females, and 22 renest attempts of P&S females. The number of females retained in each analysis varied by site, year, and female age class due to different censoring criteria and data collection methods (Table 3.3).

Table 3.3 – Number of after-second year (ASY), second-year (SY), or unknown age (Unk.) female mallards from each site and year used in the analyses of each vital rate. Females could occur multiple times in the data set due to renesting.

	Southland		Waikato		Female Age		
Analysis	**2014**	**2015**	**2014**	**2015**	**ASY**	**SY**	**Unk.**
Breeding incidence[1]	53	53	41	53	87	106	7
Renesting propensity[1]	28	27	26	34	48	64	3
Egg hatchability	50	47	40	45	93	84	5
Partial depredation	65	58	48	61	118	108	6
Daily nest survival[1]	45	47	34	41	79	84	4
Nest initiation date[1]	46	48	32	39	76	85	4
Clutch size	67	55	46	62	117	106	7

[1] Implant females only.

3.4.1 Breeding Incidence

Breeding incidence was 0.91 (182 out of 200 birds nested; 95% CI: 0.82–0.96) and was best explained by female age and body size index (Tables 3.4, A2.2); SY females and relatively smaller females were less likely to nest than ASY females and larger females, such that 11 of 15 non-breeding females were below average body size (β_{Age} = 0.79, SE = 0.57; β_{Size} = 0.56, SE = 0.26; Figure 3.1).

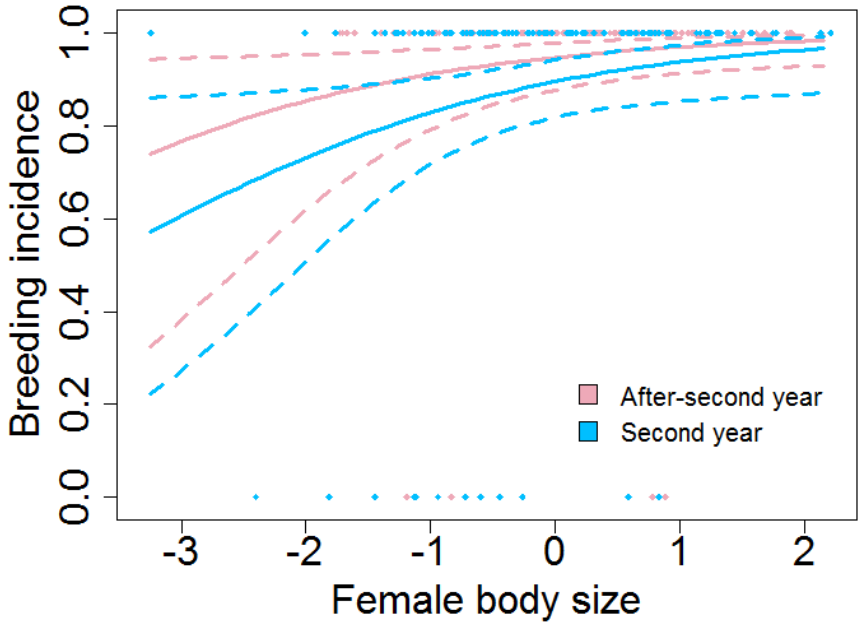

Figure 3.1 – Predicted breeding incidence in relation to age and body size (lower, negative values = smaller individuals; greater, positive values = larger individuals), for female mallards in Southland and Waikato, 2014–2015. Dots = raw values; dashed lines = 95% CI.

3.4.2 Renesting Propensity

Implanted females replaced 62% of failed first nest attempts (71/115), 30% of failed second nest attempts (15/50), 17% of failed third nest attempts (2/12), and 25% of failed broods (17/69). As determined from the best-approximating model, predicted renesting propensity averaged 0.50 (95% CI: 0.39–0.60) and was best described by female condition and the nest age, initiation date, and clutch size of the previous nest attempt (Tables 3.4, A2.3; β_{COND} = 0.35, SE = 0.24; $\beta_{Pre\text{-}Nestage}$ = -0.12, SE = 0.02; $\beta_{Pre\text{-}IDATE}$ = -0.06, SE = 0.01; $\beta_{Pre\text{-}Clutch}$ = 0.28, SE = 0.13). While approximately 90% of females renested if previous nests were lost before the 3rd of August (relative initiation date = 19), < 10% of females renested after the 13th of October (relative initiation date = 90; Figure 3.2). Approximately 75% of renesting attempts occurred if the age of the previous nest was < 14 days old at the time of nest failure (e.g., early incubation or younger; Figure 3.3). Females were more likely to renest if the clutch size of the previous nest attempt was larger (Figure 3.4), however correlations between initiation date and clutch size of the previous nest (r = -0.55, p < 0.001) may explain this relationship (i.e., earlier nests had larger clutch sizes and this was when renesting propensity was greatest). Further, females in better body condition at time of capture were more likely to renest than females in poor condition (Figure 3.5).

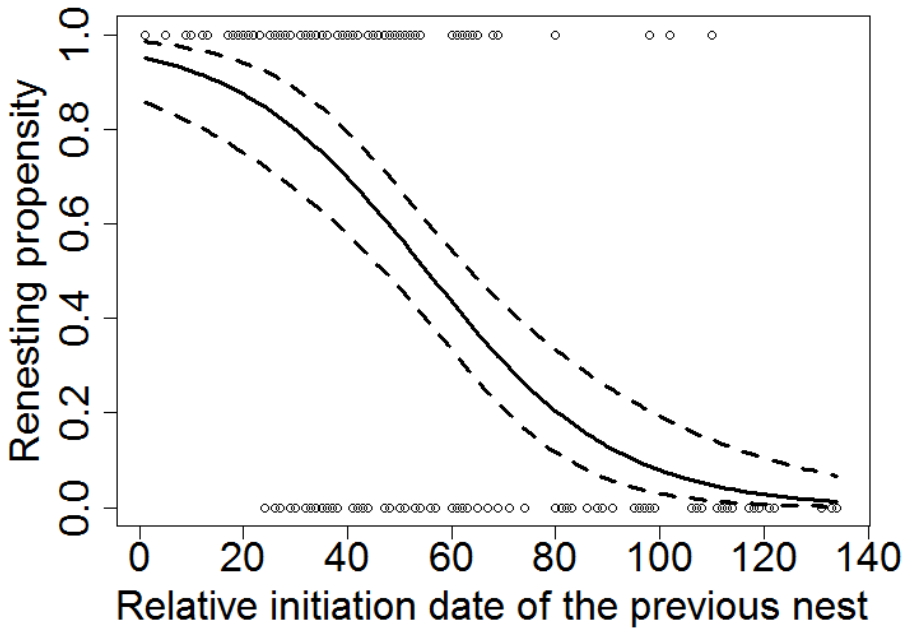

Figure 3.2 – Renesting propensity in relation to the initiation date of the previous nest attempt (relative initiation date: 1 = 15 July; 140 = 2 December), for implant females in Southland and Waikato, 2014–2015, held at mean covariate values (Pre-Nestage = 24.0; Pre-Clutch = 9.8; condition = 0.027). Dots = raw values; dashed lines = 95% CI.

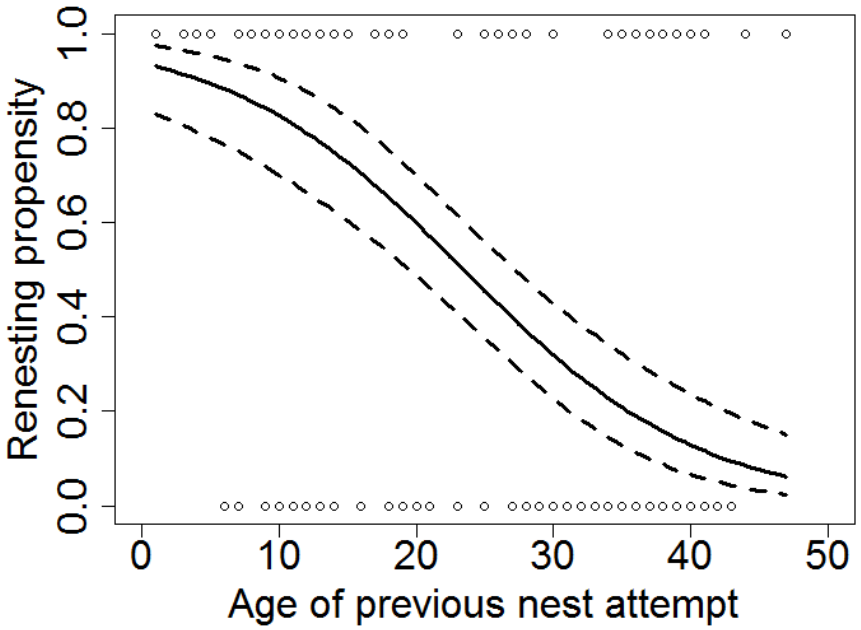

Figure 3.3 – Renesting propensity in relation to the age (days since nest initiation) of the previous nest attempt, for mallards equipped with abdominal implants, in Southland and Waikato, 2014–2015, held at mean covariate values (Pre-Initiation date = 56.5; Pre-Clutch = 9.8; condition = 0.027). Dots = raw values; dashed lines = 95% CI.

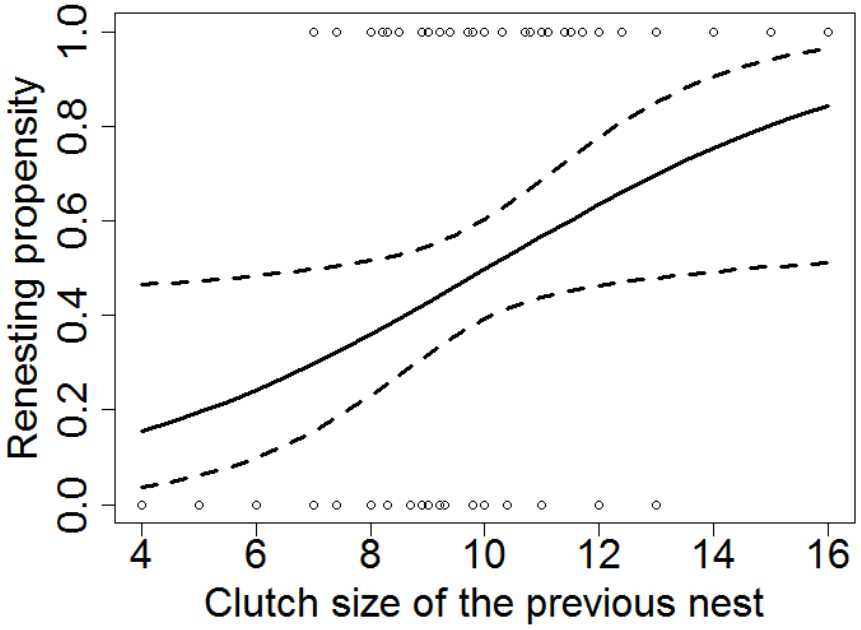

Figure 3.4 – Renesting propensity in relation to the clutch size (actual and predicted) of the previous nest attempt, for mallards equipped with abdominal implants, in Southland and Waikato, 2014–2015, held at mean covariate values (Pre-Initiation date = 56.5; Pre-Nestage = 24.0; condition = 0.027). Dots = raw values; dashed lines = 95% CI.

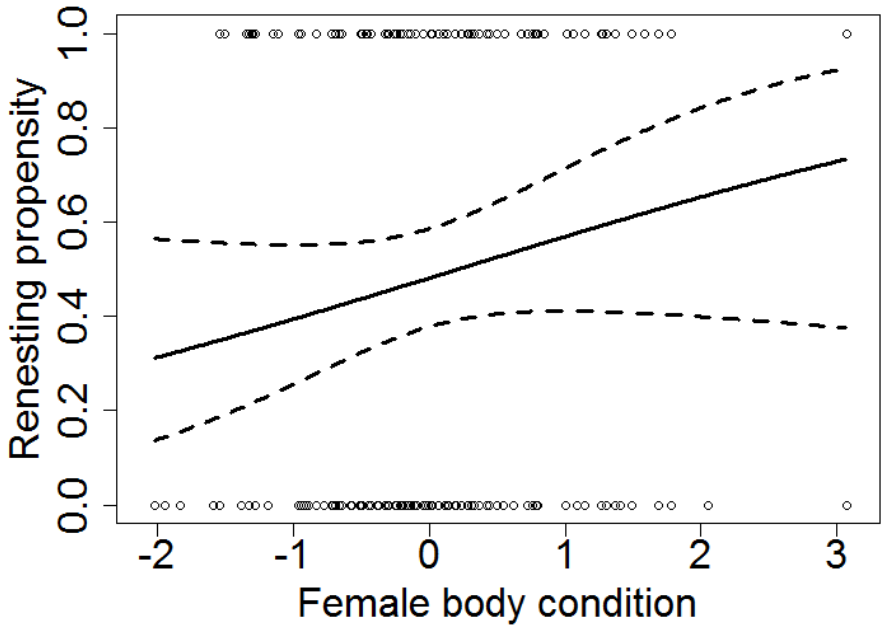

Figure 3.5 – Renesting propensity in relation to female condition (lower, negative values = poor condition; greater, positive values = better condition), for mallards equipped with abdominal implants in Southland and Waikato, 2014–2015, held at mean covariate values (Pre-Initiation date = 56.5; Pre-Nestage = 24.0; Pre-Clutch = 9.8). Dots = raw values; dashed lines = 95% CI.

3.4.3 Egg Hatchability

Females laid 2809 eggs in 270 successful nests, of which 76 eggs were partially depredated prior to hatch, 175 eggs were intact but unhatched at nest exodus, 4 eggs were damaged by investigators during trapping or measuring, and 2 nests containing a total of 16 eggs failed due to total hatching failure. My analysis of egg hatchability included 199 nests which contained 2046 eggs (Implant = 138, P&S = 61). Predicted egg hatchability was 0.93 (95% CI: 0.91–0.95) and was best explained by effects of egg volume ($\beta = 0.083$, SE = 0.069); clutches that had overall greater egg volume had higher hatchability rates (Figure 3.6; Tables 3.4, A2.4).

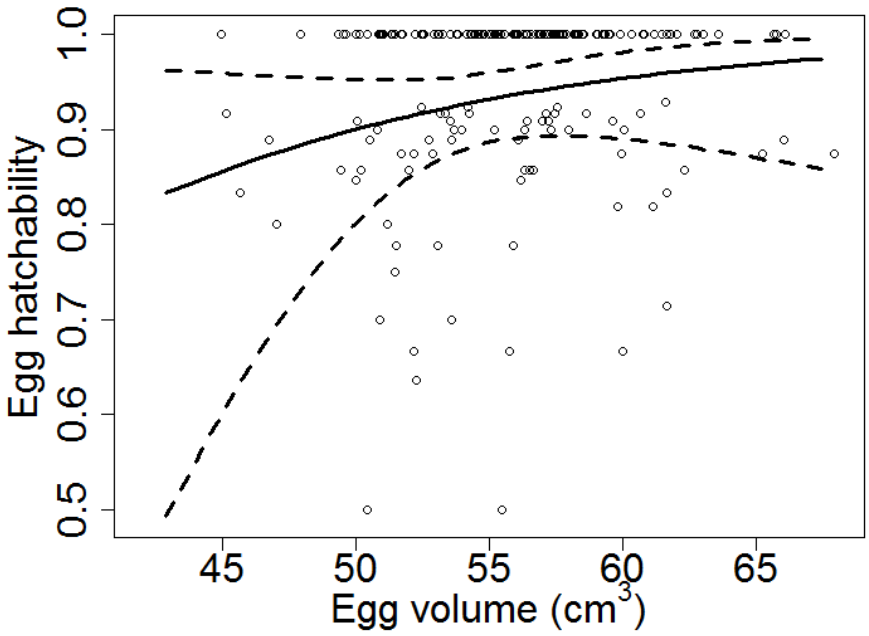

Figure 3.6 – Egg hatchability in relation to mean egg volume (0.515 * length * breath^2) of female mallards in Southland and Waikato, 2014–2015. Dots = raw values; dashed lines = 95% CI.

3.4.4 Partial Depredation

At least one depredation event occurred at 167 (39%) of the 432 nests (Implant = 239, P&S = 75; unmarked = 118) monitored in this study, whereas predators completely destroyed 98 nests by removing all eggs (n = 77) or killing the female (n = 21). Partial depredation occurred at 69 nests (16%; 95% CI: 11–18%), resulting in the abandonment of 17 nests, destruction of 15 nests, and removal or destruction of 532 eggs. Multiple depredation events were recorded at 15 nests (4%); 1 hatched, 4 were abandoned, and the remaining 10 were completely destroyed following subsequent visits by the predator(s). During partial depredation events at these nests, predators removed an average 0.33 of the clutch (SD = 0.26) or 3.23 eggs (mode = 1; SD = 2.50; range = 1–9). Partial depredation was unaffected by any measured covariates (Tables 3.4, A2.5).

Table 3.4 – Model selection results of breeding incidence, renesting propensity, egg hatchability, and partial nest depredation of female mallards in Southland and Waikato, 2014–2015. Models were ranked by differences in Akaike's Information Criterion, corrected for small sample size (AIC_c). Number of parameters (K) includes the intercept. I present the null model, top-supported (lowest AIC_c) model, and models within 2 AIC_c units of the top model unless they contained uninformative parameters.

Model	K	ΔAIC_c[a]	w_i[b]	Deviance
Breeding incidence				
Age + Size	3	0.00	0.39	113.53
Size	2	0.04	0.38	115.63
Null	1	4.87	0.07	121.20
Renesting propensity				
Pre-Clutch + Pre-IDATE + Pre-Nestage + Cond	5	0.00	0.38	137.31
Pre-Clutch + Pre-IDATE + Pre-Nestage	4	0.02	0.37	139.47
Null	1	99.64	0.00	245.37
Egg hatchability				
Egg volume	2	0.00	0.26	51.69
Null	1	0.63	0.18	54.37
Partial depredation				
Null	1	0.00	0.29	249.32

[a] Differences in AIC_c relative to the model with the lowest value.

[b] Model weight.

3.4.5 Nest Survival

I evaluated daily nest survival using a multistage approach to accommodate variations in sample sizes between nests of marked and unmarked females. Stage 1 focused on landscape-scale habitat features only, and evaluated nest survival of 7759 exposure days from 435 nests (Implant = 241; P&S = 75; unmarked = 119), including 246 nests in Southland and 212 nests from 2014. Stage 2 incorporated effects of both spatial scales and evaluated 6606 exposure days of 375 nests (Implant = 214, P&S = 73, unmarked = 88), of which 218 were in Southland and 187 from 2014. Stage 3 integrated effects of habitat and female attributes, and evaluated 5221 exposure days for 283 nests of 224 marked females, including 76 known nesting attempts of implant females (62 second nests, 12 third nests, and 2 fourth nests; Table 3.3) and 12 known renesting attempts of P&S females (2 of which were third attempts). Final nest fates included hatch (63%; n = 274), abandonment due to predators or machinery (9%; n = 41), total or partial destruction of the nest or death of the female by a predator (27%; n = 118), or complete nest failure due to non-viable eggs (< 1%; n = 2).

At the 200 m scale only (stage 1), nest survival was best explained by effects of nest age, distance to nearest road, and study site ($\beta_{NEST\ AGE}$ = 0.039, SE = 0.009; β_{Dist_Road} = -0.91, SE = 0.36; β_{WAI} = -0.28, SE = 0.16; Tables 3.5, A2.6); nest survival increased with closer proximity to primary roads (Figure 3.7), was higher in Southland, and was positively related to nest age (Figure 3.8). Results were similar in stage 2 of the analysis; in addition to nest age, distance to nearest road, and site, the best-approximating model incorporated local scale effects of grass, vegetation density, and habitat type ($\beta_{Nest\ age}$ = 0.038, SE = 0.009; β_{Dist_Road} = -0.79, SE = 0.44; β_{WAI} = -0.27, SE = 0.18; β_{Grass} = -0.35, SE = 0.22; $\beta_{Veg\_Density}$ = 0.057, SE = 0.040; β_{Hedge} = 0.49, SE = 0.26; $\beta_{Non\text{-}Linear}$ = 0.39, SE = 0.26; β_{Road} = 0.86, SE = 0.35; $\beta_{Waterbody}$= 0.085, SE = 0.25; Tables 3.5, A2.7), yet there was large uncertainty among the top models (Table 3.5). Daily nest survival increased with vegetation density (Figure 3.9), but was lowest for nests near aquatic habitats (Table 3.6). Analysis of stage 3 yielded similar results and I did not detect any effect of female attributes on nest survival (Table A2.8). As determined from the best-approximating model in stage 2, overall mean daily survival rate was 0.9789 (95% CI: 0.9646–0.9874).

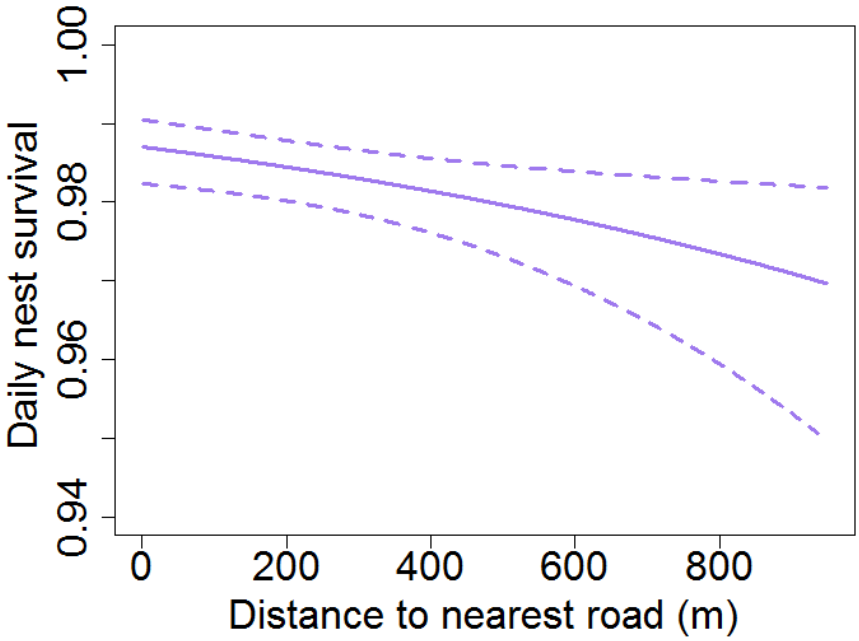

Figure 3.7 – Predicted daily nest survival rate in relation to distance to the nearest road for mallards in Southland, 2014–2015, held at mean covariate values (Pre-Nest age = 23.9 days). Dashed lines = 95% CI.

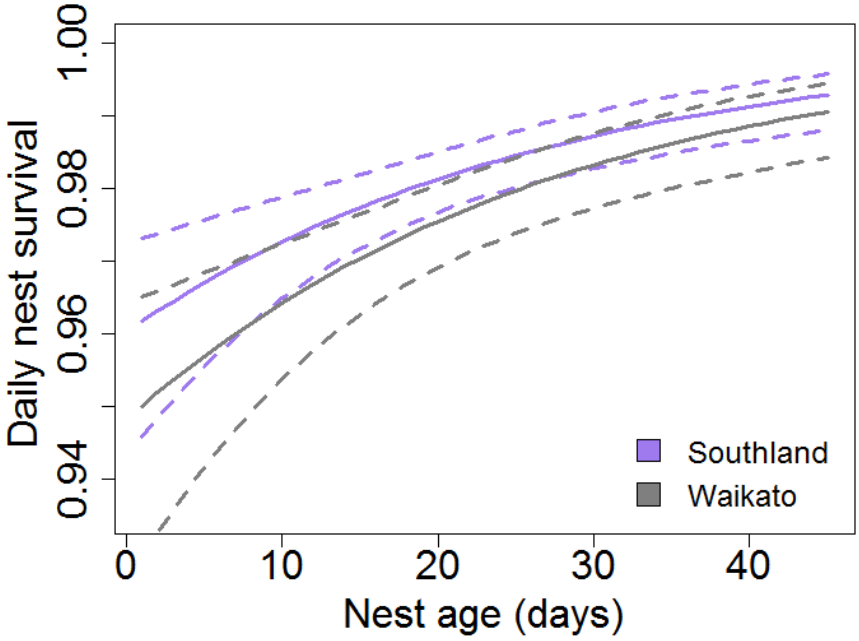

Figure 3.8 – Predicted daily nest survival rate in relation to nest age and study site for mallards in Southland and Waikato, 2014–2015, held at mean covariate values (distance to nearest road = 246.7 m). Dashed lines = 95% CI.

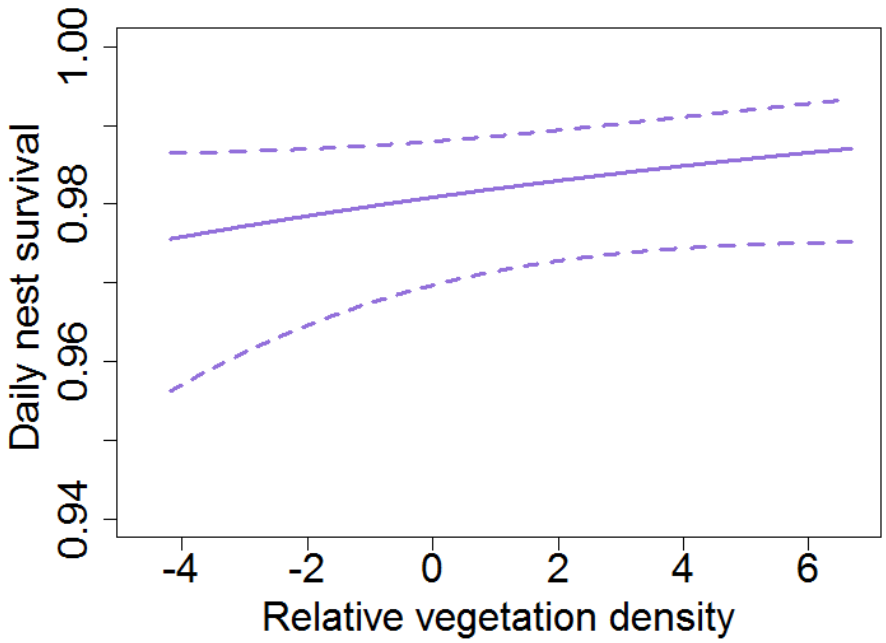

Figure 3.9 – Predicted daily nest survival in relation to vegetation density of the nest-site, for mallards nesting in drain habitat in Southland, 2014–2015, held at mean covariate values (distance to nearest road = 246.7 m; Nest age = 23.9 days; grass = 0.46) Dashed lines = 95% CI.

Table 3.5 – Model selection results of daily nest survival of mallards in Southland and Waikato, 2014–2015. Models were ranked by differences in Akaike's Information Criterion, corrected for small sample size (AIC_c). Number of parameters (*K*) includes the intercept. I present the null model, top-supported (lowest AIC) model, and models within 2 AIC_c units of the top model unless they contained uninformative parameters.

Model	*K*	ΔAIC_c[a]	w_i[b]	Deviance
Stage 1 – Landscape habitat				
Dist_Road + Nest age + Site	4	0.00	0.45	948.58
Dist_Road + Nest age	3	0.96	0.28	951.55
Null	1	26.30	0.00	980.90
Stage 2 – Landscape and local habitat				
Dist_Road + Nest age + Grass + Hab_Type + Veg_Density + Site	10	0.00	0.10	805.00
Dist_Road + Nest age + Grass + Hab_Type + Site	9	0.03	0.09	807.06
Dist_Road + Nest age + Grass + Hab_Type + Veg_Density	9	0.20	0.09	807.23
Dist_Road + Nest age + Hab_Type + Veg_Density	8	0.27	0.08	809.32
Dist_Road + Nest age + Grass + Hab_Type	8	0.69	0.07	809.75
Dist_Road + Nest age + Veg_Density	4	0.97	0.06	818.10
Dist_Road + Nest age + Grass + Site	5	1.00	0.06	816.12
Nest age + Grass + Hab_Type + Site	8	1.18	0.05	810.23
Dist_Road + Nest age + Hab_Type + Site	8	1.27	0.05	810.33
Dist_Road + Nest age + Grass	4	1.43	0.05	818.56
Dist_Road + Nest age + Hab_Type	7	1.57	0.04	812.65
Dist_Road + Nest age + Site[c]	4	1.60	0.04	818.73
Dist_Road + Nest age	3	1.82	0.04	820.96
Nest age + Hab_Type + Veg_Density + Site	8	1.82	0.04	810.88
Null	1	27.22	0.00	850.38

[a] Differences in AIC_c relative to the model with the lowest value.

[b] Model weight.

[c] Top model from Stage 1.

Table 3.6 – Site-specific cumulative nest survival (mean and lower and upper 95% confidence intervals) to 38 days (mean number of days from initiation to hatch of successful nests) in each major habitat type. Estimates were derived from the top supported model describing daily nest survival of mallards in Southland and Waikato, 2014–2015, and held at mean covariate values (distance to nearest road = 246.7 m; vegetation density = 4.97 dm; grass = 0.46).

	Southland		Waikato	
Habitat type	**Mean**	**95% CI**	**Mean**	**95% CI**
Drainage ditch	0.35	0.22–0.48	0.25	0.13–0.39
Non-linear	0.48	0.30–0.65	0.39	0.21–0.56
Hedgerow	0.52	0.37–0.67	0.42	0.23–0.61
Roadside	0.64	0.40–0.80	0.55	0.32–0.73
Waterbody	0.38	0.21–0.55	0.28	0.13–0.45

3.4.6 Timing and Duration of Breeding

Mean initiation date of 165 first detected nest attempts of implant birds was 28th August (SD = 10.2; range = 15th July–1st November). The best-approximating model incorporated effects of site, year, age, condition and size (β_{WAI} = -13.49, SE = 2.95; β_{2015} = 9.15, SE = 2.80; β_{AGE} = -11.33, SE = 2.91; β_{COND} = -3.49, SE = 1.51; β_{SIZE} = -2.52, SE = 1.47; Tables 3.7, A2.9); birds nested around 13 days earlier in Waikato but 10 days later in 2015. Further, ASY females nested approximately 11 days earlier than SY females, and birds that were larger (Figure 3.10) or in better body condition (Figure 3.11) also nested earlier.

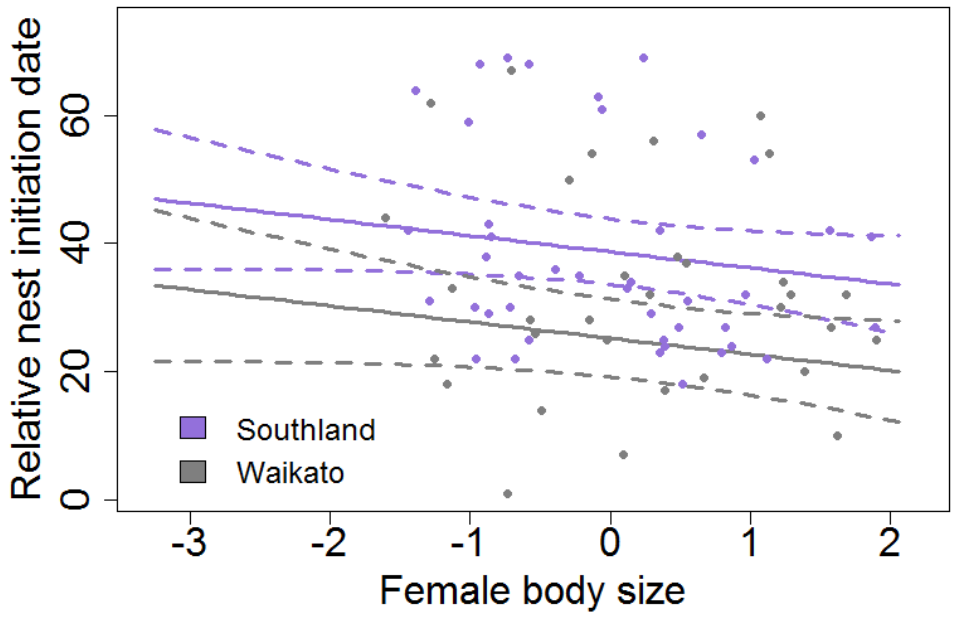

Figure 3.10 – Predicted initiation date of first nest attempts, relative to day 1 (15th July) of the nesting season, in relation to body size (lower, negative values = smaller birds; greater, positive values = larger birds) for mallards in Southland and Waikato, 2014, held at mean body condition (0). Dots = raw values; dashed lines = 95% CI.

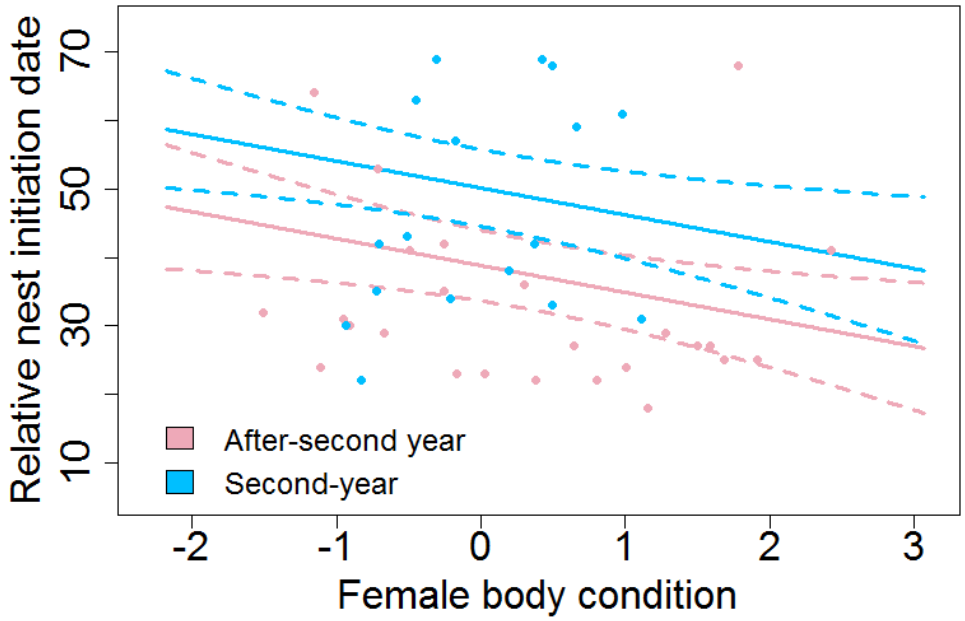

Figure 3.11 – Predicted initiation date of first detected nest attempts, relative to day 1 (15th July) of the nesting season, in relation to body condition (lower, negative values = poor condition; greater, positive values = better condition) and female age, for mallards in Southland, 2014, held at mean body size (0). Dots = raw values; dashed lines = 95% CI.

Mallards initiated nests over a period of 4.5 months from 15th July–26th November ($\bar{x}$ = 5th September, SD = 27.3 days, n = 466). Renest attempts of marked females occurred later in the year, but as early as 27th July in Waikato and 1st September in Southland. Initiation and hatch dates were confidently known for 37 nests, including nests of 25 implant females, 6 P&S birds, and 6 unmarked females (SOU = 20; WAI = 17; 2014 = 22; 2015 = 15). Incubation length averaged 27.5 days (SD = 2.0) and was best explained by effects of site (Tables 3.8, A2.10); incubation length was approximately 1.6 days longer in Southland than Waikato and averaged 28.2 (SD = 1.6) and 26.6 days (SD = 2.1), respectively.

3.4.7 Clutch and Egg Size

Overall, mean clutch size of 428 nests of marked and unmarked birds was 10.3 eggs (SD = 2.5; range = 4–18; 1 unmarked bird had a clutch size of 18). I investigated clutch size of 306 nest attempts of 226 marked females (Implant = 164; P&S = 65; Table 3.3), including 104 known renesting attempts. As determined from the best-approximating model, predicted clutch size was 10.1 (95% CI: 9.6–10.6), and was best explained by nest initiation date, transmitter type, and female age (β_{IDATE} = -0.03, SE = 0.004; $\beta_{P\&S}$ = 0.54, SE = 0.25; β_{AGE} = 0.61, SE = 0.22; Tables 3.7, A2.11); clutch size decreased with relative nest initiation date (Figure 3.12) and was greater for birds equipped with P&S transmitters. Further, clutch size of ASY females nests averaged 1 egg greater than clutches of SY females (ASY: $\bar{x}$ = 10.5, 95% CI: 10.1–11.0; SY: $\bar{x}$ = 9.7, 9.2–10.1).

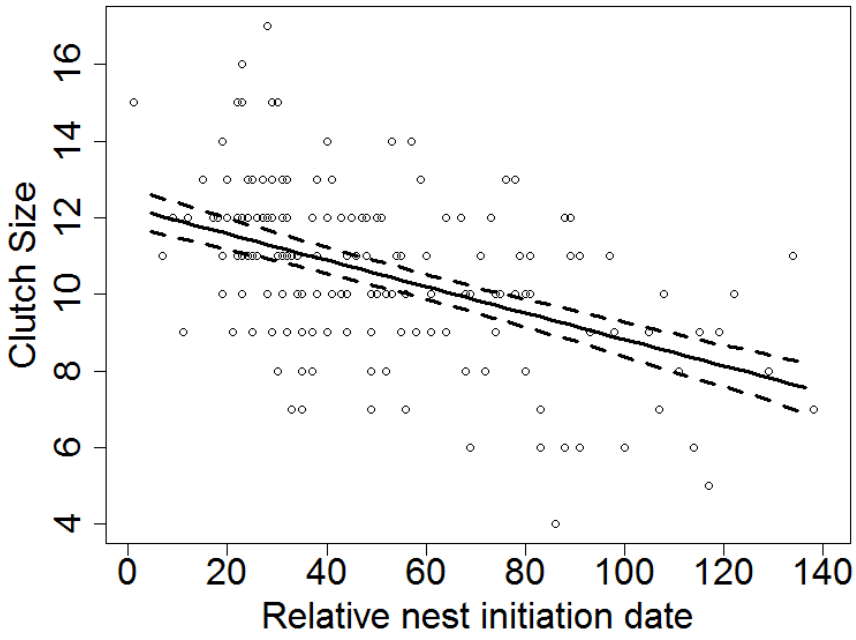

Figure 3.12 – Predicted clutch size (number of eggs) in relation to relative nest initiation date (day 1 = 15th July) of after-second year females equipped with implant transmitters, in Southland and Waikato, 2014–2015. Dots = raw values; dashed lines = 95% CI.

Predicted mean egg volume of 292 nests of marked (Implant = 175; P&S = 71) and unmarked (n = 46) females was 55.5 cm^3 (SD = 4.2) and was best explained by transmitter effects (e.g., whether bird was implant female or not), clutch size, and year (β_{Clutch} = 0.39, SE = 0.11; $\beta_{Transmitter}$ = 1.62, SE = 0.49; β_{2015} = -0.89, SE = 0.48; Tables 3.7, A2.12). Egg volume decreased with clutch size (Figure 3.13), was ~1.0 cm^3 smaller in 2015 than in 2014, and was 2 cm^3 smaller for implant females (Implant: $\bar{x}$ = 54.7 cm^3, SD = 1.1; P&S: $\bar{x}$ = 56.8 cm^3, SD = 1.1; Unmarked: $\bar{x}$ = 56.5 cm^3, SD = 0.6). Effects of initiation date was competitive with clutch size and contained in the second-best model that was within 0.08 AIC_c units of the top model and indicated that egg volume decreased with initiation date (Table 3.7; β_{IDATE} = -0.03, SE = 0.009).

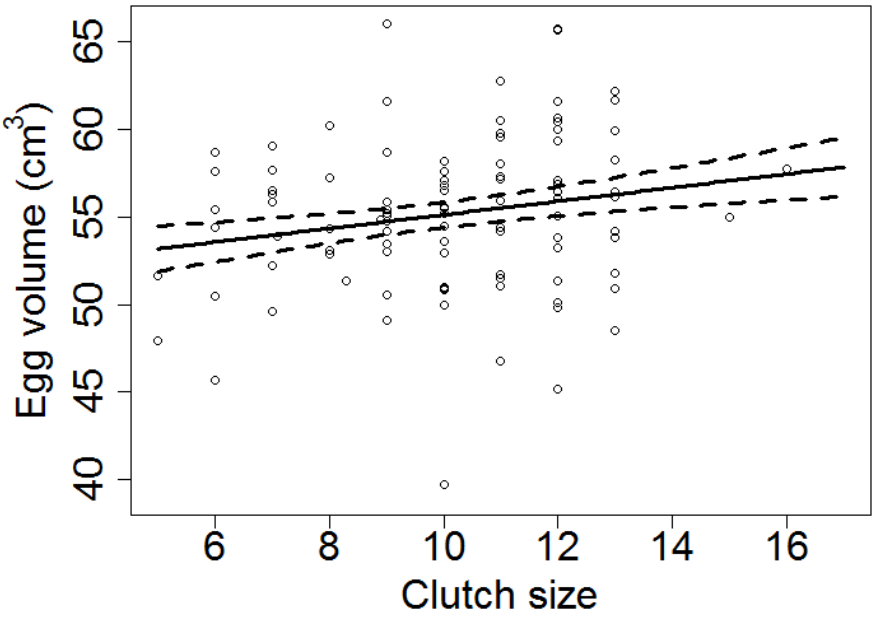

Figure 3.13 – Predicted mean egg volume (0.515 * length * breath^2) per nest in relation to clutch size, for female mallards equipped with implant transmitters, in Southland and Waikato, 2014. Dots = raw values; dashed lines = 95% CI.

Table 3.7 – Model selection results from the analysis of initiation date, incubation length, and clutch and egg size of mallards in Southland and Waikato, 2014–2015. Models were ranked by differences in Akaike's Information Criterion, corrected for small sample size (AIC_c). Number of parameters (*K*) includes the intercept and variance. I present the null model, top-supported (lowest AIC_c) model, and models within 2 AIC_c units of the top model unless they contained uninformative parameters.

Model	*K*	ΔAIC_c[a]	w_i[b]	Deviance
Initiation date				
Age + Condition + Size + Site + Year	7	0.00	0.43	1410.73
Age + Condition + Site + Year	6	0.85	0.28	1413.80
Null	2	37.82	0.00	1459.19
Incubation length				
Site	1	0.00	0.75	148.32
Null	2	4.37	0.08	152.59
Clutch size				
Initiation date + Age + Transmitter type	4	0.00	0.76	1243.91
Null	2	95.80	0.00	1345.87
Egg Volume				
Clutch size + Transmitter type + Year	5	0.00	0.31	1638.83
Initiation date + Transmitter type + Year	5	0.08	0.29	1638.91
Initiation date + Transmitter type	4	0.56	0.23	1641.47
Clutch size + Transmitter type	4	1.41	0.15	1642.32
Null	2	24.92	0.00	1668.97

[a] Differences in AIC_c relative to the model with the lowest value.

[b] Model weight.

3.4.8 Nest-site Selection

Vegetation density and composition measurements were collected at 425 nest sites and 915 random points. Females selected nest-sites that had greater amounts of vegetation density (Figure 3.14), and higher proportions of sedge and shrub vegetation ($\beta_{DENSITY}$ = 0.18, SE = 0.03; β_{SEDGE} = 1.02, SE = 0.32; β_{SHRUB} = 0.99, SE = 0.24; Tables 3.8, A2.13).

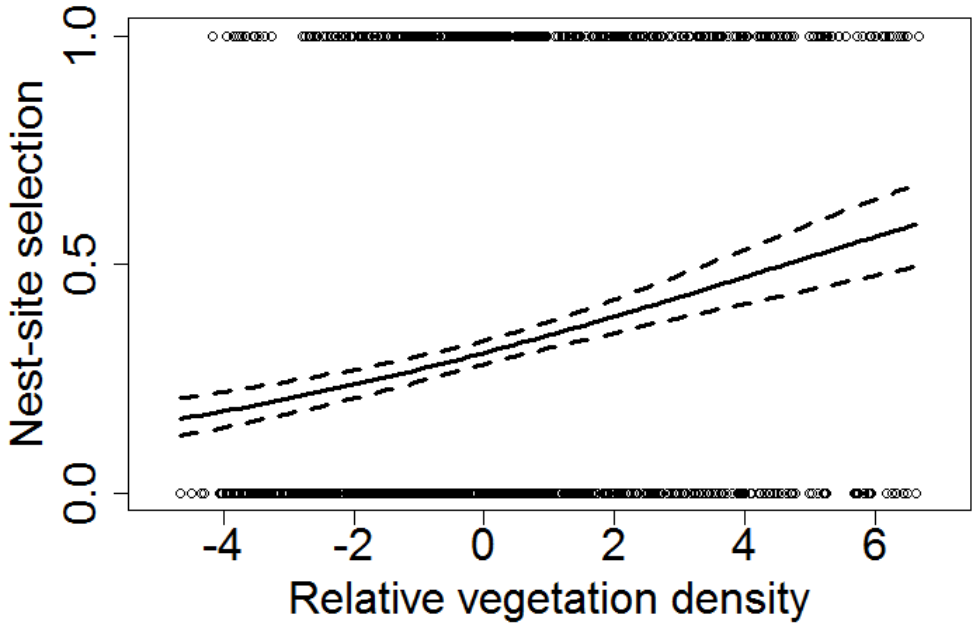

Figure 3.14 – Predicted nest-site selection in response to relative vegetation density at the nest-site, for female mallards in Southland and Waikato, 2014–2015, held at mean covariate values (sedge = 0.05; shrub = 0.14). Dots = raw values; dashed lines = 95% CI.

Analysis of nest-site selection at the 200 m landscape scale included 489 nests and 1000 random points (500 per study site). Nest-site selection at this scale was best described by the proportion of nest habitat within a 200 m radius buffer and the distance to the nearest road and waterbody (β_{Dense_Veg} = 2.36, SE = 0.57; β_{Dist_Road} = 1.41, SE = 0.26; β_{Dist_Water} = -8.41, SE = 0.77; Tables 3.8, A2.14); females selected nest sites that had higher proportions of dense habitat within the 200 m radius buffer (Figure 3.15) and were in closer proximity to road (Figure 3.16) and water habitats (Figure 3.17).

Table 3.8 – Model selection results of nest-site selection of female mallards in Southland and Waikato, 2014–2015. Models were ranked by differences in Akaike's Information Criterion, corrected for small sample size (AIC_c). Number of parameters (*K*) includes the intercept. I present the null model, top-supported (lowest AIC_c) model, and models within 2 AIC_c units of the top model unless they contained uninformative parameters.

Model	*K*	ΔAIC_c[a]	w_i[b]	Deviance
Local scale (1 m^2)				
Veg_Density + Sedge + Shrub	4	0.00	0.98	1561.60
Null	1	101.97	0.00	1669.60
Landscape scale (200 m radius buffer)				
Dist_Road + Dist_Water + Dense_Veg	4	0.00	0.99	1657.70
Null	1	221.52	0.00	1885.21

[a] Differences in AIC_c relative to the model with the lowest value.

[b] Model weight.

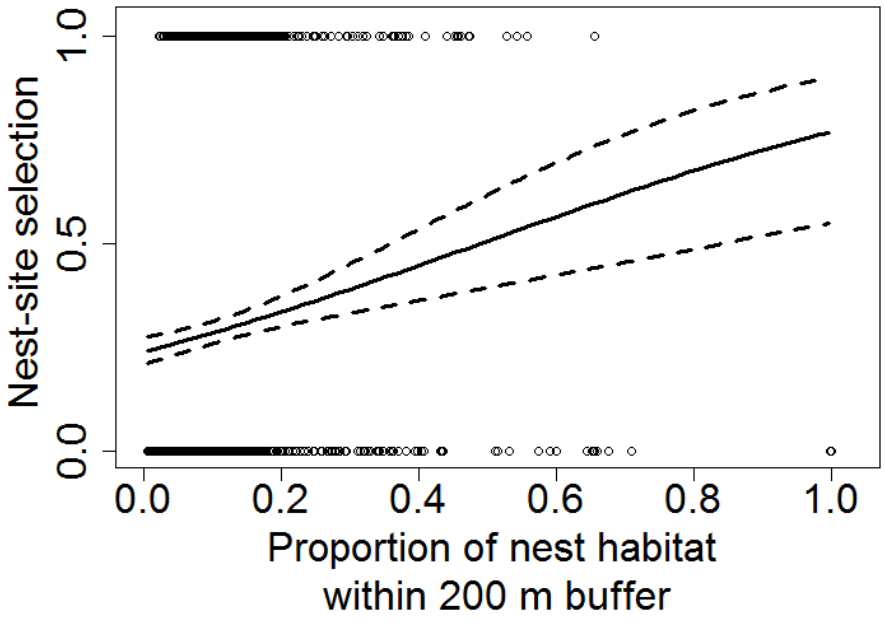

Figure 3.15 – Predicted nest-site selection in response to the proportion of dense habitat within a 200 m buffer radius of the nest-site for female mallards in Southland and Waikato, 2014–2015, held at mean covariate values (distance to nearest road = 298.6 m; distance to nearest water = 109.8 m). Dots = raw values; dashed lines = 95% CI.

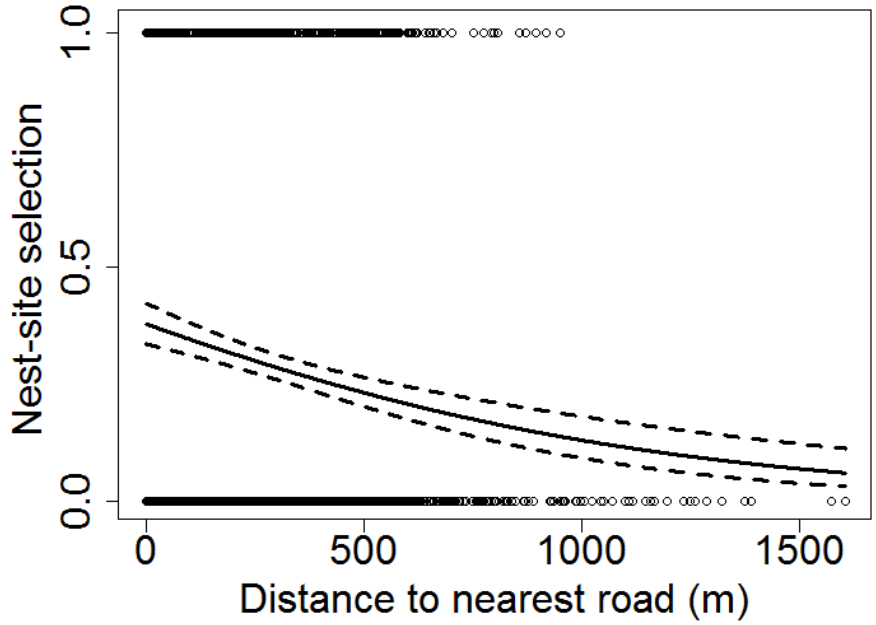

Figure 3.16 – Predicted nest-site selection in response to the distance from the nest to the nearest road for female mallards in Southland and Waikato, 2014–2015, held at mean covariate values (proportion of nest habitat = 0.10; distance to nearest water = 109.8 m). Dots = raw values; dashed lines = 95% CI.

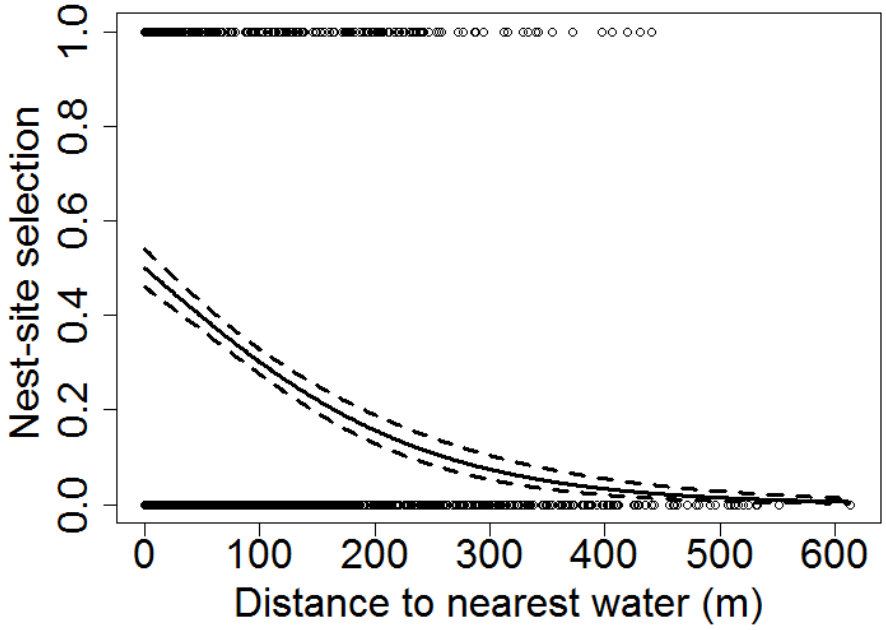

Figure 3.17 – Predicted nest-site selection in response to the distance from the nest to the nearest waterbody for female mallards in Southland and Waikato, 2014–2015, held at mean covariate values (Proportion of nest habitat = 0.10; distance to nearest road = 298.6 m). Dots = raw values; dashed lines = 95% CI.

3.4 Discussion

This study provides the first comprehensive analyses of nesting vital rates and nest characteristics of female mallards in New Zealand. Vital rate estimates provided here of breeding incidence, renesting propensity, egg hatchability, partial depredation, and nest survival greatly improve our understanding of the ecology of mallards and mallard-grey duck hybrids in NZ. These results are important to help inform conservation programs and understand population dynamics. I found that mallards in NZ selected nest-sites which conferred greater reproductive success, such that nest survival increased when birds selected sites with tall, dense vegetation in close proximity to roads. While I was unable to link selection for habitat type to survival, results indicated that females nesting in habitats such as drainage ditches and riparian margins of waterbodies had lower nest success compared to birds that nested along roadsides, hedgerows, or in non-linear habitat types. I also detected a transmitter effect where birds equipped with abdominal implant transmitters tended to have smaller clutch sizes and lower mean egg volume, than nests of unmarked birds or birds captured on the nest during late incubation (P&S females). Possibly, implant transmitters compete with the ovary and oviduct for limited space within the abdominal cavity. Also, effects of site were pronounced, such that nest survival and length of incubation were greater in Southland than Waikato, but nesting occurred earlier in Waikato. Moreover, birds tended to nest earlier in 2014, when renesting propensity and overall mean egg volume was greater. Finally, I found that smaller females were less likely to nest, but older, larger, or better-conditioned females nested earlier, renested more often, and laid larger clutch sizes than did younger, smaller females, in poor body condition.

Land-use practises and management, vegetation composition, predator communities, wetland habitat, and climatic conditions of the agriculturally dominated landscapes in which mallards inhabit year-round in NZ differ dramatically from the Prairie Pothole Region of North America in which a vast majority of research has been conducted on mallard nesting ecology (e.g., Klett et al. 1988, Arnold et al. 1987, Greenwood et al. 1995, Pasitschniak-Arts et al. 1998, Krapu et al. 2004b, Howerter et al. 2008, Arnold et al. 2010, Howerter et al. 2014). Despite introductions from game farming, introgression with native heterospecifics, and different selective pressures from hunting and agriculture, breeding season vital rates of mallards in NZ are comparable to mallards from North America (Table 3.9). Factors affecting renesting propensity were nearly identical to those of Arnold et al. (2010) who found effects of female body condition, initiation date, and previous nesting effort, but reported a

somewhat higher renesting rate of 57% for mallards in North America. Our estimates of nest survival are higher than most studies conducted in North America with the exception of Pieron and Rohwer (2010) who reported cumulative survival rates from 0.36–0.60; but their estimates were derived from sites where mammalian predators had been lethally controlled through trapping. However, in that same study system, survival rates of mallard ducklings were among the lowest ever reported in North America, and researchers found that duckling survival was the primary driver of population growth as opposed to nest survival (Amundson et al. 2013). Population growth rates of mallards may be more affected by duckling survival in systems where nest survival is high (Hoekman et al. 2002, Amundson et al. 2013), and this will be assessed in Chapters 4–5.

Table 3.9 – Mean vital rate estimates for mallards in Southland and Waikato, New Zealand (NZ), 2014–2015 compared to overall mean and a range of estimates from North American studies.

Vital Rate	NZ	North America (mean; range)	References[a]
Breeding incidence	0.91	0.81; 0.54 – 0.96	1–4
Renesting propensity	0.50	0.57; 0.46–0.67	Arnold et al. (2010)
Egg hatchability	0.93	0.90; 0.83 – 0.94	4–6
Partial depredation[b]	0.16	0.37	Ackerman et al. (2003)
Cumulative nest survival	0.43	0.17; 0.09–0.60	1–6
Clutch size	10.1	9.1; 8.6–9.8	1–6

[a] 1–Hoekman et al. (2006a); 2–Coluccy et al. (2008); 3–Devries et al. (2008); 4–Dugger et al. (2016); 5–Ackerman et al. (2003); 6–Howerter et al. (2014).

[b] Proportion of nests that experience at least 1 depredation event, which does not result in nest failure.

Trends between initiation date and female age and condition were similar to those found by Devries et al. (2008), such that females in better condition nested nearly 2 weeks earlier, but SY females nested approximately 4 days later. While average clutch size of first

nest attempts reported here (10.1 eggs) is less than other records reported in NZ (12.4 eggs, Balham 1952; 13 eggs, Williams 1981), it is greater than average clutch sizes of breeding mallards in North America (Table 3.9). Islandic waterfowl tend to lay larger eggs and smaller clutches; generally 2–3 eggs less than ancestral stock (Lack 1970, Rohwer 1988). As mallards were introduced to NZ in 1867, their evolutionary biology may not hold true in this regard. Further, recently released mallards reportedly maintain their large clutch sizes when breeding on oceanic islands (Weller 1980), yet mallards became widely established in NZ > 50 years ago. Possibly, larger clutch sizes in NZ are related to optimal food availability during laying or brood-rearing (Rowher 1992).

Information on adaptive habitat use of mallards in NZ is sparse; mallards reportedly nest close to water, favouring nest-sites in small bushes, at the base of hedges, or in the open amongst tall grass (Williams 1981), but nests in sedges, debris from fallen trees or scrap timber have also been reported (Balham 1952). Aside from the positive response of selection and survival to vegetation density and distance to roads, the adaptive significance of nest-site selection in this study was ambiguous. Survival of nests located along roadsides was nearly twice as high as those along drainage ditches (Table 3.6), but I did not detect selection of these habitat types. Further, mallards selected nest-sites that had higher relative amounts of shrub or sedge habitat within 1 m^2, but again, I did not find selection for these features. Possibly, predators avoid busy roads (Bergin et al. 2000) or prefer to search habitats that are closer to water, which may explain higher nest survival along roadsides but reduced survival along drains and other waterbodies. However, longer overland travel to nearby ponds or drainage ditches may reduce duckling survival (Bloom et al. 2012), thus mallards may nest near drains to improve future brood survival, a stage-specific habitat-selection trade-off which should be evaluated further (Sheppard 2013, Gibson et al. 2016a). Typically, the riparian margin of drainage ditches was half as wide as roadside habitat (Figure A1.1), which may possibly create an exceptionally easy target for predators. I did not relate specific attributes of each habitat type (e.g., width, length, area, mean vegetation height, or vegetation composition) to nest survival because this information was not consistently collected during the course of field work. But understanding how habitat-specific attributes influence predator abundance or use, and the associated effect on nest survival is warranted if nest survival is driving population growth rates of mallards in NZ.

There were 9 degrees difference in latitude (~1,000 km) between our two study sites, and site effects were prevalent such that nesting occurred earlier in Waikato (the lower latitude site), but nest survival was greater in Southland despite longer incubation periods. However, among waterfowl, synchronous nesting over large latitudinal ranges is more common (Wishart 1983, Gurney et al. 2011). Mallards have occupied NZ for over 130 years, providing sufficient time to adjust their timing of breeding to reflect the climatic conditions of the Southern Hemisphere and nest during the warmer months of the year, as they do in their native habitat. Contrary to reports of Cumming et al. (2016) who found that mallards in Africa nested in the middle of Austral-summer (January), mallards in this study tended to avoid nesting in the middle of Austral summer and instead, nested during Austral late-winter or early-spring. Similar to the only other estimate of season length in NZ (130 days; Williams 1981), I reported that the nesting season was 134 days long, but local farmers and hunters have reported mallards nesting as early as March, while others have reported seeing young ducklings in April (Bell 2017). This may be the longest reported nesting season of any wild waterfowl species (Williams 1981), but could be a genetic artefact of the game-farm birds used to establish the population (i.e., captive-reared birds may nest throughout the year). Alternatively, the timing of breeding of mallards in NZ may be in response to expected juvenile food availability in spring and early summer, lower perceived depredation rates during late winter and spring for nesting females and juvenile ducklings, avoidance of overheating while brooding in the middle of summer, or optimal moult period during early to mid-summer (Cumming et al. 2016); hypotheses which should be explored further.

Climatically, Southland is colder and wetter than Waikato. During the 6 months prior to nesting (February–June), the total precipitation and the number of wet days was greater, while the mean monthly temperature and soil moisture deficit was lower, in Southland than Waikato (Table A3.1). Colder temperatures in Southland likely contributed to the delayed onset of breeding and longer incubation periods observed in the study area. Higher amounts of precipitation in Southland post-nesting possibly created optimal food resources for laying females and may explain why female body condition at time of marking, and perhaps nest survival, was greater in Southland. Further, temperatures were warmer in 2014 than 2015, and may explain why birds nested earlier and more often in 2014 than 2015. The annual climate of NZ was near average in terms of rainfall and temperature in 2014, but an El Niño event occurred in June 2015, which resulted in a below normal year for rainfall; this was reflected in drier than normal soil moisture levels and above normal sunshine for most of the

country (NIWA 2016). Nest failure due to flooding did not occur in our study, which is what Williams (1981) attributed as the cause of failure for 25% of first nests in NZ. Average height of nests above water when measured at nest exodus was 127.9 cm (SD = 147.0), and an increase in water level by 45 cm during nesting would have possibly destroyed 25% of nests that were located along drains or waterbodies (Appendix A1.4). Thus, it is possible that nest failure from flooding is a common event during excessively wet years, which could greatly reduce nest survival rates; such stochastic events should be accounted for in future models which assess population growth rates.

3.4.1 Management Recommendations

Nesting vital rates studied here were most affected by variations in female age and habitat use. Older females had higher breeding effort; they nested earlier, laid larger clutches, and successfully hatched more eggs per nest. Habitat enhancement or predator control programs that target nests or nest predators could improve female survival during nesting and allow more ASY females to successfully reproduce. Nest survival was highest when birds selected nesting sites with relatively greater vegetation density along roadsides, but lower when they nested along drainage ditches. Drainage ditches are typically associated with agricultural land, and the width of the riparian margin and required fencing regimes differs among each region. To improve nest survival, habitat managers should advocate for the additional planting and restoration of native shrubs, sedges, and rank grass in prime nesting habitats. Additionally, during peak nest initiation (late August – late September) managers should discourage disturbance to areas that have been identified as nesting habitats including: i) mowing, spaying, or haying of roadsides; ii) pruning of hedgerows; iii) modification of drains (dredging or spraying); iv) the burning of brush piles; and, v) harvesting of forest lots. Identifying and controlling nest predators may increase female survival during nesting and ultimately improve reproductive outputs. To fully assess how population growth may be constrained for mallards in NZ, other demographic rates including adult female and duckling survival should be fully evaluated and per capita productivity should be determined (sensu Hoekman et al. 2002, but see Chapter 5).

Chapter 4

4. Factors Affecting the Survival and Detection of Mallard Broods and Ducklings in New Zealand

4.1 Introduction

Ideally, game bird managers can use breeding populations and annual recruitment estimates to set harvest regulations or to identify conservation priorities (Cowardin and Blohm 1992). Age ratios of juvenile to adults birds derived from hunting reports (i.e., band returns, diary surveys, Parts Collection Surveys) are useful when estimating fecundity and recruitment and setting management plans (Zimmerman et al. 2010). However, using age ratios from hunting data limits inference about the current population status because: i) numbers that are obtained following a breeding and hunting season provide little information to predict the next years' reproductive output; ii) the number of adult to juvenile birds is a product of numerous fecundity components (i.e., breeding incidence, nest survival, brood survival, breeding season survival) and short-comings of fecundity are not measured; iii) and, age ratios from migratory species are obtained from a mixture of breeding, transitional, and wintering habitats, as such, they are difficult to associate with any single breeding population. For management actions to be effective, estimates of recruitment should be timely, associated with a particular location, and derived from vital rates that have a large influence on population growth rates (Morris and Doak 2002). For gamebirds, offspring survival is one of the most important parameters that affect population dynamics (Clark et al. 2008, Coluccy et al. 2008, Sandercock et al. 2008, Wilson et al. 2012, Dugger et al. 2016). Thus, managers are able to estimate recruitment by measuring ratios of breeding pairs to offspring survival or brood abundance and incorporating this information into population models (Cowardin and Blohm 1992, du Rau et al. 2003). But for waterfowl species, the secretive nature of broods may result in imperfect counts, poor detection probabilities, and biased estimates of productivity or abundance (Cowardin and Johnson 1979, du Rau et al. 2003). Hence, it is essential that researchers are able to simultaneously estimate survival and associated detection

probabilities, especially when results will be used to inform population models or derive annual productivity estimates.

In NZ, hunting seasons and bag limits of waterfowl are based on perceived population size, but managers are beginning to use demographic-based population models to estimate annual productivity, which in turn can be used to modify harvest regulations. Yet, such methods require that managers are able to link vital rates to measurable or predictable environmental factors so they can react to conditions and set regulations accordingly (Singer et al. 2016). Such knowledge enables managers to implement management programs that conserve and promote important habitats, and ultimately improve productivity. For example, research in North America has linked annual variation in waterfowl populations to wetland conditions (e.g., density, cover, and permanency) during the breeding season (Singer et al. 2016). In particular, survival of mallard ducklings improves with greater abundance of seasonal and semi-permanent wetlands (Rotella and Ratti 1992, Pietz et al. 2003, Krapu et al. 2006, Amundson and Arnold 2011, Howerter et al. 2014). Understanding how wetland types influence duckling survival is particularly important if wetland vegetation and water permanency can be managed to benefit broods and ultimately improve population growth rates (Davis et al. 2017).

Agricultural intensification and wetland drainage have reduced the amount of wetland habitat in NZ by around 90%, and recently as little as 5% and 16% of historic wetlands remained on the North and South Island, respectively (Ausseil et al. 2011). Although most of the remaining wetlands are manged by local governments, nearly 60% of land coverage in NZ is comprised of agriculturally dominated rural landscapes, which are privately owned and managed (MacLeod et al. 2008, Ausseil et al. 2011). Within the rural landscape complex, some small ponds (including natural, stock, hunting, or dairy effluent) remain, but most waterbodies are constrained within a vast network of drainage ditches or channelised streams and creeks (Miskell 1993, Nguyen and Sukias 2002). As a consequence of severe wetland depletion, mallards and other native waterfowl, including paradise shelduck and brown teal (*Anas chlorotis*), tend to use damp pastoral areas during brood-rearing (Williams 1979, David and Murray 2002, Garrick et al. 2017). Thus, management actions directed at the maintenance or protection of permanent and semi-permanent wetlands may not confer desired benefits for brood-rearing females if they use these alternative habitats.

In North America, duckling survival is positively related to wetlands that are semi-permanent or temporary and have wide peripheral margins of flooded emergent vegetation (Krapu et al. 2006, Raven et al. 2007, Bloom et al. 2012). In NZ, nearly all wetlands are permanent but ephemeral wetlands become abundant following heavy rain. Within NZ, ephemeral wetlands occur across a range of rainfall zones and temperatures, and the productivity of invertebrate and plant communities may vary with wind, sunlight, soil substrate, and adjacent habitat types (Johnson and Rogers 2003). However, delineation of ephemeral wetlands via remote tools has been inconsistent, so reliable identification and quantification requires arduous field work (Johnson and Rogers 2003, Ausseil et al. 2011). Moreover, predicting the presence and abundance of ephemeral wetlands is difficult due to the dynamic nature of the wetlands and the various factors that influence them (Johnson and Rogers 2003). Therefore, understanding how weather (temperature and rainfall) affects duckling survival in NZ might be a valuable surrogate for water conditions to predict survival rates under certain climatic conditions, which may be used to focus management goals (Singer et al. 2016).

During their first week of life, precocial offspring have underdeveloped thermoregulatory ability and cold, wet weather may increase the chance of hypothermia or result in additional brooding which ultimately reduces feeding time (Sedinger 1992, Krapu et al. 2000, Krapu et al. 2006). For instance, research in North America found that precipitation during the first 3 days post-hatch reduced survival of dusky Canada geese (*Branta candadensis occidentalis*) offspring (Fondell et al. 2008), while cold temperatures reduced survival of mallard ducklings (Howerter et al. 2014). Conversely, survival of white-cheeked pintail (*Anas bahamensis*) ducklings in Puerto Rico was positively related to daily precipitation, which possibly increased cover and access to food amid interspersed vegetation in flooded areas (Davis et al. 2017). In NZ, mallards nest during Austral winter and brood-rearing occurs during Austral late-winter to early-summer, thus some ducklings are hatching during the coldest time of the year. However, NZ has milder weather than North America and possibly more stable food sources for ducklings (Garrick et al. 2017). Although Garrick et al. (2017) reported no effect of precipitation on duckling survival in NZ, their study focused on 1 site during 1 year, did not incorporate effects of temperature, and was designed to test for adverse effects of rainfall (i.e., mean 10 day rainfall was weighted such that it was deemed more important early in life). Yet, in milder climates, precipitation may be advantageous to ducklings (Davis et al. 2017), and this warrants further investigation.

Total brood loss (simultaneous loss of the entire brood) is an important biological component of offspring mortality, but cannot be measured if ducklings or the attending female is unmarked (T. Arnold, University of Minnesota, unpubl.). To avoid underestimation of total brood loss, marked individuals are required to obtain counts (or no counts) of offspring and to account for this heterogeneity. Yet, markers adversely affect duckling survival (Amundson and Arnold 2010) so researchers must mark parents and use tracking techniques (i.e., telemetry) to locate, identify and count surviving offspring. Although fates of individual ducklings are often correlated with brood mates (Amundson and Arnold 2011), knowledge of both brood survival (whether $\geq$1 duckling survived to fledge) and duckling survival (the proportion of ducklings in a brood that survives to fledge) can provide important information to waterfowl managers. Understanding factors that affect total brood loss enable managers to implement programs that result in higher brood survival, whereas duckling survival is required to understand the reproductive output and expected production of females in response to various management strategies. For instance, efficient brood predators (i.e., American mink; *Neovison vison*) may eliminate an entire brood such that attrition from large brood sizes is irrelevant. As such, understanding predator habitats and cycles may help link brood survival to habitat type or landscape composition and provide further justification for management actions (Krapu et al. 2004a). In North America, Krapu et al. (2004a) found that brood survival increased with seasonal wetlands when mink populations were low, but found that during years when wetland conditions were optimal for duckling growth, brood survival remained low due to permanent waterbodies that provided mink refugia. As such, they recommended that waterfowl managers conserve and restore seasonal wetlands while maintaining the dynamic integrity of wetlands. Similarly, Bloom et al. (2012) found that duckling survival rates were greater on seasonal wetlands that had larger, central expanses of open water and wide peripheral rings of emergent vegetation and suggested that duck production could increase if upland management programs were directed in landscapes with abundant seasonal wetlands.

Obtaining successful counts of ducklings requires that the female can be located and that observers are able to see and count all surviving offspring. But, imperfect detection can occur if females leave ducklings during brood-breaks (Raven et al. 2007), or if observers are unable to locate and count all ducklings (i.e., ducklings are hidden, travelling through dense habitats, or temporarily separated). As such, incomplete or counts of zero offspring are obtained, resulting in imperfect detection of broods and ducklings, which may lead to an

underestimate of young that are still alive when they are last surveyed (Lukacs et al. 2004, Brudney et al. 2013). For instance, Brudney et al. (2013) found that chick survival of piping plovers (*Charadrius melodus)* was underestimated by 4% because brood counts were often incomplete, and censoring decisions of uncertain fates led to higher bias. Thus, detection probability should be quantified simultaneously to reduce bias in studies that mark breeding females and rely on resights of unmarked offspring.

In 2014–2015, I initiated a 2-year telemetry study to investigate breeding ecology of mallards on 2 study sites in NZ, of which 1 site-year of these data has already been published (Garrick et al. 2017). Here, I examined effects of female age, brood attributes (e.g., hatch date, brood age), weather (e.g., rainfall and temperature), study site, and year on the daily survival of broods and ducklings. I included effects of female age, site, and year to understand differences and to derive age-specific site-year estimates of cumulative duckling survival, so to parse error into process and random components for use in concurrent productivity models. Additionally, I modelled detection probability of broods and ducklings in response to duckling age and site-year (to represent observer differences) to obtain unbiased estimates of survival. I combine mallards and mallard-grey duck hybrids (hereafter mallards) in this study because they are combined for management and monitoring throughout the country (Rhymer et al. 1994, McDougall and Amundson 2017).

4.2 Methods

4.2.1 Field Methods

During 2014–2015, 304 female mallards were captured from study areas in Southland (46°12’S, 168°20’E) and Waikato (37°55’S, 175°18’E), NZ (Chapter 2 – Figures 2.1, 2.2). Each year, 60 pre-breeding female mallards per study area were captured and marked during June or July and equipped with a 22 g intra-abdominal radiotransmitter (hereafter implant; Model IMP/150, Telonics, Mesa, Arizona, Rotella et al. 1993, Paquette et al. 1997). To monitor survival and to locate nests, females were intensively tracked with hand-held and truck-mounted radio-telemetry systems (Kenward 1987). From late August to early November, nests of unmarked mallards were located using a combination of techniques including beating vegetation with sticks during foot searches and using well-trained pointing dogs. Attending females were captured on the nest during late incubation and equipped with a 9 g back-mounted prong-and-suture radiotransmitter (hereafter P&S; Model LB-66, Telonics, Mesa, Arizona; Rotella et al. 1993, Paquette et al. 1997). Study sites, capture and marking

procedures, and tracking regimes of pre-nesting and nesting birds are described in detail in Chapter 2, Chapter 3 – section 3.2.1 and Chapter 6 – section 6.4.1. Due to the increased risk of mortality, ducklings were not equipped with transmitters or marked for future identification (Krapu et al. 2006, Amundson and Arnold 2010).

When nests were located, eggs were counted, candled to determine development stage (Weller 1956), and measured (length and breadth, to nearest 0.1 mm using electronic or Vernier calipers) to calculate egg volume. Nests were subsequently checked every 7–10 days until fate was determined and the number of eggs was recorded during each visit. Nests were passively checked using telemetry on the estimated day of hatch and every day thereafter until the female and ducklings left the nest (Chapter 2 – section 2.2). Investigators then approached the nest to confirm that the nest hatched and to count the remaining eggs and hatched membranes to determine initial brood size. Following hatch, brood-rearing females were tracked every 1–3 days until the brood was 10 days of age, and then every 5–7 days thereafter until radio loss or failure occurred or the female: died; re-paired or flocked once ducklings were 45 days old or more; lost all the ducklings (e.g., complete brood mortality); or, successfully fledged at least 1 duckling (55–83 days post-hatch). Tracking abruptly ceased for 11 females that went missing before brood loss or a final count could be confirmed and for 2 broods that relocated to restricted land.

During brood observations, investigators used binoculars or spotting scopes to obtain a full count of the surviving ducklings without disturbing the female and brood, but due to the secretive nature of broods and the landscape of the study areas, this was not always possible. At approximately 10, 30, 45, and 60 days of age, or whenever total brood failure was suspected, more invasive techniques (i.e., double observer methods, pushing/flushing broods towards hidden observers, closely approaching and flushing broods, or beat-outs) were implemented in attempt to obtain full counts of the surviving ducklings. Brood observations were classified as: i) full count, if investigator was confident in their count and could clearly see all ducklings present; ii) partial count, if investigator was uncertain of the count, the count was deemed incomplete, or the entire brood could not clearly be seen (i.e., visually blocked by vegetation, landscapes, or other structures); or, iii) mixed count, if ducklings were seen with more than 1 female and brood amalgamation was suspected, but separate counts of individual broods could not be obtained. Additional attempts were made to see the entire brood if a partial count was suspected. If no sighting was obtained, the location of the female was estimated and 0 was logged as the count for ducklings.

4.2.2 Model Structure

I used the exposure interval between two consecutive brood observations as the sampling unit, defined as an observation interval. I created interval-specific observation matrices of offspring counts and covariate information and used a recently developed model structure fitted by a Bayesian framework that simultaneously examines daily duckling and brood survival, and individual duckling and brood detection (T. Arnold, University of Minnesota, unpubl. data). The model is an extension of the Cormack-Jolly Seber model and followed methodologies of Lukacs et al. (2004) such that broods were assumed to be independent and reliably associated with the marked female, but relaxed the assumption that all young are counted at every occasion. Further, the model assumed that: i) broods were closed to immigration (i.e., brood mixing did not occur); and, ii) after accounting for individual covariates, whole-brood mortality and observation failure, individual survival and detection probabilities of offspring were similar for each observation interval (T. Arnold, University of Minnesota, unpubl. data). Further, the model allowed for irregular intervals between counts such that exposure days were equal to the interval size. Interval censoring, whereby the midpoint of the interval is used to calculate exposure days, is frequently used in survival studies but can bias estimates if interval periods are longer than a few days (Dinsmore et al. 2002).

I estimated interval-specific brood and duckling survival by treating consecutive brood observations as intervals. If a brood survived a given observation interval, then survival was reflected as interval-specific individual duckling survival, whereas if the brood failed during the interval (i.e., complete brood loss during a single event), individual duckling survival was irrelevant. If at least 1 duckling survived, brood detection probabilities were modelled using a single Bernoulli trial (0 = brood not seen; 1 = brood detected), and the probability of detecting an individual duckling was the product of brood and duckling detection probability. This method permitted the use of staggered survival data, irregular interval lengths, and incomplete or missed brood counts (i.e., inability to detect all or some of the surviving offspring).

Covariates were chosen *a priori* based on previous research (see section 4.2.3). I used daily survival rates and detection probabilities to determine cumulative survival to 30 and 45 days post-hatch. Models were implemented using JAGS (Plummer 2003) run through jagsUI (Kellner 2015) in R*3.3.0 (R Development Core Team 2015). I assigned uniform priors from 0.5 to 1 for daily brood and duckling survival rates or 0 to 1 for brood and duckling detection

probabilities; priors for survival and detection parameters were set on the real scale and then transformed to the logit scale (e.g., logit (S) = log(S/(1-S)). I assigned covariates to uniform priors in the interval -2 to 2 (logit scale), and continuous covariates were standardised to have mean = 0 and SD = 1 to aid in model convergence. I ran 50,000 iterations of 3 MCMC chains and removed the first 5,000 iterations as burn-in. The posterior distribution was calculated from every fifth iteration (i.e., thin rate = 5), thus the joint posterior was determined from 27,000 samples. I assessed model convergence by visually inspecting trace plots and ensuring all $\hat{R}$ values were < 1.1 (Gelman and Rubin 1992). I defined supported covariates as those with coefficients that had 95% credible intervals that did not overlap zero.

4.2.3 Brood and Interval-specific Covariates

For each survival and detection parameter for broods and ducklings, I included biologically relevant covariates reported to influence duckling and brood survival rates or detection probabilities in similar studies (Table 4.1). Ducklings are most susceptible to mortality early in life and a strong relationship between brood age and survival has been consistent in the literature (Talent et al. 1983, Gendron and Clark 2002, Bloom et al. 2012, Garrick et al. 2017). Thus, I included brood age as a covariate for all model parameters. I considered female age as after-second year (ASY) or second year (SY) in my analysis because older females may be more attentive to broods and some studies have linked female age to duckling survival rates (Gurney et al. 2012, Garrick et al. 2017). I was unable to confidently classify the age of 5 brood-rearing females (~2.6%) because wing or bursal characteristics were not recorded or were indeterminate. Rather than remove these birds from analyses, I ran 2 separate models and pooled unknown aged birds with ASY and SY females, respectively. Differences between resultant model parameters were negligible ($\leq$ 0.02), so I present results of the latter model that combines unknown-aged females with SY females because deviance information criteria (DIC; Spiegelhalter et al. 2002) value was 20.7 units lower for this model. In North America, offspring survival is often positively related to earlier hatch dates (Dzus and Clark 1998, Amundson and Arnold 2011, Brudney et al. 2013; but see Howerter et al. 2014). Although Garrick et al. (2017) found no effect on hatch date for brood survival in Southland, I examined hatch date effects using a larger sample size collected over multiple sites and years to confirm this result. I determined seasonal hatch date relative to 1st September (first day of Austral spring and the day before the earliest hatch date recorded for this study). I included site and year in the analysis of duckling survival to evaluate potential

site and year-specific differences and to obtain separate site-year estimates for estimating process variation in Chapter 5.

Table 4.1 – Brood and interval-specific covariates used to evaluate brood and duckling survival and detection.

Parameter	Brood-specific covariates	Interval-specific covariates
Daily brood survival	Hatch date	Brood age
Daily duckling survival	Female age, site, year	Brood age, rainfall, temperature
Brood detection	Site, year	Brood age
Duckling detection	—	Brood age

For each observation interval, I determined the: i) number of ducklings observed; ii) number of days between observations (interval length); iii) age of the brood at the beginning of each interval; iv) mean lowest daily temperature (°C), averaged across interval length; and, v) mean daily rainfall (mm), averaged across interval length. I was interested in evaluating interval-specific rainfall and temperature because inclement weather may be detrimental to young broods (Bloom et al. 2012) but rainfall might provide additional food and cover in regions with milder temperatures (Davis et al. 2017). Daily records of precipitation and minimum air temperature were obtained from the National Climate Database (National Institute of Water and Atmospheric Research Ltd, 2015, cliflo.niwa.co.nz), using data collected from the nearest weather station for each study site (Southland: Winton2, Agent no. 5768; Waikato: Hamilton Aws, Agent No. 2112).

Survival rates and resultant productivity estimates are biased when detection probabilities are low (Cowardin and Blohm 1992), because ducklings that are not observed are assumed not to be dead or non-existent. As such, it is essential that researchers incorporate detection probabilities when estimating offspring abundance or survival rates to measure productivity (Lukacs et al. 2004, Pagano and Arnold 2009). Brood size tends to decrease with brood age because of high duckling mortality rates during the first 10 days of life (Bloom et al. 2012), so I included duckling age as a covariate for both individual and total brood survival. I expected that individual ducklings would be more difficult to detect at younger ages because of their small size and cryptic nature (Walker et al. 2013), but that the brood would be more readily detected shortly after hatch because larger brood sizes increase detectability (Pagano and Arnold 2009). Further, brood detection can vary with observer

experience, time of day, brood size, weather, and habitat types (Pagano and Arnold 2009). Identification of observers conducting brood observations was not recorded during the first year of the study, so I was unable to test for observer-specific differences in detection. Instead, I tested for effects of site and year because observers varied by site-year, additional training was provided in 2015, and each year the most experienced observers were generally based in Waikato. I dismissed weather effects from my *a priori* predictions on detection probabilities because of similar rainfall during brood-rearing among sites and years (Appendix 3 – section A3.2), and weak or equivocal results between weather variables and detection probabilities from previous research (Giudice 2002, Pagano and Arnold 2009).

4.2.4 Data Censoring and Considerations

I combined 2 broods that became and remained amalgamated throughout the entire brood-monitoring phase and treated them as a single large brood because: i) they had the same hatch date; ii) telemetry data indicated that the 2 implant females remained together from capture until the end of the study; iii) nests were within 4 m of each other; and, iv) although individual broods could not be discriminated, adequate counts and information on the mixed-brood was obtained throughout the brood-rearing period. I censored all records of a 3rd brood which amalgamated with other unmarked brood(s) immediately following hatch because reliable counts could never be obtained. Aside from the 3 broods that mixed immediately following hatch, only 3% of observations reported brood-mixing. I censored counts of temporary brood amalgamations if it was impossible to obtain a reliable count of each brood. Four broods became habitually mixed after 41 or more days of age, so I right-censored these data to include only the observations prior to brood amalgamation (n = 8 observations). Eight females died during brood-rearing: 5 had ducklings < 21 days old at time of mortality; 2 were found dead at brood age 30, but were last reported alive at brood age 24 and 26 days, respectively; 1 died at brood age 60. Gendron and Clark (2002) reported survival of ducklings abandoned from 23 days of age, thus if a female died during brood-rearing, I assumed complete brood loss if ducklings were younger than 23 days. To evaluate detection, I retained partial counts and zero counts (i.e., no ducklings observed because of total brood loss or failed detection) in my analysis.

4.3 Results

My analysis included 175 radiomarked female mallards (Implant = 123; P&S = 52; ASY = 90; SY = 80; Unknown age = 5), 190 broods (i.e., 15 females had 2 broods each), 1780 ducklings ($\bar{x}$ = 9.3 per brood; SD = 2.6; range = 2–15, excluding amalgamated brood of 18), and 2,243 observations or attempted observations of broods. Mean number of observations per brood was 11.8 (SD = 5.7, range = 1–24) and the average interval between observations was 1.5 days (SD = 0.8; range = 1–9) for broods < 10 days old and 4.5 days (SD = 2.4; range = 1–24) for broods > 10 days old. Mean age of successful broods at cessation of tracking was 56.2 days (SD = 11.9, range = 30–83). Excluding the amalgamated brood that had 14 surviving ducklings, the average number of surviving ducklings detected in final brood observations was 3.7 (SD = 2.6, range = 1–10) and total brood loss was reported for 101 females including 5 females that died during brood-rearing when ducklings were < 21 days post-hatch. Mean lowest temperature and rainfall during observation intervals was 6.8°C (SD = 3.0; range = 1.9–14.6°C), and 3.2 mm (SD = 4.1 mm; range = 0–58.6 mm), respectively.

Mean daily brood survival was 0.9816 (95% CI: 0.9746–0.9875) and 30-day and 45-day cumulative brood survival was 0.50 (95% CI: 0.39–0.61) and 0.43 (95% CI: 0.31–0.57), respectively. Daily duckling survival ranged from 0.9536 (95% CI: 0.9409–0.9643) for SY females in Waikato in 2015 to 0.9688 (95% CI: 0.9610–0.9756) for ASY females in Southland. Brood and duckling survival both increased with duckling age (Figure 4.1). Cumulative duckling survival was higher in Southland than Waikato and older females had higher duckling survival rates (Table 4.2); thus, daily duckling survival was greatest for ASY females in Southland but lowest for SY females in Waikato (Figure 4.2). Duckling survival was unaffected by year, rainfall, or temperature and brood survival was not related to hatch date (Table 4.3). Overall, detection probability of ducklings was 0.77 (95% CI: 0.75–0.79) while detection of broods differed by site and year such that brood detection probabilities were lowest in Southland in 2014, but greatest in Waikato in 2015 (Table 4.4). Finally, detection of individual ducklings decreased with duckling age (Figure 4.3), whereas detection of broods increased with age (Table 4.3).

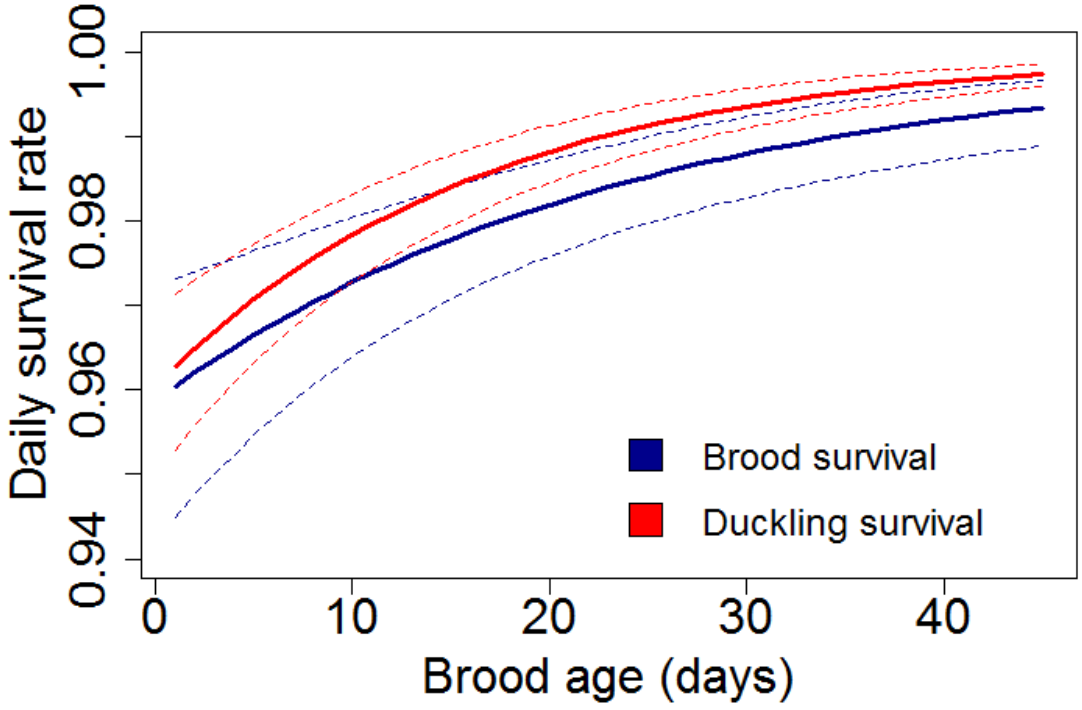

Figure 4.1 – Daily survival rate of broods (averaged over sites, years, and age class) and ducklings (after-second year females in Southland 2014), in relation to brood age. Dashed lines = 95% CI.

Table 4.2 – Mean posterior 30-day and 45-day cumulative duckling survival ± associated standard deviation for after-second year (ASY) and second-year (SY) female mallards in Southland and Waikato study areas in 2014–2015 in response to brood age.

	Southland		Waikato	
	30 day	**45 day**	**30 day**	**45 day**
ASY 2014	0.30 ± 0.04	0.25 ± 0.04	0.21 ± 0.04	0.17 ± 0.04
ASY 2015	0.29 ± 0.04	0.24 ± 0.04	0.20 ± 0.04	0.16 ± 0.04
SY 2014	0.25 ± 0.04	0.20 ± 0.03	0.17 ± 0.04	0.13 ± 0.04
SY 2015	0.25 ± 0.04	0.20 ± 0.03	0.16 ± 0.04	0.12 ± 0.0.3

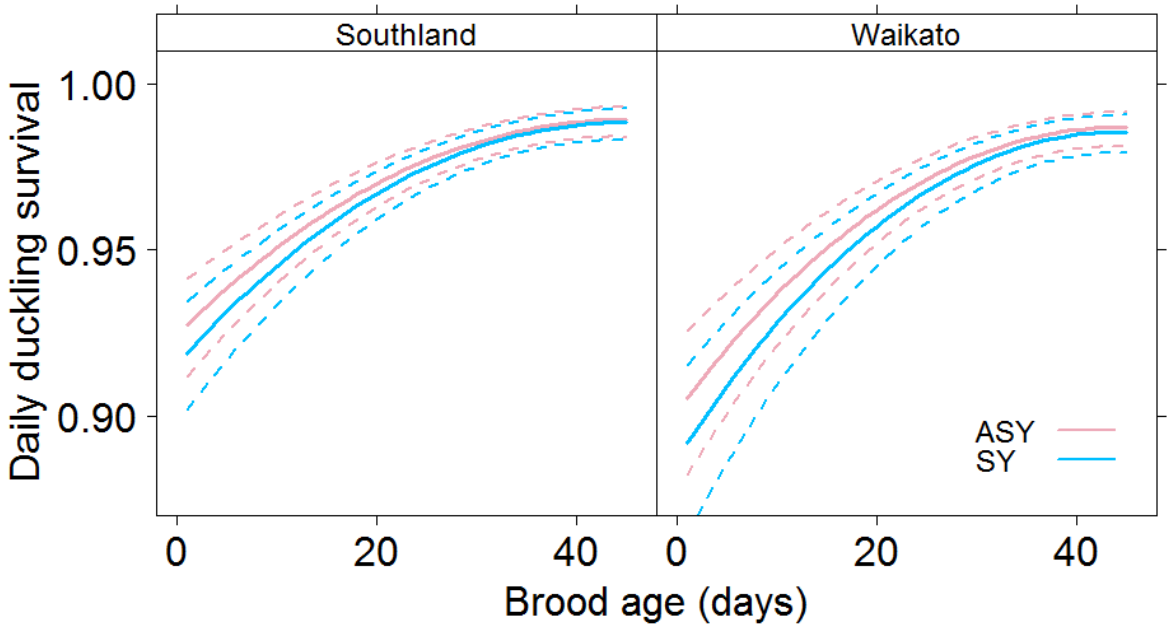

Figure 4.2 – Daily duckling survival for after-second year (ASY) and second-year (SY) female mallards in Southland and Waikato study areas in 2014–2015, in response to brood age. Dashed lines = 95% CI.

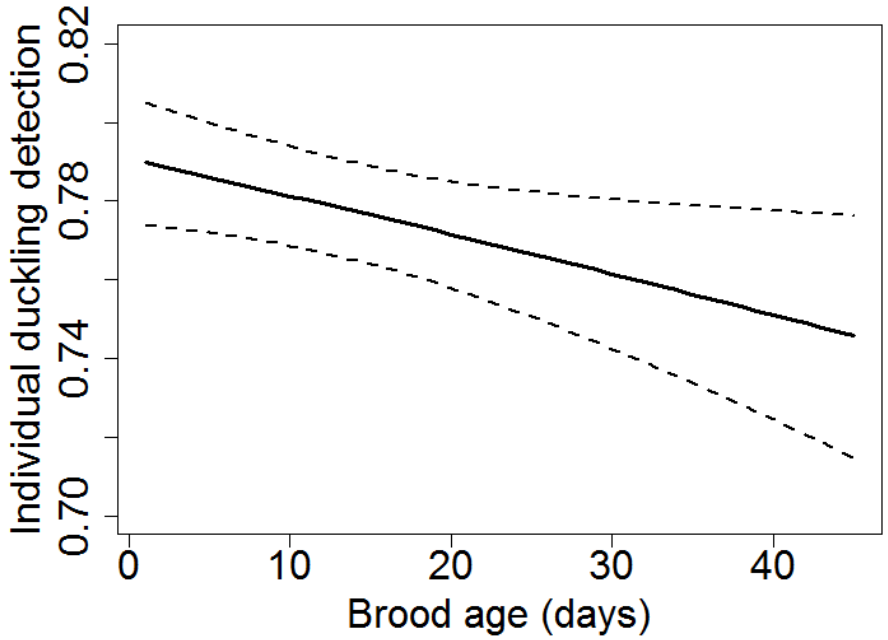

Figure 4.3 – Probability of detecting individual ducklings in relation to brood age in Southland and Waikato study areas in 2014–2015. Dashed lines = 95% CI.

Table 4.3 – Posterior mean and 95% confidence intervals for logit-scale model parameters used in the evaluation of duckling and brood survival and detection.

Parameter	Posterior Mean	LCI	UCI
Duckling Survival			
Intercept	2.676	2.292	3.070
Brood age	0.062	0.051	0.075
Female age (SY)	-0.231	-0.399	-0.0650
Site (Southland)	0.512	0.303	0.725
Year (2015)	-0.0559	-0.224	0.110
Rainfall	0.015	-0.015	0.047
Temperature	-0.0037	-0.049	0.043
Brood Survival			
Intercept	3.240	2.920	3.574
Brood age	0.0422	0.0263	0.0600
Hatch date	-0.0748	-0.295	0.149
Duckling detection			
Intercept	1.327	1.230	1.424
Brood age	-0.0055	-0.0101	-0.0005
Brood detection			
Intercept	1.179	0.922	1.441
Brood age	0.0032	-0.0043	0.0108
Site (Southland)	-0.635	-0.892	-0.380
Year (2015)	1.017	0.758	1.284

Table 4.4 – Mean posterior brood detection probabilities and lower (LCI) and upper (UCI) confidence intervals.

Site	Year	Mean	LCI	UCI
Southland	2014	0.65	0.60	0.69
Southland	2015	0.84	0.80	0.87
Waikato	2014	0.78	0.73	0.82
Waikato	2015	0.91	0.88	0.93

4.4 Discussion

This study is the first to evaluate duckling and brood survival of mallards in NZ while accounting for detection probabilities. I found that duckling survival increased with brood age and was higher for older females, but was not related to hatch date or precipitation. These results are consistent with the only other study on duckling survival in NZ (Garrick et al. 2017), and their data has been incorporated and reanalysed here alongside 3 additional site-years of data. Similar to previous studies, brood and duckling survival increased with brood age (Talent et al. 1983, Gendron and Clark 2002, Hoekman et al. 2004, Bloom et al. 2012). Conversely, effects of female age on duckling survival has been ambiguous; some studies found similar effects of increased survival among older females (e.g., Gurney et al. 2012), while others found no relationship (Krapu et al. 2000, Hoekman et al. 2004, Bloom et al. 2012). Possibly, older females are more experienced and better able to direct their ducklings to abundant food sources that optimise growth, or they are more effective at evading predators. Alternatively, Bloom et al. (2012) hypothesised that in North America older females might breed earlier and resultantly have higher duckling survival. However, this hypothesis does not fit well in NZ given that I detected no relationship between hatch date and survival. In North America, studies on many avian species found positive effects of earlier hatch dates on brood survival but this appears to be most pronounced at northern latitudes where wetland conditions fluctuate annually (Dzus and Clark 1998). Brood-rearing habitats within NZ probably have more stable food sources due to a milder climate and may explain why survival rates are consistent throughout the season (Garrick et al. 2017). Finally, inclement weather may be detrimental to duckling survival (Bloom et al. 2012), or conversely, rainfall may benefit ducklings by creating favourable brood-rearing habitat in tropical climates (Davis et al. 2017). However, duckling survival was not related to interval-

specific weather variables in this study, which may also be a reflection of the milder climate and stable food sources (Garrick et al. 2017). Thus, rainfall and temperature patterns may not be a suitable method for predicting offspring survival and/or productivity of mallards in NZ.

Duckling survival rates reported here are among the lowest reported for mallards. Cumulative duckling survival to 30-days post-hatch ranged from 0.16–0.30, which is within the range reported by Amundson and Arnold (0.07–0.34; 2011), who reported some of the lowest duckling survival rates of mallards in North America. Other North American studies have reported 30-day duckling survival rates from 0.33–0.58 (Pietz et al. 2003, Hoekman et al. 2004, Bloom et al. 2012). Low duckling survival reported here may result from different predator assemblages, unproductive brood-rearing habitat, or inadequate food sources. Amundson and Arnold's (2011) low estimates yielded from a study system where nest predators were trapped and removed but brood predators such as raptors and mink were not controlled. Causes of duckling-specific mortality in NZ are unknown, although during this study I witnessed duckling depredation by Australasian harriers and the killing of ducklings by pukekos. Further, stoats, weasels, ferrets, and feral cats are abundant within NZ and are known predators of waterbirds (O'Donnell et al. 2015) and future research should evaluate the effectiveness of predator control. The 45-day brood survival estimates presented here are similar to those reported by Dugger et al. (0.50; 2016) who found that broods in Washington, USA used unproductive drainage ditches and linear features with low vegetation cover. Broods in NZ use similar habitats (Chapter 2; Appendix 1 – section A1.5), but the quality of these habitats were not measured here. However, linking duckling and brood survival to habitat selection would provide useful management recommendations and should be considered in future studies.

Higher duckling survival in Southland may be related to differences in habitat, predator communities, or food sources. Although habitat composition appeared similar between study areas (Chapter 2 – Table 2.1), habitat use by brood-rearing females may have differed. For instance, Garrick et al. (2017) found that brood use of abundant ephemeral wetlands in Southland was positively related to duckling survival. Ephemeral wetlands were uncommon in Waikato and instead, brood-rearing females tended to use effluent or stock ponds and drainage ditches. Predator communities or available food required for duckling growth may differ among waterbody type and may explain the site-specific difference in duckling survival that were observed in this study; hypotheses which should be explored further. Also, Garrick et al. (2017) found that duckling survival in Southland was negatively

related to the proportion of dense habitat (i.e., hedgerows and margins of road, drains and wetlands) within brood habitats. Composition of brood-rearing habitat within Waikato has not yet been quantified, but observed differences in duckling survival might be explained if higher proportions of dense habitat exists within brood-rearing habitats in Waikato.

The main benefit of this model was that it adjusted survival estimates for imperfect detection, as opposed to assuming perfect detection or adjusting incomplete counts based on subsequent surveys (i.e., Brudney et al. 2013). Studies that estimate survival without accounting for imperfect detection may bias brood survival low (Brudney et al. 2013). Indeed, Garrick et al. (2017) reported that in areas without ephemeral water, duckling survival of ASY and SY females in Southland in 2014 was 0.26 and 0.11, respectively. Although they used different covariates, I used nearly the exact same data (i.e., I did not censor as many broods because I was able to account for imperfect detection) and reported that in Southland in 2014, duckling survival was 0.29 and 0.24 for ASY and SY females, respectively. Brood detection probabilities reported here (range = 0.65–0.91) are greater than those reported by Pagano and Arnold (2009) who detected 0.30–0.35 of unmarked mallard broods, and 0.50–0.60 of unmarked broods of diving ducks. However, broods in their study were unmarked and used wetlands with abundant emergent cover, whereas observers in this study had a good idea of where to look for radiomarked broods even if they were not currently visible and most brood were observed using drainage ditches or pastureland (Appendix 1 – Section A1.5); habitats that might increase detection because of inadequate cover. Detection in response to habitat use was not assessed here but could inform waterfowl managers about the effectiveness of ground-based brood-surveys if they are used as a tool for measuring productivity in the future (Pagano and Arnold 2009). Although brood monitoring protocols were consistent among sites and years, observer experience and training regimes differed, which likely attributed to the differences in brood detection among site-years. These results are consistent with Pagano and Arnold (2009) who found that detection probability of experienced observers was 0.11 higher than for inexperienced observers. Observers in Southland in 2014 were the least experienced and received little to no training, as such, detection probabilities for that season were the lowest of any site-year. These results support recommendations of other researchers that highlight the importance of measuring observer-specific detection probabilities and advocate that adequate training be provided to ensure consistency among personnel conducting counts on cryptic offspring (Giudice 2002, Pagano and Arnold 2009).

4.4.1 Management Recommendations

These results demonstrate that duckling survival is low in NZ, which may have important implications for population growth; a population demographic model will be constructed in Chapter 5 to assess this impact. Management actions aimed at improving duckling survival (e.g., predator control or habitat enhancement) should be implemented consistently and effectively throughout the brood-rearing period (September–December in this study) because survival rates appear constant during this time (i.e., no hatch date effect), although emphasis should focus on the peak brood-rearing period (September–November). Predator control can be costly and may not always improve duckling survival rates (Amundson et al. 2013), so the effectiveness of prolonged predator control programs should be examined before widespread applications are implemented. On-going habitat and enhancement programs should focus on promoting adaptive brood-rearing habitat. In North America, seasonal and semi-permanent wetlands that have peripheral rings of emergent vegetation are beneficial to broods (Bloom et al. 2012). Until the adaptive significance of brood-rearing habitats have been assessed in NZ, waterfowl managers should advocate against wetland drainage such that ephemeral wetlands are created during wet periods, while also promoting planting of semi-aquatic (i.e., emergent) vegetation. Finally, high brood detection probabilities illustrated here suggest that brood counts might provide a reliable field measure when estimating recruitment and setting hunting regulations. Thus, if managers wish to calculate annual productivity from brood: pair ratios, then detection among common habitats should be assessed and a standardised roadside survey should be created that will allow mangers to incorporate these detection probabilities into the study design (Pagano and Arnold 2009).

Chapter 5

5. Productivity of Mallards in New Zealand

5.1 Introduction

Mallards were introduced to NZ in the late 1860's for sport-hunting (Dyer and Williams 2010). The eventual wide-spread establishment of mallards in NZ resulted from the release of 25,000 individuals during 1940–1960 and the extensive hybridisation and introgression with the native grey duck (Williams and Basse 2006, Dyer and Williams 2010). Today, mallards and mallard grey-duck hybrids (hereafter mallards) are a culturally valued game species and the most abundant and widely harvested game bird in the country (Williams 1981, Caithness 1982, Robertson 2007, Dyer and Williams 2010). Because it is difficult to differentiate mallards and grey ducks from hybrids (Guay et al. 2014) they are combined for managing and monitoring purposes (Rhymer et al. 1994, McDougall and Amundson 2017). Also, mallards are the primary driver of game bird license sales (McDougall and Amundson 2017), attracting approximately 40,000 hunters and generating an average $2.6 million in license sales annually (R. Sowman, NZ Fish and Game, pers. comm.). New Zealand Fish and Game Council is a non-profit organisation that is government-mandated to protect habitats and sustainably manage populations of game birds and freshwater sport fish. Season lengths and bag limits are based on perceived population trends and are independently set by 12 self-governing regional councils that comprise Fish and Game (McDougall and Amundson 2017). However, few regions have successfully established long-term banding or monitoring programs, thus little is known about the population dynamics of mallards in NZ (McDougall 2012). To effectively manage populations and ensure harvest rates are set appropriately, waterfowl managers need to estimate annual production (Krapu et al. 2006).

Stage-specific vital rate information (e.g., clutch size, egg hatchability, survival of females, nests, and offspring) can be used to inform demographic population models and determine population growth rates (λ; Morris and Doak 2002). Sensitivity and elasticity analyses can identify which vital rates have the greatest influence on population growth and

provide a basis for developing biologically sound management and conservation initiatives (Coluccy et al. 2008, Dugger et al. 2016). Further, life-stage simulation analysis can incorporate process variation of vital rates and simulate how sensitivity and elasticity vary across parameters (Hoekman et al. 2002). In North America, sensitivity analyses of mallard populations highlight the importance of female survival, duckling survival, and nest success on population growth rates (Coluccy et al. 2008, Howerter et al. 2014). For instance, in the Great Lakes Region of North America, high sensitivities of population growth rates to survival of non-breeding females and ducklings warranted management of populations through harvest regulations, but also emphasised the importance of wetland protection, enhancement, and restoration of brood-rearing habitats (Coluccy et al. 2008). Conversely, population dynamics of Mid-continental mallards in North America are most sensitive to changes in nest success and female survival during the breeding season, so conservation initiatives are directed at grassland management and enhancement of nesting habitats (Reynolds et al. 2001, Hoekman et al. 2002). For conservation programs to be effective, it is necessary that wildlife managers direct efforts to improving vital rates that have the most influence on population growth. Currently, waterfowl managers in NZ are unsure whether conservation efforts should focus on habitat enhancement and restoration that may improve survival of nests and/or ducklings, or if hunting regulations should be adjusted to allow more females to survive the hunting season. Incorporating vital rate information into a perturbation analyses will greatly improve the current understanding of population growth rates of mallards in NZ and will highlight effective management regimes.

During 2014–2015, I conducted a 2-year study to investigate factors that influenced the survival of female mallards, nests, and ducklings in NZ. During this time, 304 female mallards were radiomarked and tracked for up to 10 months each year to examine breeding season vital rates. Results suggested that mallards in NZ tend to have relatively high nest survival (Chapter 3), whereas duckling survival is low (Chapter 4; Garrick et al. 2017). Further, McDougall and Amundson (2017) reported that high hunting rates reduced survival of second-year females, which may reduce recruitment into the breeding population. Currently, it is unknown if high nest survival rates can offset lower duckling survival rates, or whether breeding success of older females can sufficiently compensate for low survival of second-year females during hunting. Thus, my objectives were to synthesise vital rate estimates from Chapters 3 and 4 with annual survival information derived from ongoing banding programs to: i) develop a stage-based demographic population model to estimate

age-specific population growth rates; ii) identify vital rates that have the greatest influence on population growth based on analytic sensitivity; iii) determine how sensitivities of vital rates varied across parameters using life-stage simulations; and, iv) recommend options to increase mallard populations.

5.2 Methods

5.2.1 Field Methods

From June 2014 to January 2016, pre-breeding and nesting female mallards were captured throughout 2 study sites in NZ and intensively radio-tracked to monitor the survival of females, nests, and ducklings. One site was located on the South Island, approximately 30 km north of Invercargill in Southland (46°12'S, 168°20'E) and the other site on the North Island, approximately 20 km south of Hamilton in the Waikato (37°55'S, 175°18'E; Chapter 2 – Figures 2.1, 2.2). Each year, approximately 60 female mallards per study site were equipped with a 22 g intra-abdominal radiotransmitter (hereafter implant; Model IMP/150, Telonics, Mesa, Arizona, Rotella et al. 1993, Paquette et al. 1997). From late August to early November, roadsides, riparian edges of drainage ditches, lakes, ponds, and other suitable nesting habitats were searched to find nests of unmarked mallards. Unmarked nesting females (n = 61) were captured on their nest during late incubation and equipped with a 9 g back-mounted (prong-and-suture) radiotransmitter (hereafter P&S; Model LB-66, Telonics, Mesa, Arizona; Rotella et al. 1993, Paquette et al. 1997). During marking, females were aged as after-second year (ASY) or second-year (SY) based on cloacal examination (Hochbaum 1942) and wing feather characteristics (Carney 1992).

The day following transmitter deployment, implant females were radio-tracked every 2–3 days using hand-held and truck-mounted radio-telemetry systems (Kenward 1987) to determine the onset of nesting and to monitor nesting behaviour and female survival. Once located, nests were subsequently checked every 7–10 days until fate was determined and the number of eggs was recorded during each visit to determine clutch size, hatching success, and initial brood size. Following hatch, brood-rearing females were tracked every 1–3 days until 10 days post-hatch and every 5–7 days thereafter until brood fate was known. Following failure of nests or broods, females were tracked weekly to detect renesting attempts and to monitor survival. All females were tracked until they died, left the study area, or the transmitter no longer emitted a detectable signal following a weakening pulse rate. Study areas, capture and marking techniques, and tracking regimes are described in detail in Chapter 2, Chapter 3 – section 3.2.1, Chapter 4 – section 4.2.1, and Chapter 6 – section 6.4.

5.2.2 Model Structure

I developed a female-based matrix model ($\boldsymbol{A}$) derived from age-specific vital rate estimates and a pre birth-pulse census where, F and S represent mean age-specific fecundity and survival probabilities for ASY and SY females, respectively:

$$\boldsymbol{A} = \begin{bmatrix} F_{SY} & F_{ASY} \\ S_{SY} & S_{ASY} \end{bmatrix}$$

Variance of an estimate is comprised of both true biological variation (σ_p, process variation) and sampling error (SE), the latter which results from measurement error (Burnham et al. 1987). Because this study took place at 2 sites, over 2 years, I was able to decompose site-year means and associated variances of each parameter into sampling and process components using variance decomposition procedures (White 2000) implemented in JAGS (Plummer 2003) run through R*3.3.0 (R Development Core Team 2015). For each vital rate (excluding clutch size), I assigned uniform priors from 0 to 1 for the mean and from 0 to 0.3 for σ_p and SE; given only 4 site-years, estimates of σ_p were affected by very vague priors. Thus, I used semi-informative priors based on previous research on mallards in North America such that my priors were at least three times larger than process variation reported for various vital rates by Hoekman et al. (2002), Coluccy et al. (2008), and Howerter et al. (2014). For clutch size, I assigned uniform priors of the mean from 0 to 20 (biologically realistic based on mallard ecology) and 0 to 0.6 for σ_p and SE. I ran 6,000 iterations of 3 Markov chain Monte Carlo (MCMC) runs simultaneously, and removed the first 1,000 iterations as a burn-in. The posterior distribution was calculated from every second iteration (i.e., thin rate = 2), thus the joint posterior was determined from 7,500 samples, and mean and process variation were derived for each vital rate (Table 5.1). I assessed model convergence by visually inspecting trace plots and ensuring all $\hat{R}$ values were < 1.1 (Gelman and Rubin 1992).

Annual survival (Sa) is a product of breeding (Sb_i) and non-breeding survival (Sn_i), and in NZ breeding and non-breeding seasons comprise approximately 6 months of the year. Thus, I obtained estimates of age-specific (i) annual survival rates from 15 years of mark-recapture banding data in the Waikato Region (McDougall 20012, M. McDougall, Eastern Fish and Game, unpubl.) and similarly decomposed estimates to obtain mean and process variation (Table 5.1). Because there are no long-term banding programs in Southland, I

assumed that survival estimates from Waikato were representative of both regions. I then calculated mean non-breeding survival as:

$$Sn_i = {}^{Sa}/_{Sb_i}$$ (Hoekman et al. 2002),

and process variation of non-breeding survival as:

$$Sn_{\sigma p} = \frac{\sqrt{(Sa^2_{\sigma p} - (Sn^2 * Sb^2_{\sigma p}))}}{(Sn^2 - Sb^2_{\sigma p})}$$ (Hoekman et al. 2002),

I then used the values from Table 5.1 to inform a beta or normal (clutch size only) distribution, conducted a Monte Carlo simulation of 10,000 replicate sets to generate a distribution of parameter estimates, and calculated 10,000 estimates of age-specific fecundity using the following equations:

$$F_i = [0.5 * cs * e * Sd * h * Sp * Sb\ ], \text{ and}$$

$$h = hs' + hs"$$

Whereby:

0.5 = presumed offspring sex ratio (Johnson et al. 1987),

$cs =$ clutch size,

$e =$ egg hatchability, the proportion of eggs that hatch within successful nests,

$Sd =$ duckling survival rate to 60 days post-hatch,

$h =$ hatched nests per breeding female,

$hs' =$ the proportion of females that hatched 1 nest,

$hs" =$ proportion of females that hatched 2 nests (i.e., producing a second brood given complete failure of the first brood),

$Sp =$ post-fledging survival rate from 60 days post hatch until 15 July (start of next breeding season),

$Sb =$ breeding season survival rate of females.

Table 5.1 – Means and process variation of age-specific vital rates used to investigate population growth rates of after-second year (ASY) and second year (SY) mallards in New Zealand.

Parameter	Mean	Process Variance
Clutch Size		
ASY	10.273	0.153
SY	9.660	0.159
Egg Hatchability		
ASY	0.925	0.018
SY	0.936	0.021
Proportion of females that hatched 1 nest		
ASY	0.848	0.052
SY	0.714	0.064
Proportion of females that hatched 2 nests		
ASY	0.157	0.091
SY	0.109	0.074
Duckling Survival (45 day)		
ASY	0.201	0.061
SY	0.165	0.058
Post-fledging Survival		
ASY	0.506	0.011
SY	0.509	0.011
Breeding Survival		
ASY	0.741	0.063
SY	0.832	0.042
Annual Survival		
ASY	0.51	0.005
SY	0.57	0.006
Non-breeding Survival		
ASY	0.689	0.063
SY	0.689	0.063

For each of the 10,000 replicate sets, I calculated the population growth rate (λ) as the product of age-specific breeding season survival (Sb_i) and non-breeding survival (Sn_i) plus the number of surviving female recruits (F_i):

$$\lambda_i = (Sb_i * Sn_i) + F_i$$

I obtained estimates of clutch size, egg hatchability, and duckling survival from marked females for each site in each year (see Chapters 3 and 4). Females tend to gradually leave ducklings from 45 days post-hatch which creates difficulties in obtaining counts and survival estimates to 60 days post-hatch (Talent et al. 1983). As such, I assumed that 45 day survival estimates obtained from Chapter 4 were representative of 60 day duckling survival. This assumption was reasonable given that daily duckling survival increased with age (Chapter 4) and previous research reported little mortality between 30- to 45-days post-hatch (Rotella and Ratti 1992). All other fecundity parameters were determined from implant females that were tracked throughout the breeding season (i.e., I did not consider 3 birds that were on restricted land, 5 birds that died from capture-related mortality, or 12 birds that went missing prior to 15th July). I censored an additional female that was shot in Southland in 2014 during the on-going hunting season in July. Although hunting during breeding could cause additive mortality, the duration of the Southland season has since been reduced and hunting beyond 15th July is no longer typical throughout NZ.

I used generalised linear models (GLM) to examine hatched nests per female and breeding-season survival. I modelled response variables using a binomial distribution with a logit link and incorporated effects of age, site, and year to aid in the decomposition of process variation. To determine post-fledging survival, I used estimates of annual survival of hatch-year females (0.32; derived from Waikato banding data) to determine a constant daily survival rate ($DSR = Sa^{(1/365)}$), which I applied to the total number of days from fledging (60 days post-hatch) to the start of the next breeding season (15th of July), defined as ($Dpfledge$). Thus, brood-specific post-fledging survival was calculated as: $DSR^{Dpfledge}$. This method allowed me to accommodate the large variation in hatch dates (range = 12th August –3rd January) and resulted in a distribution of rates, which I incorporated into the GLM.

Approximately 25% of females who experience brood failure renested (Chapter 3 – section 3.4.2), so I defined hatched nests per female as the number of hatched nests per radiomarked female that survived the nesting season. This method assumes a maximum of 2

broods and allows successful renesting only if the first brood failed, thus it was a combination of females that hatched 1 nest *(h')* and those that hatched 2 nests *(h")*. For my analysis of *h'*, I censored 15 females that went missing during the breeding period, 3 females who abandoned their only detected nests due to investigator disturbance, and 35 birds that died during nesting or brood-rearing (their failure to produce offspring was captured by including breeding season survival as a component of fecundity – see Hokeman et al. 2002). For analysis of *h"*, I censored females that were unable to renest because they died during brood-rearing (n = 7) or if brood fate was unknown (e.g., female went missing, unable to track due to land restrictions, transmitter no longer emitted a detectable signal following a weakening pulse rate; n = 10).

I defined the breeding season from 15th July (earliest onset of nesting) to 15th January (time when most birds had finished brood-rearing). During this study, nest initiation beyond November was not detected, so I assumed non-brood-rearing females that went missing (or transmitter no longer emitted a detectable signal following a weakening pulse rate) after 1st December (n = 11) were moulting at sites outside the study area and had survived the breeding-season. I also considered two females that died after they successfully fledged ducklings but before 15th January to have survived the breeding season because they were known recruiters. However, I censored females that went missing during 15th July–1st December for which final fate could not be determined (n = 20), unless they had already hatched a brood (e.g., hatched nests per female was already known; n = 3).

The fecundity equation represented the pathway by which individuals are recruited as breeding females in the following year (SY stage) and the model represented the functional relationship between each time step (Figure 5.1). Juvenile females enter the SY age-class at their first breeding season and SY females enter the ASY age-class at their second breeding season. I assumed that females that died during the breeding season contributed nothing to recruitment, thus only females that survived the breeding season could contribute to the fecundity equation (although the two aforementioned females which died after successfully fledging ducklings were an exception). This method avoids confounding nest or brood failure with female mortality during breeding and does not require corrections to compensate for underestimation of fecundity (Hoekman et al. 2006b).

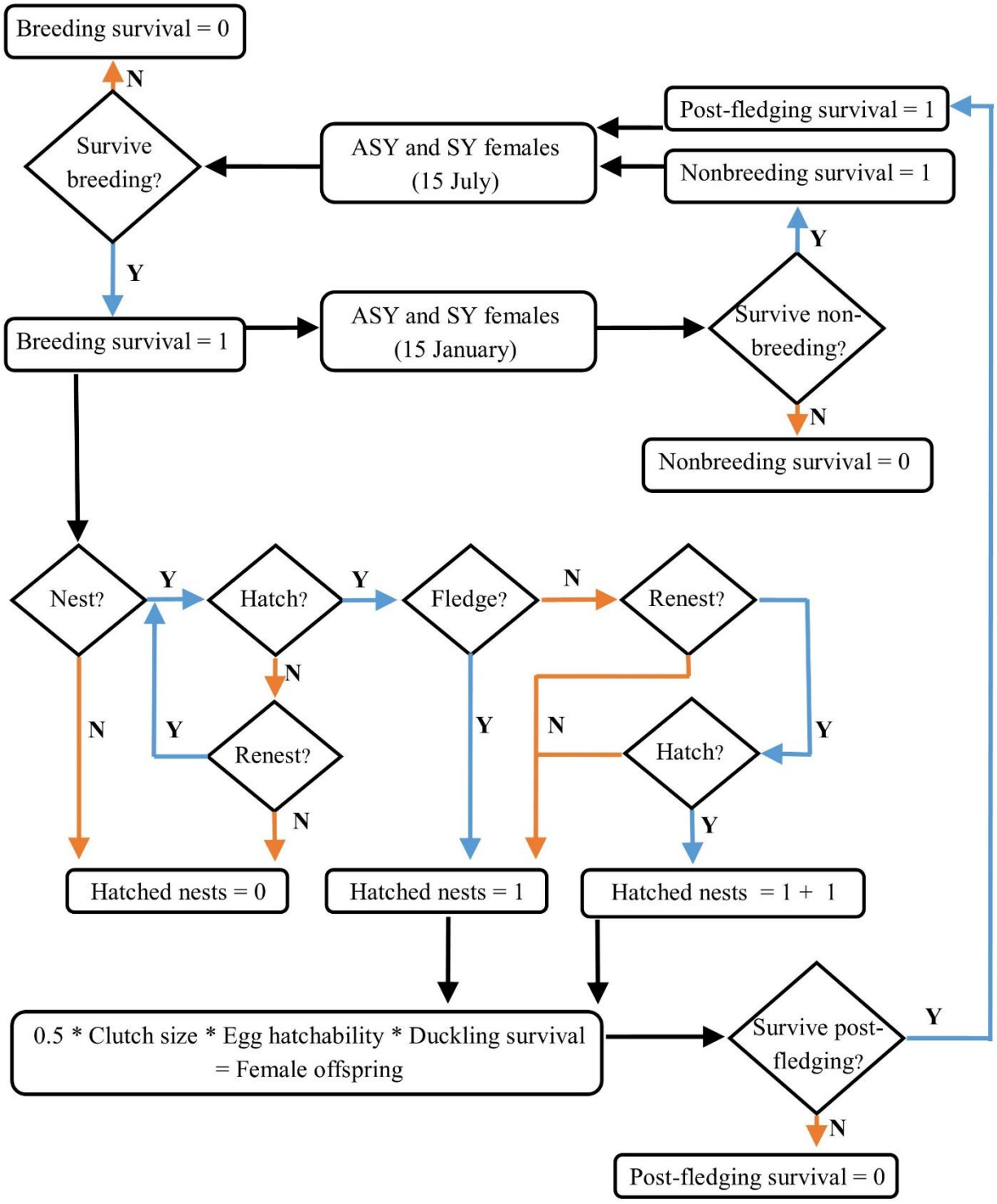

Figure 5.1 – Flow diagram for an age-specific model of mallard females in New Zealand, showing the functional relationship between parameters, where N = no and Y = yes.

5.2.3 Sensitivity and Life-stage Simulation Analyses

I calculated analytic sensitivities for each model parameter to assess the contribution of each vital rate (θ) on λ. Sensitivity is used to describe the absolute rate of change in λ in response to absolute change of a given vital rate, whereas, elasticity is a unit-less measure of the proportional change of λ in response to an infinitesimal proportional change in each vital rate (de Kroon et al. 2000). However, elasticity is uninformative in this model because fecundity is the product of various reproductive vital rates, which results in identical elasticities for each parameter of fecundity. As such, I only consider sensitivity here. I used the 'popbio' package (Stubben and Milligan 2007) in R*3.3.0 (R Development Core Team 2015) to calculate sensitivity for each of the 10,000 replicates of λ, whereby sensitivity was defined as:

$$Sensitivity = \frac{\Delta\lambda}{\Delta\theta}$$ (de Kroon et al. 2000).

I further explored the contribution of influential vital rates on λ by conducting a life-stage simulation analysis (Wisdom et al. 2000). Here, I took the 10,000 replicates of vital rates and resulting λ across their range of process variation and calculated coefficients of determination (r^2). Coefficients of determination indicate the amount of variation in population growth that is attributable to the range of variation in each parameter (Mills and Lindberg 2002, Amundson et al. 2013). I modelled the input range of the most influential vital rate while holding all other vital rates constant at mean values and plotted r^2 as a function of an iterative increase (0.05 interval) to visually assess its contribution to λ (Hoekman et al. 2002, Amundson et al. 2013).

5.2.4 Hypothetical Examples

To aid management initiatives and directions and to understand the practicality of increasing sensitive vital rates through management actions, I created hypothetical scenarios. I recreated 10,000 realisations of λ, whereby mean values of various vital rates were increased by 5% until they approached 1 and were allowed to vary with existing process variation. Given observed life-history variation in mallards, vital rates that approach 1 are unrealistic, but I allowed them to approach this level to illustrate whether or not management actions would be viable (i.e., if λ never equalled one despite excessively high vital rates then management actions may need to be directed elsewhere).

Although other vital rates might increase in response to management actions that target a single vital rate (i.e., enhancement of duckling habitat may improve feeding efficiency of females or create favourable nesting habitat), stage-specific habitat-selection

trade-offs may limit these benefits (Gibson et al. 2016a). Further, duckling predators often differ from nest predators, so predator control programs may only affect 1 vital rate while having minimal effect on other rates. Because it is unknown how other vital rates would respond to changes in a given vital rate without testing for trade-offs, I left all other vital rates and associated process variance constant. Management actions are likely to affect both age classes, however, age-specific effects are unknown. Therefore, I averaged vital rates between age classes. I considered 3 different scenarios that focused on likely management actions in response to results presented here:

1. Increased duckling survival – If efforts were focused on restoration and enhancement of habitats that improve duckling survival or on predator control programs that target duckling predators, then hypothetically, duckling survival rates would increase. To demonstrate this scenario, I averaged duckling survival across age classes and increased it from 0.12 (lowest 45-day cumulative survival reported in Chapter 4) to 0.97.

2. Increased breeding survival – Large-scale predator control programs that target nest predators would improve survival of breeding females but duckling predators may not be affected. To illustrate this scenario, I averaged breeding survival of both age classes and increased it from 0.74 (representative of the lowest mean observed survival rate across age classes) to 0.99.

3. Increased non-breeding survival – Changes to harvest regulations could increase non-breeding survival of females. To mimic this scenario, I averaged non-breeding survival of both age classes and increased it from 0.59 to 0.99.

5.3 Results

Age-specific estimates for clutch size and egg hatchability were derived from Chapter 3 and averaged 10.0 and 0.93, respectively (Table 5.1), while duckling survival estimates were derived from Chapter 4 and averaged 0.18 between age classes. I determined remaining vital rates of 205 (ASY = 90; SY = 107; unknown age = 8) abdominally implanted radiomarked female mallards that were tracked throughout the breeding season. Following censoring, I evaluated the proportion of females that hatched nests (n = 171); probability of hatching one nest averaged 0.77 (SE = 0.06) across age classes. The probability that a female successfully produced a second clutch following complete brood failure was 0.15 (SE = 0.08); 52 females did not renest, whereas 17 initiated another nest, of which 10 hatched at least one egg. I calculated post-fledging survival from 85 females that were confirmed to have successfully raised broods to $\geq$ 30 days post-hatch. On average, the post-fledging period was 218 days (SD = 22.0; range = 158–255) and survival during this time was 0.51 (SE = 0.008). Mean breeding season survival was 0.79 (SE = 0.06). During the 180-day breeding season period, 161 females survived and 43 females died; 26 females died during nesting, 5 during brood-rearing, and 12 during various transition stages (i.e., after failure of nest or brood but before the onset of renesting). Annual survival estimates were obtained from banding data and averaged 0.51 for adult females, which yielded non-breeding survival estimates of 0.69 for both age classes (Table 5.1).

At mean parameter values the matrix took the form:

$$\boldsymbol{A} = \begin{bmatrix} 0.25_{SY} & 0.36_{ASY} \\ 0.57_{SY} & 0.51_{ASY} \end{bmatrix},$$

with λ = 0.84 (95% CI: 0.69–1.03). Sensitivity of λ was driven most strongly by duckling survival, followed by breeding-season survival of ASY females (Table 5.2; Figure 5.2). Sensitivities were moderate for duckling and breeding-season survival of SY females, post-fledging survival of ASY females, and non-breeding survival of both age classes (Table 5.2; Figure 5.2). Sensitivities of remaining vital rates were low and did not exceed 0.23.

Table 5.2 – Mean sensitivity and associated standard deviation (SD) of each vital rate for after-second year (ASY) and second-year (SY) female mallards.

	ASY females		SY females	
	Mean	**SD**	**Mean**	**SD**
Clutch size	0.02	0.004	0.01	0.005
Egg hatchability	0.23	0.05	0.10	0.05
Duckling survival	1.10	0.20	0.54	0.12
Hatched nests per female	0.22	0.04	0.12	0.06
Post-fledging survival	0.42	0.08	0.18	0.10
Breeding survival	0.73	0.07	0.37	0.09
Non-breeding survival	0.48	0.06	0.31	0.06

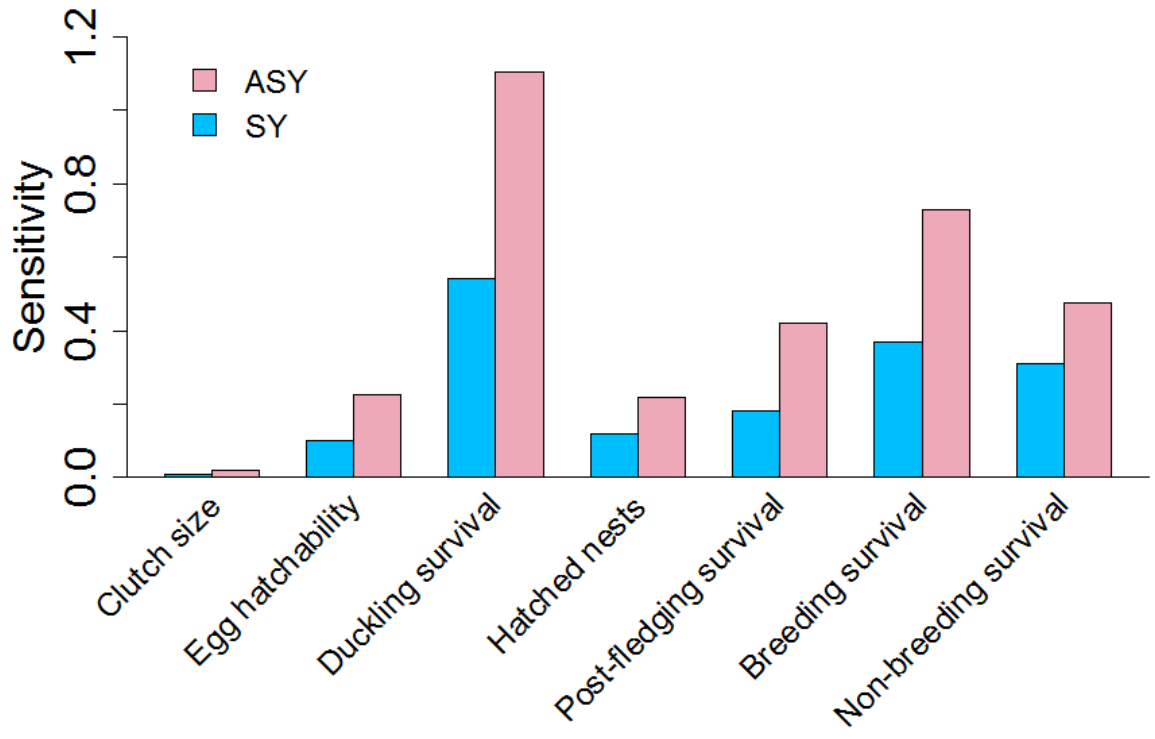

Figure 5.2 – Sensitivity of age-specific vital rates (ASY = after-second year; SY = second year) at mean values.

When I conducted simulations to assess life-table responses, I found that duckling survival of ASY and SY females accounted for 0.61 and 0.14 of variation in λ, respectively. Remaining variation was attributable to hatched nests per ASY females (0.7) and non-breeding and breeding survival of both age classes which accounted for 0.3–0.4 each; all other vital rates contributed little (< 0.02; Figure 5.3). As ASY duckling survival approached its upper limit within its range of process variation, the influence of SY duckling survival on λ plateaued, while the influence of hatched nests per ASY females continued to increase and almost surpassed the importance of SY duckling survival (Figure 5.4). However, the coefficients of determination of other vital rates did not exceed 0.13 (Figure 5.4).

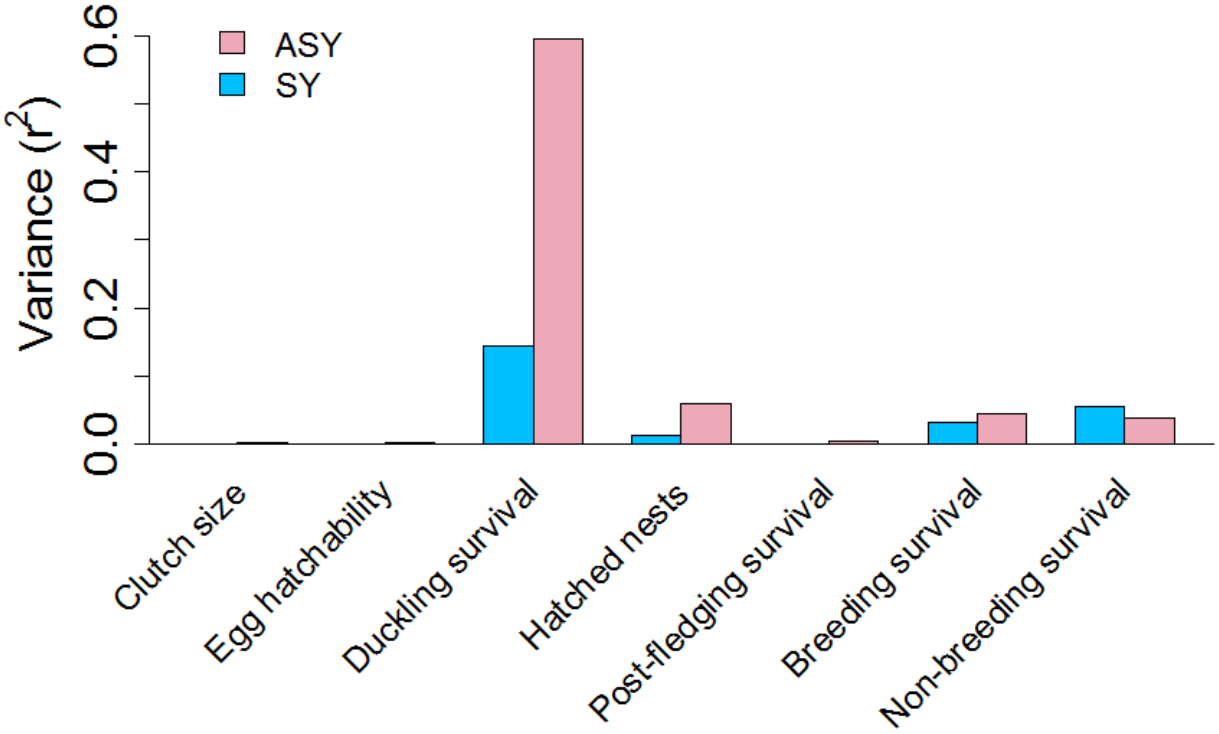

Figure 5.3 – Variance of sensitivity for age-specific vital rates (ASY = after-second year; SY = second year) at mean values.

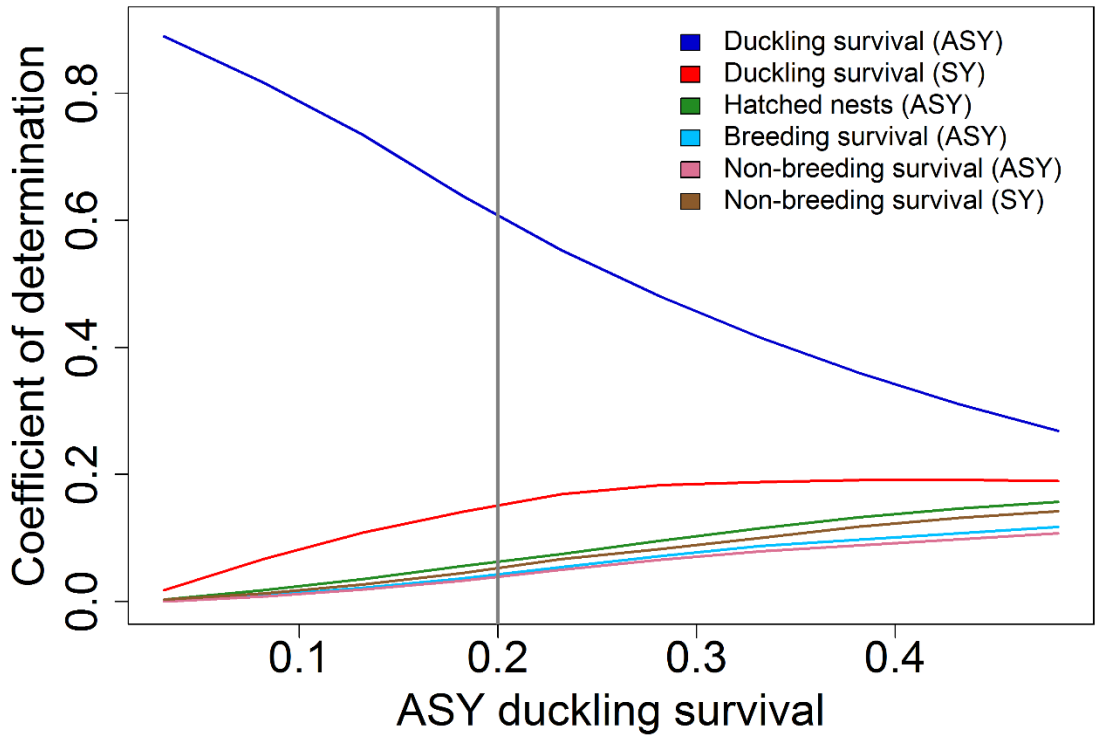

Figure 5.4 – Coefficient of determination with finite population change of the 6 most influential vital rates for mallards in NZ, including duckling survival of after-second year (ASY) and second-year (SY) females and hatched nests, breeding and non-breeding survival of ASY females; as determined from a life-stage simulation analysis conducted across the range of process variation of duckling survival for ASY females. Grey line represented current mean duckling survival of ASY females.

5.3.1 Scenario 1 – Increased Duckling Survival

Given current estimates of duckling survival (0.18 when averaged between age classes), duckling survival would need to increase by 0.14 to 0.28 for mean λ to equal 1 (Figure 5.5).

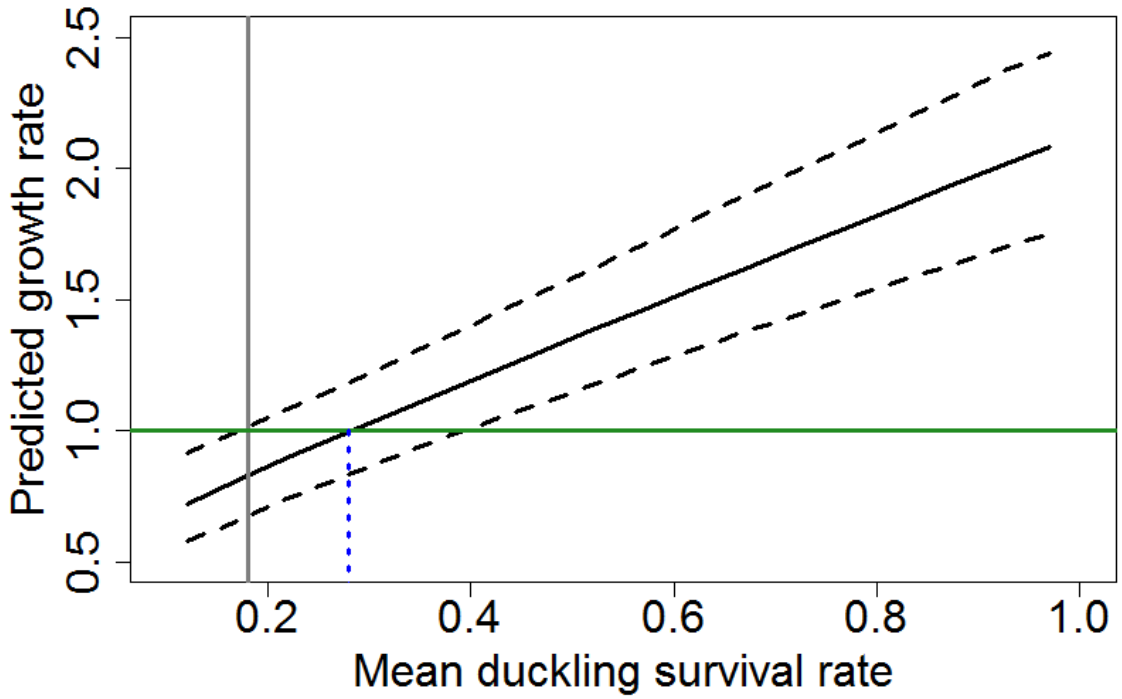

Figure 5.5 – Predicted population growth rate in response to a hypothetical increase in duckling survival averaged between female age classes. Grey line = current duckling survival rate (averaged between female age classes); green line = λ equal to 1; blue dotted line = mean duckling survival needed to reach population stability; dashed lines = 95% CI.

5.3.2 Scenario 2 – Increased Breeding Survival

Increasing mean breeding-season survival between ASY and SY age classes (0.79) to a hypothetical value of 0.91 resulted in a stable population (Figure 5.6).

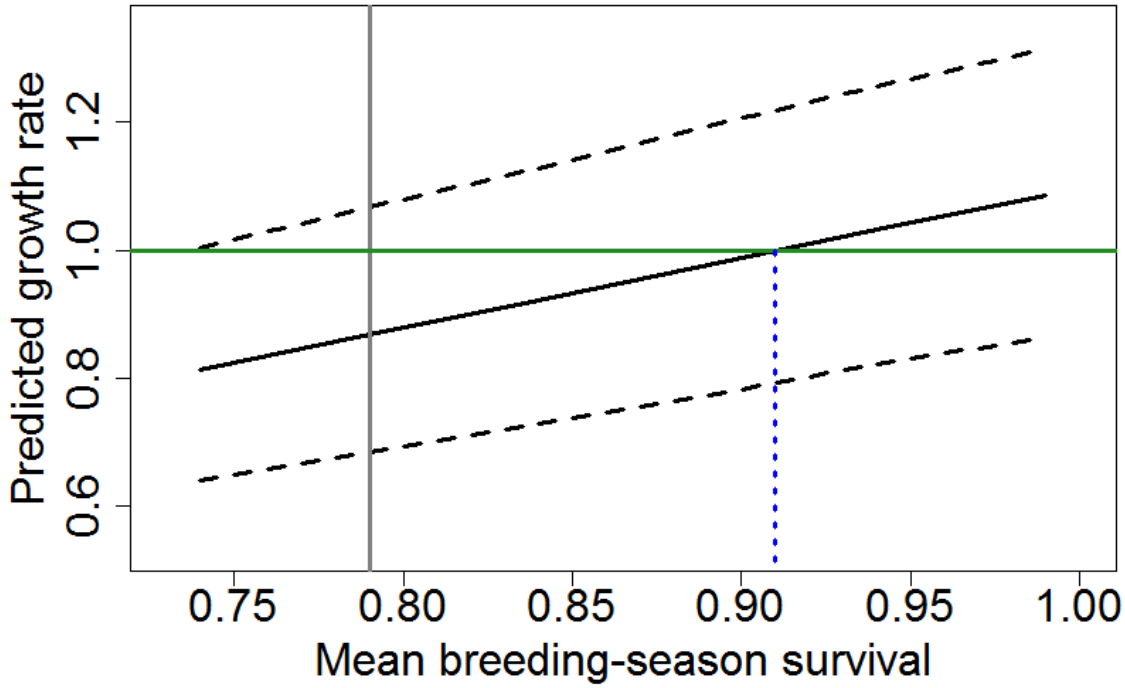

Figure 5.6 – Predicted population growth rate in response to a hypothetical increase in breeding survival averaged between female age classes. Grey line = current breeding-season survival rate (averaged between female age classes); green line = λ equal to 1; blue dotted line = mean breeding-season survival needed to reach population stability; dashed lines = 95% CI.

5.3.3 Scenario 3 – Increased Non-breeding Survival

Manipulation of non-breeding survival resulted in a stable population growth rate when non-breeding survival increased from 0.69 to 0.89 (Figure 5.7).

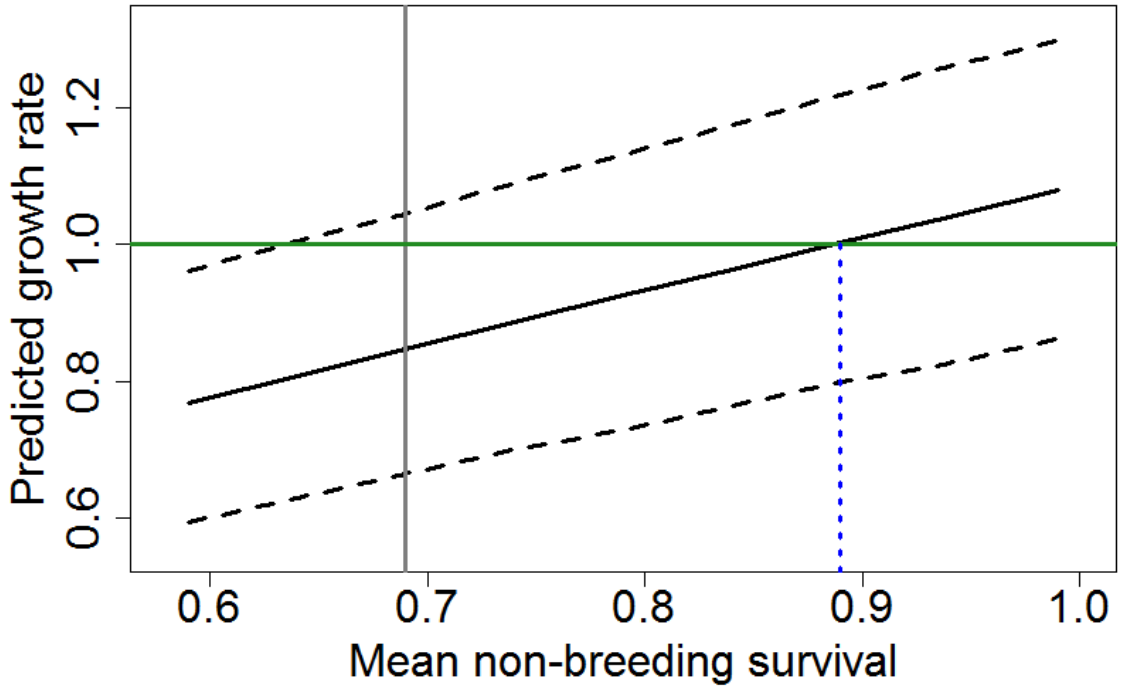

Figure 5.7 – Predicted population growth rate in response to a hypothetical increase in non-breeding survival averaged between female age classes. Grey line = current non-breeding survival rate (averaged between female age classes); green line = λ equal to 1; blue dotted line = mean non-breeding survival needed to reach population stability; dashed lines = 95% CI.

5.4 Discussion

This is the first comprehensive analysis of vital rates and population growth rates of mallards in NZ. I found that fecundity was greater for ASY females, whereas SY females had higher annual survival (because they invested less in reproduction). This resulted in different contributions to population growth such that mean age-specific λ was 0.86 (95% CI: 0.67–1.12) and 0.82 (95% CI: 0.62–1.07) for ASY and SY females, respectively. Overall, model-predicted population growth rates presented here (0.84) implies that the population is decreasing by 0.16 annually, which is lower than what is indicated by banding data or perceived by waterfowl managers (M. McDougall, Eastern Fish and Game, pers. comm.; D. Klee, Auckland/Waikato Fish and Game, pers. comm.). Finally, duckling survival was the most influential factor affecting population growth, followed by breeding season survival of ASY females and duckling survival of SY females. Given the vital rates presented here, a stable (i.e., $\lambda = 1$) population can be reached if duckling survival increased from current estimates of 0.18 to 0.28.

Breeding vital rates presented here are comparable to similar studies of mallards in North America. Mean clutch size is slightly larger, whereas egg hatchability and the proponents that contribute to hatched nests per female (breeding incidence, renesting propensity, and nest success) are within the range reported by North American researchers (Chapter 3 – Table 3.9). Conversely, my estimates of duckling survival (Chapter 4) are among the lowest reported for breeding mallards (Krapu et al. 2006, Stafford and Pearse 2007, Amundson and Arnold 2011) and likely explain the large influence of this vital rate on λ. Birds in this study renested following brood failure (0.15), whereas in North America < 0.01 of females had $\geq$ 1 brood (Arnold et al. 2010). However, intensive renesting and high nest success were not sufficient to offset low duckling survival rates. Further, estimates of breeding survival (0.79) were also similar to those from North America (0.74, Coluccy et al. 2008; 0.77, Howerter et al. 2014; 0.90, Dugger et al. 2016), but annual (0.51) and non-breeding (0.69) survival estimates were lower. For instance, annual survival of implant females in Canada was 0.73 (Arnold and Howerter 2012) and Hoekman et al. (2002) reported annual and non-breeding survival rates of 0.54 and 0.80, respectively. Further, McDougall and Amundson (2017) reported that annual survival in Eastern region was 0.63. As such, low annual survival rates in Waikato resulted in low non-breeding survival rates (i.e., non-breeding survival was calculated from annual and breeding survival). Possibly, prolonged

hunting seasons or persistent hunting pressure may reduce female condition and subsequently affect survival in the Waikato region.

Given comparable estimates of most vital rates, mean estimates of λ presented here (0.84) are within the range reported by studies of mallards in North America (0.82, Hoekman et al. 2002; 0.77, Amundson et al. 2013; 0.95, Howerter et al. 2014; 0.88, Dugger et al. 2016). Although estimates of λ provided by these studies suggested population declines, populations have not decreased due to the migratory nature and cyclic population trends of waterfowl in North America. For instance, estimates provided by Hoekman et al. (2002) and Howerter et al. (2014) were derived using data collected from breeding females in the Canadian Prairie Parklands during 1993–2000, but low production during this time-frame was offset by a large production of ducks that simultaneously occurred within the United States (Williams et al. 1999, Hoekman et al. 2002). Similarly, results of Amundson et al. (2013) were akin with U.S. Fish and Wildlife Service Waterfowl Breeding Population and Habitat Surveys that also indicated population decreases during the time of the study (2006–2007), which were offset by immigration to the study area in subsequent years (Amundson et al. 2013). In New Zealand, mallards are sedentary (McDougall 2012), so immigration from adjacent local populations would need to occur for the population to stabilise. Possibly, population growth rates presented here are biased low due to transmitter effects or are an inadequate representation of spatiotemporal variation. For instance, many of the vital rates that I analysed here were largely based on implant females and may not be fully representative of the unmarked population. Females equipped with abdominal implant transmitters tended to have smaller clutch sizes and lower mean egg volume than nests of unmarked birds or birds equipped with P&S transmitters, suggesting that implant transmitters might compete for oviduct space (Chapter 3). Also, this demographic model was based on data collected over 2 years in 2 sites only, so the full spectrum of variation in vital rates may not be captured here and results may not be representative of long-term trends. Climatically, the first year of the study (2014) experienced near normal rainfall and temperatures, but was preceded by the third-warmest year on record in NZ when drought was common, and followed by another dry year that was also drought-stricken (NIWA 2013, 2014, 2015). Reproductive output and survival rates may differ substantially during excessively wet or dry years (Krapu et al. 2006), and waterfowl managers in NZ believe that wet conditions during 2016–2017 may yield greater reproductive outputs (D. Klee, Auckland/Waikato Fish and Game, pers. comm.). Thus, duckling survival during wet years may be higher than reported here and could explain

why current population trends are inconsistent with my findings. Given the cyclic nature of waterfowl populations, it is likely this study was conducted during years of lower production and higher production in subsequent years could offset the low population growth rates reported here.

In North America, most studies reported that λ was most sensitive to nest, non-breeding or breeding season survival rates of females (Hoekman et al. 2002, Coluccy et al. 2008, Dugger et al. 2016; but see Amundson et al. 2013). Given that sensitivity and life-stage simulation analyses highlighted the importance of duckling survival, management initiatives should focus efforts on promoting duckling survival or investigating factors that decrease or limit duckling growth and/or survival, such as reduced food availability, maladaptive habitat selection, or ineffective anti-predator behaviour. In particular, nutrition greatly influences duckling growth rate, size at fledging, and future life-history parameters (Sedinger 1992). Arguably, there are fewer wetlands in NZ than in areas where mallards have been studied in North America (e.g., the Prairie Pothole Region), and seasonal or semi-permanent wetlands were virtually non-existent during the course of this study. Non-permanent waterbodies are positively associated with abundant aquatic invertebrates and are beneficial to ducklings (Dzus and Clark 1997, Cox et al. 1998, Krapu et al. 2004a, Bloom et al. 2012, Davis et al. 2017). This may explain why Garrick et al. (2017) reported that duckling survival was higher in areas where ephemeral wetlands were present. Further, permanent waterbodies (which are common in NZ) may have higher populations of pest-fish which may compete for food and decrease macroinvertebrate communities (Garrett-Walker 2014, Maceda-Veiga et al. 2017), ultimately reducing duckling growth. During the course of this study, investigators (particularly in Waikato) frequently reported that ducklings were smaller than expected for their age, and mean fledging did not occur until 68.6 days post-hatch (SD = 10.2), which is nearly 19 days later than mean age of fledging of mallards in North America (Ball et al. 1975). Linking duckling growth rates to food abundance of various waterbodies and brood habitats may highlight necessary management actions.

Predator communities in NZ also differ from those in North America. Although predator densities were not quantified during the course of fieldwork, pukeko and Australasian harriers appeared to be prolific and were frequently reported during brood observations. Cats and mustelids are also believed to have been plentiful; they were identified as the primary cause of female mortality (Sijbranda 2015, Sriram 2017) and were likely the predominate brood-predator (Chapters 4). Causes of duckling-specific mortality in NZ are

unknown, but high populations of brood predators may explain similarities between low duckling survival and λ reported here and those reported by Amundson et al. (2013). In the latter study, nest predators were trapped and removed from the study area but brood predators (e.g., raptors and mink) were not controlled, which may have accounted for the low duckling survival rates they observed (Amundson and Arnold 2011). These results led them to report that duckling survival was most influential in a predator-removal study where nest survival estimates were comparatively high (0.60–0.72; Pieron and Rohwer 2010). In NZ, rural landowners trap predators on their own accord (MacLeod et al. 2008), but feral cats, stoats, weasels, and ferrets likely evade most traps. Possibly, increasing bag limits of pukeko could aid in alleviating duckling predators but efforts to contain mammalian brood-predators will also be necessary. As such, cause-specific mortality and the efficiency of predator control should be explored further, because factors that result in 0.10 cumulative mortality of ducklings could be targets for management programs.

The foraging efficiency of predators may be related to landscape characteristics, which may ultimately impact duckling and female survival. Predators thrive in highly-fragmented agricultural areas that have an abundance of linear habitat features (Pasitschniak-Arts et al. 1998, Bergin et al. 2000), whereas expansive fields of grass and numerous wetlands (i.e., as in the Prairie Pothole Region of North America) likely alleviate depredation pressure by providing duck refugia. Further, Garrick et al. (2017) found that duckling survival in Southland was negatively related to the proportion of dense cover (i.e., hedgerows and margins of road, drains, and wetlands) within brood habitats, and nesting and brood-rearing females frequently used linear drainage ditches during the course of this study (Table A1.2). As such, drainage ditches may be an ecological trap for brood-rearing females (Schlaepfer et al. 2002), and the adaptive significance of these and other well-used brood-rearing habitats (i.e., effluent ponds, pasturelands) should be quantified.

The survival of females during the breeding and non-breeding periods were also integral components of mallard population growth, suggesting that waterfowl managers should also direct efforts at promoting female survival rates. Females are most susceptible to depredation during nesting so the most effective management option is to target nest predators (Pieron and Rohwer 2010, Arnold et al. 2012). Of the 42 females that died during the breeding period in this study, 9 were laying, 9 were incubating, 8 were brood-rearing, and the nesting stage of the remaining 15 was unknown (i.e., nest could not located, eggs were not candled to determine nest age, all eggs were destroyed upon discovery of the dead

females). However, as demonstrated in scenario 2, increased survival of breeding females will not yield $\lambda \geq 1$ unless survival rates reached 0.91, which is biologically unlikely. Conversely, a stable population could be obtained if mean non-breeding survival increased from 0.69 to 0.89, but again, this may not be a realistic value given the life-history and game-status of mallards. However, in conjunction with improved duckling survival rates, increased survival of females during the breeding and non-breeding periods should enhance duck production.

The non-breeding period ranges from January to July and includes harvest, which occurs in May and the feasibility of reducing hunting pressure should be considered. Currently, hunting regulations are based on perceived population size and not on adaptable harvest-management strategies derived from mallard ecology. Bag limits and season lengths vary among regions and change frequently, and in Eastern region, illegal hunting accounted for 13% of harvest (McDougall and Amundson 2017). In NZ, changes to hunting regulations (i.e., gender-based limits, shorter seasons) may only be effective in conjunction with widespread hunter education, stricter compliance and monitoring, and overall reductions in season lengths and bag limits. Further, given that harvest in NZ occurs immediately prior to (or something during) nesting, the timing of the hunting season may also impact female survival and subsequent productivity through pair-bond disruption and widowing. Mallards are seasonally monogamous and pair-bonds remain intact throughout renesting attempts (Brasher et al. 2006). Once paired, male mallards are highly vigilant and protective of females (Portugal and Guillemain 2011) and females reportedly have higher reproductive investment and success when paired to higher quality males (Sheppard et al. 2013). In North America, mate loss has been linked to reductions in clutch size and egg viability, selection of inferior males, and decreased female survival (Lercel et al. 1999, Nicolai et al. 2012). The effects of widowing immediately prior to or during the onset of the breeding season should be investigated and the timing of hunting in NZ should be re-evaluated.

5.4.1 Management Recommendations

This study suggests that duckling and female survival are the vital rates that are most likely to drive variation in λ. I demonstrated that a stable population is unlikely to be obtained by increasing breeding and non-breeding survival of females alone (i.e., duckling survival would have to increase simultaneously). Ultimately, management strategies that improve and promote duckling survival may be the most viable method of increasing population growth. Managers should increase current efforts of enhancing the quality of wetlands, ponds, and

drainage ditches, which are typically used during brood-rearing. For instance, waterfowl densities on constructed ponds in Waikato were positively associated with lower fish biomass, higher macroinvertebrate abundance, increased marginal fencing, and greater wetland areas (Garrett-Walker 2014). Similarly, researchers in Finland also found that mallards used habitats that had large numbers of emerging insects (Nummi et al. 2013), while researchers in North America found that broods selected wetlands with large central expanses of open water and wide peripheral margins of flooded emergent vegetation (Raven et al. 2007); a habitat that was later linked to increased duckling survival (Bloom et al. 2012). Also, duckling survival in Puerto Rico was positively related to shallowly flooded habitats which resulted in interspersed emergent vegetation and allowed ducklings more access to food by providing additional cover (Davis et al. 2017), while numerous studies in Canada and USA have indicated a positive association between wetland density and duckling survival (e.g., Krapu et al. 2006, Bloom et al. 2012, Amundson et al. 2013). The Waikato Region has an abundance of peat lakes, yet brood-rearing females did not appear to readily use these areas, possibly because of low macroinvertebrate abundance and/or high densities of pest-fish that compete for invertebrates. The removal of pest-fish, particularly koi carp, gambusia, and goldfish, and the retention or expansion of riparian areas around well-used brood-habitats will likely improve duck densities (Garrett-Walker 2014). Pest-fish may not be able to survive in temporary wetlands and may explain higher duckling survival rates associated with shallow, temporary wetlands in Southland (Garrick et al. 2017).

Alternatively, large-scale predator removal programs may help eliminate brood or nest predators and increase duckling and female survival rates. For instance, researchers in Saskatchewan, Canada found that removal of nest predators, including striped skunk (*Mephitis mephitis*), raccoon (*Procyon lotor*), coyote (*Canis latrans*), and American badger (*Taxidea taxus*) improved survival of ducklings from 0.36 on control sites to 0.57 on predator-trapped sites (Pearse and Ratti 2004). However, in North Dakota, USA, a similar study found that removal of nest predators greatly increased nest survival, but duckling survival was among the lowest ever observed and was unaffected by predator removal (Amundson et al. 2013). Yet, in NZ, predator removal has been effective in controlling mammalian nest predators (Whitehead et al. 2008, Innes et al. 2015), although the underlying impact of wetland predators has yet to be evaluated (O'Donnell et al. 2015). In NZ, brood predators are poorly understood, but efforts to identify and control them could prove useful. Lethal control programs may effectively reduce overall predator assemblages within the

landscape, ultimately improving duck production, but the effectiveness of large-scale predator removal programs should be evaluated (*sensu* Pearse and Ratti 2004, Amundson et al. 2013). For instance, designing a study with predator-trapped and control blocks or researching brood survival within well-established predator-control sanctuaries (i.e., Maungatautari Ecological Reserve, Serpentine Lake/Rotopiko Sanctuary), will enable managers to gauge the cost-effectiveness of implementing predator control programs.

Chapter 6

6. Effects of Surgically Implanted Transmitters on Reproduction and Survival in Mallards

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6.1 Abstract

Abdominally implanted radiotransmitters have been widely used in studies of waterbird ecology; however, the longer handling times and invasiveness of surgical implantation raises important concerns about animal welfare and potential effects on data quality. Although it is difficult to assess effects of handling and marking wild animals by comparing them to unmarked controls, insights can often be obtained by evaluating variation in handling or marking techniques. Here, we used data from 243 female mallards and mallard-grey duck hybrids equipped with fully encapsulated abdominally implanted radiotransmitters from 2 study sites in New Zealand during 2014–2015 to assess potential marking effects. We

evaluated survival, dispersal, and reproductive effort (e.g., breeding propensity, nest initiation date, clutch size) in response to 3 different attributes of handling duration and procedures: i) processing time, including pre-surgery banding, measurements, and blood sampling of un-anaesthetised birds; ii) surgery time from initiation to cessation of anaesthetic; and, iii) total holding time from first capture until release. We found no evidence that female survival, dispersal probability, or reproductive effort were negatively affected by holding, processing, or surgery time and concluded that we collected reliable data without compromising animal welfare. Our results support previous research that fully encapsulated abdominal-implant radiotransmitters are a suitable technique that enables researchers to obtain reliable estimates of reproductive performance and survival.

6.2 Introduction

Over the past 50 years, ecologists have used radio-telemetry to study survival, movement, and behaviour of waterbirds, including shorebirds, cranes, grebes, loons, ducks, geese, swans, albatrosses, penguins, and alcids (e.g., Greenwood and Sargeant 1973, Korschgen et al. 1984, Klugman and Fuller 1990, Meyers et al. 1998, Kenow et al. 2002, Green et al. 2004, Mulcahy et al. 2011). In particular, telemetry-based breeding-season survival rates and habitat selection patterns have informed management and conservation practices of game birds (Cowardin et al. 1985, Davis et al. 2014, Howerter et al. 2014, Gibson et al. 2016a). Usually, investigators make the fundamental assumption that capture and marking techniques do not bias parameters of interest such as behaviour, reproductive effort, survival, or movement (Barron et al. 2010). In a recent meta-analysis, Barron et al. (2010) suggested that implanted and anchored transmitters had the greatest reported device-induced mortality when compared to other attachment methods (e.g., harness, collar, glue, and tail-mounted). Conversely, White et al. (2013a) demonstrated that externally attached devices had consistent detrimental effects on body condition, survival, and reproduction, and suggested that implant-transmitters are preferable. Equivocal results create difficulties when deciding which marking techniques are most appropriate for a given study. Thus, researchers should test assumptions of marker effects on parameters of interest to prevent unreliable conclusions being drawn from their biased data (Barron et al. 2010).

Initially, radiomarkers designed for waterfowl were externally mounted (e.g., backpacks or back-mounted), but adverse effects such as mass loss, feather wear, and abnormal behaviour (Dwyer 1972, Greenwood and Sargeant 1973, Perry 1981) led researchers to develop abdominally implanted transmitters (Korschgen et al. 1984). Since

then, surgical techniques have been modified and refined to minimise handling stress and mortality, including use of general anaesthesia, intubation and heart-rate monitoring, and improved aseptic and sterilisation methods (Mulcahy and Esler 1999). Abdominal-implant techniques involve a relatively invasive surgical procedure requiring more facilities, additional personnel, and specialised equipment. As a result, handling and holding duration is often increased, and risks to study animals may be greater than for other attachment techniques (Olsen et al. 1992, Esler et al. 2000a). In combination with additional data collection (e.g., collection of biometric measurements and blood samples), handling and holding times of birds may be overly prolonged and unknowingly affect individual welfare or measured vital rates.

Although earlier studies reported greater survival, return rates, and reproductive effort of waterfowl when equipped with abdominally implanted transmitters as opposed to back-mounted or harness-style devices more recent investigations into effects of abdominally implanted transmitters have been ambiguous (Rotella et al. 1993, Dzus and Clark 1996, Paquette et al. 1997, Esler et al. 2000a). For instance, abdominally implanted transmitters did not affect survival of tundra swans (*Cygnus columbianus*; Ely and Meixell 2016) or short-term survival, behaviour, time budgets, or fecundity of Canada geese (Branta canadensis; Hupp et al. 2003, Hupp et al. 2006). Further, researchers detected no difference in survival among surf and white-winged scoters (*Melanitta perspicillata* and *M. fusca*, respectively) equipped with external (prong-and-suture) or internal transmitter types (Iverson et al. 2006). In contrast, common eiders (*Somateria mollissima*) exhibited lower first-year survival, behavioural changes, reduced foraging, and adverse physiological responses after surgical implantation of satellite transmitters with percutaneous antennas (Latty et al. 2010, Fast et al. 2011, Latty et al. 2016). Despite the wide application of surgically implanted transmitters, studies rarely address the potential effects that variations in processing, surgical, and total holding time have on study subjects (McMahon et al. 2011) even though post-surgery censor periods may be required (Latty et al. 2016). More importantly, understanding how marker effects influence demographic parameters of interest is especially paramount if conservation and management decisions are derived from research programs (e.g., Hooijmeijer et al. 2014, Uher-Koch et al. 2014, Hupp et al. 2015).

Evaluating population vital rates often requires that individuals can be identified, which creates difficulties when assessing effects of marking wild animals because vital rates of unmarked controls are difficult to establish. Fortunately, variations in capture and handling

techniques during a given procedure can be used as metrics to evaluate subsequent survival and reproductive performance. Mallards were introduced to NZ in the late 1800's (Dyer and Williams 2010) and have since become an economically important game bird (McDougall and Amundson 2017). We combined mallards and mallard-grey duck hybrids (hereafter mallard) in our study because females of both species are phenotypically similar (Guay et al. 2014), largely introgressed (Williams and Basse 2006), and jointly managed and monitored throughout the country (McDougall and Amundson 2017). In 2014, we initiated a 2-year telemetry study to investigate habitat selection and breeding ecology of mallards on 2 study sites in NZ. Here, we examine the effects of variations in capture and handling procedures during abdominal implantation of radiotransmitters on subsequent survival, dispersal, and reproductive effort of wild female mallards. Specifically, we tested the assumption that longer processing, surgery, and holding times have no effect on post-surgical survival, dispersal or site-fidelity, breeding propensity (i.e., whether or not a female initiated at least one clutch), nest initiation date (i.e., day first egg was laid relative to start of breeding season), and first clutch size.

6.3 Study Areas

During 2014–2015, we captured pre-breeding mallards throughout 2 study areas in NZ. One site was located on the South Island, approximately 30 km north of Invercargill in Southland (SOU; 46°12'S, 168°20'E) and another on the North Island, approximately 20 km south of Hamilton in the Waikato (WAI; 37°55'S, 175°18'E; *see* Fig. 1.1 and 1.2). We baited 4–6 trap sites within each study area with corn or barley from 6 weeks prior to trapping through to completion of trapping (range: 5–19 days) during which time traps were rebaited every 1–3 days. Study area boundaries differed by site and year (SOU_{2014} = 3,000 ha; SOU_{2015} = 4,900 ha; WAI_{2014} = 25,800 ha; WAI_{2015} = 19,200 ha) because of land-owner permission, trap locations, and bird movement.

6.4 Methods

6.4.1 Capture, Handling, and Surgical Procedures

We trapped birds beginning in early July in Southland and early June in Waikato using baited funnel traps that were placed on the edge of refuge ponds (i.e., ponds that were not hunted during the most recent hunting season). Each year, we marked ~60 female mallards per study area and equipped them with a 22-g intra-abdominal very-high frequency (VHF) radiotransmitter (Model IMP/150, Telonics, Mesa, Arizona, Rotella et al. 1993, Paquette et

al. 1997). Transmitters were fully encapsulated (i.e., no percutaneous antenna), equipped with mortality sensors that were activated after 8-hr of inactivity, and programmed with a 12-hr on, 12-hr off (in 2014) or 14-hr on, 10-hr off (in 2015) duty cycle. Upon removal from the trap, time of day was recorded and females were placed in a communal holding pen to await processing and surgical implantation of transmitters. In Southland, we transported birds < 5 km before being placed in the holding pen and performed surgical implantation under aseptic field conditions in a converted sheep-shearing shed that served as a fixed-location surgery unit. In Waikato, we processed birds near the trap locations; we performed surgical implantation under similar conditions in a converted horse-trailer that served as a mobile surgery unit.

We defined ***processing time*** as the time elapsed from when a bird was removed from the holding pen until it was placed on the surgical table for implantation. During processing, we equipped all birds with a NZ Department of Conservation steel leg band and a coloured-auxiliary wrap-around band (in 2015 only), weighed them with electronic scales (± 1 g), and used a ruler to measure wing chord (± 1 mm) from the end of the carpo-metacarpus to the tip of the longest primary feather. With electronic calipers (± 0.1 mm,) we measured (i) head length from the back of the head to the tip of the bill, (ii) culmen length (total length of the upper part of the bill), (iii) tarsus length (i.e., length of the tarsometatarsal bone, excluding joints), and (iv) keel length from the tracheal pit to the hind margin of the sternum. We classified female age as either after-second year (ASY) or second-year (SY) based on cloaca (Hochbaum 1942) and wing feather characteristics (Carney 1992). We collected the 2nd greater secondary covert feather for additional verification of age assignments (Krapu et al. 1979). We also collected 5–7 flank feathers and < 3 mL of blood from each bird for related studies. Processing time depended on the number and experience of personnel, but could be confounded by the behaviour of the bird (e.g., whether she struggled or remained calm), and time necessary to collect blood. Following processing, birds were handed to a 3- or 4-person surgical team who immediately began implantation surgery.

Protocols for surgical implantation followed Olsen et al. (1992) with the following exceptions: we used a C-Pram breathing circuit (SurgiVet, Smiths Medical PM, Inc. Norwell, MA USA), a modified canine mask hooked to the anaesthetic machine, and a 2.0 mm endotracheal tube for intubation. We placed the mask over the bird's bill and anaesthesia was induced using isoflurane delivered at a flow rate of 4% until the bird appeared unconscious based on toe-pinch and wing extension reflexes ($\bar{x}$ = 4.6 mins, SD = 1.5). Once intubated, the

anaesthetist closely monitored breathing and heart rate using an oesophageal audio-patient monitor and adjusted the flow of Isoflurane when required (Korschgen et al. 1996); we used 70% isopropyl alcohol and Betadine® (7.5% w/v povidone-iodine) to soak the surgical area and CIDEX® OPA (0.55% Ortho-phthalaldehyde; Advanced Sterilization Products, Irvine, CA, USA.) to cold-sterilise instruments and transmitters. We injected 0.2–0.4 mL of a local anaesthetic (Marcain; 0.5% bupivacaine hydrochloride; AstraZeneca Ltd, Auckland, NZ) subcutaneously around the incision site between the posterior end of the sternum and the pubic bone (Korschgen et al. 1996). Immediately following intubation, we used a scalpel and tissue scissors to make a 2–3 cm incision in the skin layer, lifted the muscle layer with forceps before opening the coelomic cavity, and inserted the transmitter dextral to the liver (Korschgen et al. 1996). We closed the surgical site with a continuous suture pattern of 2 separate layers (subcutaneous muscle and tissue layer followed by skin layer) using absorbable monofilament suture and immediately administered pure oxygen following closure of the skin layer. Once birds became alert following surgery they were placed in solitary holding pens for $\geq$45 min, after which they were released provided they were fully alert. Birds that were not fully alert after 45 min were checked every 10 min until they appeared ready for release (Korschgen et al. 1996). We recorded the time at 9 different stages of the surgical procedure: i) when the mask went on and the administration of anaesthesia began, ii) bird was deemed unconscious, iii) bird was intubated, iv) incision was made, v) transmitter was fully inserted, vi) body wall was closed and tied-off, vii) skin layer was closed, viii) bird was extubated, and ix) bird was placed in a recovery pen.

The time from when the bird became unconscious after the placement of the mask to when the bird was extubated prior to regaining consciousness was considered ***surgery time*** and depended on the: i) speed at which a bird became unconscious, which could be an artefact of body mass, body condition, behaviour (i.e., birds that appeared more agitated would often take longer to become anesthetised) or the experience of the anaesthetist; ii) period it took the surgeon to implant the transmitter and tie the sutures, and; iii) time it took for the bird to regain consciousness, which could be a result of the amount of Isoflurane administered or individual attributes such as body size. We defined ***holding time*** as the time elapsed from when we checked traps and removed birds to the time the bird was finally released after surgical implantation. Holding time varied depending on the number of females captured and marked in a given day (range = 1–28), the state of those birds (i.e., excessively

muddy birds were cleaned and dried prior to processing), and the order in which females were selected from the holding pen for processing.

6.4.2 Tracking and Monitoring Procedures

The day following transmitter deployment, we began radiotracking birds to monitor survival and determine the onset of breeding and clutch size of the first detected nest attempt. We tracked females every 1–3 days using hand-held telemetry or locations were triangulated using truck-mounted, null-array antenna systems (Kenward 1987) and Location of a Signal Software, version 1.03 (LOAS; Ecological Software Solutions, Hegymagas, Hungary). If females went missing during ground tracking, we searched for them extensively during road searches throughout the study area and beyond until they were relocated, or the nesting period had nearly completed (end of November). Additionally, during the peak breeding season, we conducted 1–3 aerial telemetry flights at each site by searching parallel transects up to 10 km outside of the study area boundary at an average height of 300 m above ground (Gilmer et al. 1981). Females were tracked until they died, were not located within 10 km of the study area, or the transmitter no longer emitted a detectable signal following a weakening pulse rate.

Whenever a female was triangulated to the same location between consecutive tracking attempts, we approached the female on foot. To minimise disturbance and investigator-induced nest abandonment, we attempted to locate the nest without flushing the female, checked nests remotely every 1–7 days via telemetry, and, visited nests directly only if the female was absent or if a week or more had passed since the last visit. Once the majority of birds had begun nesting (early September), we obtained a visual sighting of all remaining non-breeding females weekly.

Mean age of nests at first visit was 15.4 days (SD = 9.0), which minimised the risk of investigator-induced abandonment (Howerter et al. 2014), but increased the probability that some nests may have been destroyed before we discovered them; however, apparent nest success was relatively high in our study areas (0.63; Chapter 3), so few nests are likely to have failed before discovery. During each visit to the nest, eggs were counted and candled to determine stage of incubation (Weller 1956). We calculated nest initiation date (IDATE) as the date the first egg was laid based on the number of eggs and stage of incubation upon discovery, assuming a laying interval of 1 egg per day and absence of partial nest predation unless we noted evidence of egg fragments or shells.

6.4.3 Data Preparation and Censoring

Approximately 10% (n = 26) of our marked birds went missing from our study sites during the pre-breeding period, and we were unable to locate them despite numerous searches using truck-mounted and aerial telemetry throughout the study areas. Thus, we wanted to evaluate whether dispersal of these birds from the study areas was a result of capture or handling effects. To avoid confounding missing birds with birds that dispersed from the study site following nest failure, we defined the pre-breeding period as the time from marking until onset of nesting or until 95% of birds had initiated their first nest attempt in each site (90 days post-marking in Southland, 115 days post-marking in Waikato). We monitored frequencies of missing birds continuously during the post-marking and breeding seasons and defined a bird as missing if we were not able to detect a signal for $\geq$2 weeks (Esler et al. 2000b, Iverson et al. 2006). We included missing birds in analyses of dispersal and our calculations of body size and condition indices, but excluded them from analysis of breeding propensity. Of these 26 missing birds, we also excluded 11 from survival analysis because they went missing within 1 week of marking, thus we did not have sufficient data to model survival. We omitted an additional 11 birds from analysis of breeding propensity; 2 that we were unable to track due to restricted access to private land and 9 that died before they had an opportunity to nest (i.e., mortality occurred before the majority of birds had initiated their first nest attempt). We excluded an additional 7 birds from the analysis of processing time because the time at which they were removed from the holding pen was not recorded. Finally, 1 bird was euthanised because it failed to fly away due to post-operative complications and was therefore removed from all analyses.

6.4.4 Statistical Analysis

We examined daily survival of birds prior to nesting (i.e., from capture to 30-days post-marking), seasonal dispersal, breeding propensity, Julian nest initiation date (IDATE; range = 196–297, whereby 196 = 15 July), and initial clutch size (CLUTCH; range = 6–17 eggs) as response variables in generalised linear mixed models using binomial (logit link: survival, dispersal, breeding propensity) or Gaussian (identity link: nest initiation date, clutch size) distributions. Although processing and surgery time were components of total holding time, holding and surgery time were negatively correlated (Pearson's: $r = -0.32$, $p < 0.001$) and processing time was not correlated with holding or surgery time (Pearson's: $r = 0.002$, $p = 0.72$; $r = -0.007$, $p = 0.92$, respectively), so we treated all 3 measures as independent predictor variables. We estimated daily female survival from the date trapped to 30 days post-

marking using logistic regression where we treated the number of days a bird lived (i.e., successes) relative to the number of days monitored (i.e., trials) as a binomial response variable (Arnold et al. 2012). Capture date differed depending on site, year, weather, and trap locations within each study site. To allow for the possibility that individuals captured on the same day may have been similarly affected by these or other unmeasured factors, we considered each trap date in each year to be a separate event (TRAP EVENT) and included this as a random effect in all analyses.

Individual female attributes often have a pronounced effect on initiation date and clutch size (Krapu et al. 2004b, Devries et al. 2008). Consequently, subtle effects of capture and handling times could be masked by more pronounced variation in female quality. Thus, we incorporated female attributes (i.e., age class, body condition, and body size), trap date, study area, year, and an interaction between study area and year as covariates in all models except for survival analyses where we removed site effects because there were no reported mortalities in Waikato during the first 30 days following capture. For analyses of clutch size, we included nest initiation date as a covariate because clutch size in North American mallards decreases throughout the breeding season (Devries et al. 2008), and we anticipated a similar effect in New Zealand. We defined body size as the first eigenvalue of a principal component analysis (PCA) using wing, keel, and head length measurements. All variables had positive factor loadings (wing = 0.54; keel = 0.56; head = 0.62), and PC1 explained 57% (SD = 1.30) of the variation among the 3 measurements. We regressed log body mass on PC1 and used residuals from the resulting equation (predicted log(mass) = 7.00 + 0.045*PC1; $r^2 = 0.43$) as an index of body condition (Devries et al. 2008, Arnold et al. 2010).

For each response variable, we evaluated 3 models that incorporated the 3 measures of processing, surgery, and holding times separately. Because distributions were right-skewed, we used the $\log_e$-transformation of processing, surgery, and holding time in each model, and back-transformed estimates when presenting results. We plotted model-based estimates of response variables using the mean value of covariates and excluded 5% of observations from the right tail of the distribution so that relationships would not be driven by extreme outliers (Arnold et al. 2012). To assess their effects on response variables, we examined regression coefficients (β, SE) for processing, surgery, and holding times and concluded they had a significant effect if their 95% confidence intervals excluded 0. We completed analyses using PROC GLIMMIX in SAS® software, Version 9.4 (SAS Institute Inc., Cary, NC, USA).

6.5 Results

We radiomarked 243 female mallards (106 ASY; 137 SY) between 4 June and 7 July 2014–2015 (SOU_{2014}: $\bar{x}$ = 5 July, SD = 2.6 days; SOU_{2015}: $\bar{x}$ = 2 July, SD = 1.3; WAI_{2014}: $\bar{x}$ = 7 June, SD = 5.5; WAI_{2015}: $\bar{x}$ = 6 June, SD = 4.0). The average processing, surgery, and holding times were 18.2 mins (SD = 5.3, range = 7.4–41.0), 21.2 mins (SD = 5.9, range = 12.0–44.4), and 300.3 mins (SD = 180.4, range = 89.0–1663.0), respectively. Processing and surgery times were 1–4 min shorter, and total handling times were approximately 100 min longer in Southland versus Waikato, and similar-sized differences occurred between years (Table 6.1). During the 30-day period post-marking, 3 birds died within 2 days of marking: 1 bird was killed by a predator following a normal surgery and release; 1 bird had a deformed keel which resulted in the transmitter being inserted lower than normal, exhibited laboured flight upon release, and was subsequently killed by a predator; 1 was extremely muddy and wet upon capture, was lethargic upon release, and post-mortem examination suggested the bird had died from hypothermia. Of the remaining 2 females that died, 1 female was killed by a mammalian predator 9 days post-marking and 1 was shot during the on-going hunting season 15 days post-marking. We found no effect of processing, surgery, or holding time on female survival, dispersal, breeding propensity, initiation date, or clutch size of the first detected nest attempt (Table 6.2; Figure 6.1).

Table 6.1 – Estimates (mean ± SD) of processing, surgery, and holding times for each site (SOU = Southland; WAI = Waikato) and year for female mallards captured and equipped with fully encapsulated abdominally implanted radiotransmitters in Southland and Waikato, 2014–2015.

Variable	*n*	Processing Time	Surgery Time	Holding Time
Site				
SOU	122	17.5 ± 4.9	19.4 ± 5.3	346.5 ± 220.9
WAI	109	19.3 ± 5.7	23.2 ± 5.8	243.6 ± 105.7
t		- 2.51	-5.24	4.43
P		0.013	< 0.001	< 0.001
Year				
2014	114	17.2 ± 5.6	22.0 ± 0.5	271.4 ± 125.1
2015	117	19.4 ± 4.9	20.4 ± 6.6	323.9 ± 223.4
t		-3.30	2.13	2.17
P		0.001	0.035	0.029

Table 6.2 – Regression coefficients (β) and **standard errors (SE) derived from models evaluating effects of processing, surgery, and holding times on breeding propensity, dispersal, survival, initiation date, and clutch size of mallards.**

	Processing		Surgery		Holding	
Response variable[1]	**β**	**SE**	**β**	**SE**	**β**	**SE**
Female survival	-2.22	1.77	-0.62	2.00	-0.04	0.82
Dispersal	-0.59	0.77	-0.53	1.08	0.68	0.48
Breeding propensity	0.03	0.10	0.08	1.27	-0.28	0.51
Initiation date	-5.58	5.05	-7.98	6.58	-2.98	2.72
Clutch size[2]	-0.56	0.55	-0.15	0.73	0.25	0.29

[1] All models include intercept, female age, body condition, body size, trap date, site, year, an interaction between site and year, and a random effect of trap date.

[2] Models evaluating clutch size also included nest initiation date as a covariate.

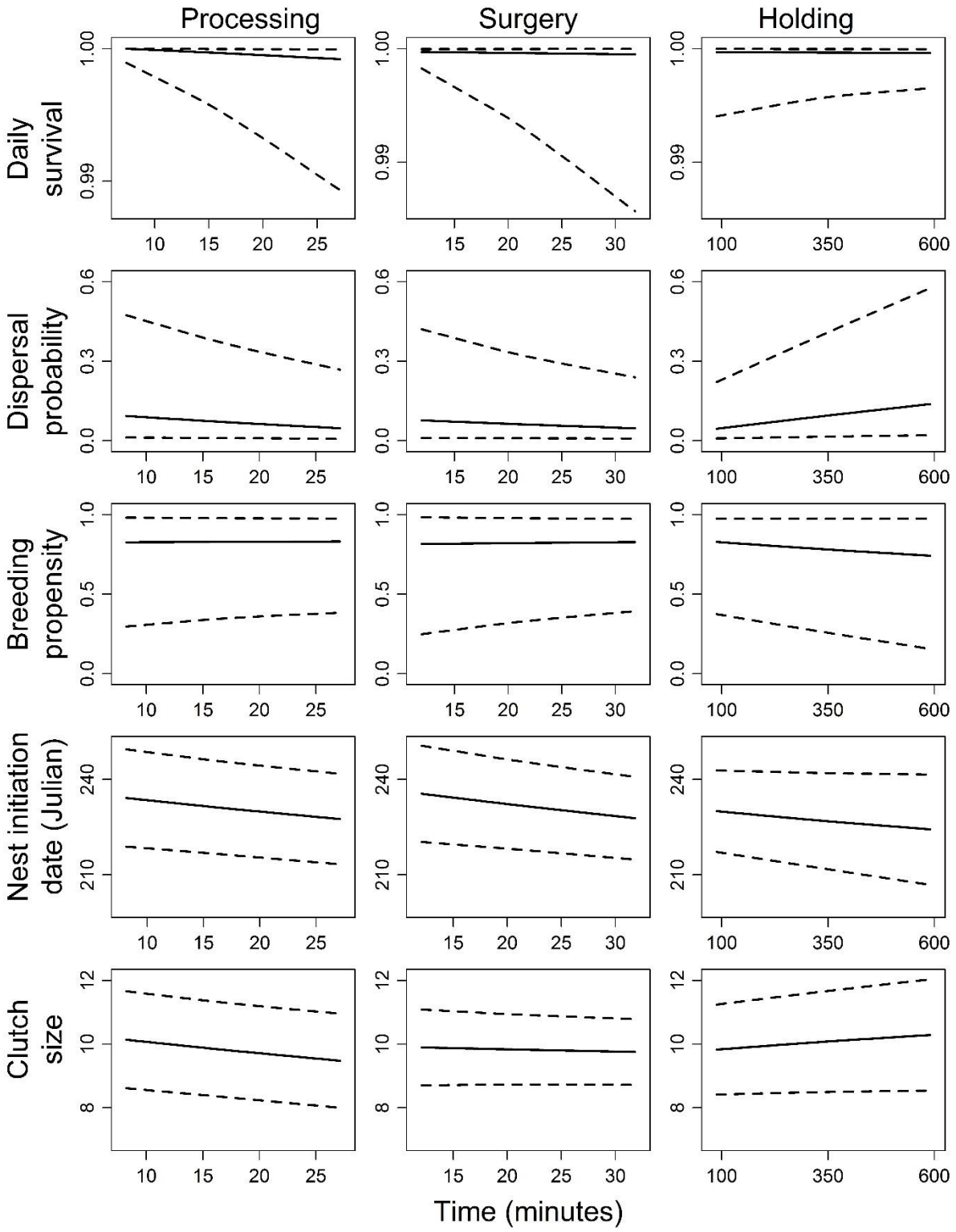

Figure 6.1 – Predicted effects of processing, surgery, and holding time (mins) on daily female survival, dispersal probability, breeding propensity, initiation date, and clutch size of first detected nest of female mallards in Southland and Waikato, 2014–2015. Estimates were derived using mean covariates from after-second year females in Waikato, 2015. Dashed lines = 95% CI.

6.6 Discussion

Despite the reputable advantages of abdominal-implant transmitters (Rotella et al. 1993, Dzus and Clark 1996, Paquette et al. 1997), few researchers have evaluated the variations of capture and handling duration during transmitter attachment on subsequent vital rates of birds. Our results suggest that additional processing, surgery, and holding times associated with implant transmitters did not affect survival, breeding propensity, initiation date, or clutch size of female mallards; thus, we have no indication that any measure of breeding ecology was compromised by our capture and handling methods. Additionally, the quality of data collected was not influenced by marking techniques as we found no pronounced effect of prolonged processing, surgery, or holding times on dispersal probability.

We found no demonstrable effect of holding or handling times on female survival to 30 days post-marking. Although mortality may have been greater during the first 2 days post-release (3 of 6 birds died during this period), it was unrelated to processing, surgery, or holding times. We attributed 1 of these deaths to hypothermia as a result of becoming wet and muddy in the bait trap (we censored another bird that died under similar conditions in 2015), and another bird had an obvious deformity; we should not have radiomarked birds that had physical deformities or were excessively wet and muddy upon capture. We therefore recommend that researchers implement a post-release interval before measuring survival. Short-term effects of prolonged processing and holding times have been reported to decrease survival of pin-tailed sandgrouse (*Pterocles alchata*) and increase capture myopathy and mobility functions of little bustards (*Tetrax tetrax*; Ponjoan et al. 2008, Casas et al. 2015). Additionally, Cox and Afton (1998) found that short-term survival of female northern pintail (*Anas acuta)* decreased when large numbers of waterfowl were captured concurrently, which subsequently increased holding times, but they did not detect an effect on survival when smaller numbers of birds ($\leq$ 172) were captured. In our study, we did not exceed 95 birds per trap event. Aside from Olsen et al. (1992) who reported 18–24 hr holding time for canvasbacks (*Aythya valisineria*), average holding time of birds in this study surpassed mean holding times reported by other researchers (76 mins, Nicholson et al. 2000; 43.7 mins, Ponjoan et al. 2008). For instance, Mulcahy et al. (2011) reported average holding times of 151.4 ± 60.4 mins from capture to release of abdominally implanted bar-tailed godwits (*Limosa lapponica*), which is approximately half of our average holding time. Because we pre-baited at our trap sites, birds in our study had access to supplementary food for up to 6-weeks prior to capture and this may have increased condition and subsequent survival rates.

Whether trap methods that provide access to supplemental food sources affects survival and reproduction is unknown, but should be investigated.

Generally, few data are gleaned from VHF marked birds that disperse or are un-trackable, and this may require researchers to mark additional individuals to obtain sufficient data, which opposes the ethical goal of sample size reduction for animals used in research ("Guidelines for the treatment of animals" 2015). Although holding times employed here exceeded that of similar studies, we found no adverse effect on dispersal rates. In NZ, mallards tend to be non-migratory, yet 14% of band recoveries collected in May–June (pre-breeding) indicate movements of >50 km from banding sites (McDougall 2012). The maximum distance from our trap sites to study area boundaries was 15 km and aerial flights expanded up to 10 km beyond the boundary, thus our maximum tracking range only covered a 25-km radius from trap sites. Though little is known about dispersal and movement between the pre-breeding and nesting stages, from band recovery data, we expected that some birds would disperse beyond our tracking capabilities.

The long-term effects of surgical time are not widely discussed in the literature and surgical times in this study were on par with times reported by Olsen et al. (1992; 18.2 min) and Mulcahy et al. (2011; 25 min). While our results indicate that researchers need not worry about the amount of time a bird is under anaesthesia during abdominal-implant procedures, we recommend that future researchers monitor and record surgical times to make sure they are consistent with previous studies. On average, processing time in this study (18.2 mins) was less than processing times reported for little bustards (27.2 mins; Ponjoan et al. 2008) but nearly twice as long as processing times of least terns (*Sternula antillarum*) and snowy plovers (Charadrius nivosus; 12.8–14.1 mins; Hill and Talent 1990). Although prolonged processing times did not affect the parameters we measured in this study, we strongly encourage other researchers to minimise processing times and reduce unnecessary stress to birds by collecting only the most relevant data. Overall, our results support previous research that abdominal-implant radiotransmitters are a suitable technique that enables researchers to obtain reliable estimates of reproductive performance and survival (e.g., Rotella et al. 1993, Dzus and Clark 1996, Korschgen et al. 1996, Paquette et al. 1997, White et al. 2013b). Furthermore, our results support the notion that capture and handling effects should be quantified in wildlife studies (Barron et al. 2010, McMahon et al. 2011), specifically when outcomes will be used to inform conservation and management decisions.

Chapter 7

7. General Discussion

Science-based management decisions can be used to set appropriate hunting regulations and to direct management programs. As such, the overall goal of this study was to evaluate population vital rates and ultimately understand drivers that affect population growth. Throughout 2 sites in 2 years, I collected data on 304 radiomarked female mallards, 495 nests, and 190 broods. Throughout the course of this study, I followed females for up to 10 months each year to investigate nesting and brood-rearing ecology. I integrated this information with estimates of banding data to obtain a snapshot of the annual cycle and the vital rates which have the greatest influence on population growth rates. Along the way, I tested for bias associated with the marking and capture techniques employed as part of this study.

In Chapter 3, I examined the effects of study site, year, and female attributes on nesting vital rates. I also investigated nest characteristics including initiation date of the first detected nest attempt, incubation and season lengths, and clutch and egg size. I found that older females had higher breeding effort and reproductive success; they nested earlier, laid larger clutches, and successfully hatched more eggs per nest. Further, nest survival and length of incubation was greater in Southland than Waikato, but nesting occurred earlier in Waikato, possibly because it is more equatorial. Also, birds tended to nest earlier in 2014, when renesting propensity and overall mean egg volume was greater. I found that nesting vital rates were within the ranges of those reported by studies of mallards in North America with the exception that clutch and egg size was greater in NZ. I also found that mallards selected nest-sites which conferred greater reproductive success, such that nest survival increased when birds selected sites with tall, dense vegetation in close proximity to roads. My results also indicated aquatic habitats had lower nest success compared to nests located along roads or within hedgerows and non-linear habitat types. Additionally, frequent use of drainage ditches by brood-rearing females, and low duckling survival rates reported here, imply these habitats

could be ecological traps (i.e., possibly foraging efficiency of predators is greater in drainage ditches). Management efforts to improve nest or female breeding survival rates should be directed during peak nesting (late August–late October) and the mowing or disturbance to roadsides and other suitable nesting habitats should be discouraged.

In Chapter 4, I evaluated brood and duckling survival to 30-day and 45-days post-hatch. I also examined brood and duckling detection probabilities, which allowed me to obtain less-biased estimates of offspring survival. I found that duckling survival increased with brood age, was greater in Southland and for older females, but was not related to hatch date or precipitation. Detection probabilities of ducklings and broods were affected by brood age but not hatch date, and site-year specific brood detection rates differed such that they were lowest in Southland in 2014 but highest in Waikato in 2015. I found that duckling survival rates in NZ were among the lowest reported for mallards in the world, which may result from different predator assemblages, unproductive brood-rearing habitat, or inadequate food sources.

In Chapter 5, I developed a stage-based demographic population model to determine factors important in affecting population growth rates. I decomposed nesting vital rates (Chapter 3) and duckling survival estimates (Chapter 4) to obtain mean estimates and process variance. I also used data collected during the course of this study to evaluate breeding survival and obtained estimates of annual survival from 15 years of banding data, which I used to determine post-fledging and non-breeding survival. I conducted sensitivity and life-stage simulation analyses to identify the vital rates that have the highest influence on λ. Consistent with higher reproductive effort and success of older females, I found that fecundity and annual survival were also greater for older females, which resulted in different age-specific contributions to population growth. The population growth rates derived from the model suggested an annual decrease of 0.16 per year, and indicated that duckling survival, particularly of older females, was the most influential factor regulating growth of mallard populations. This was followed by breeding season survival of ASY females and duckling survival of SY females. Finally, I demonstrated that increasing duckling survival may improve population growth, but increased breeding or non-breeding survival alone would not sufficiently offset the low duckling survival rates in this study.

Finally, in Chapter 6, I evaluated variations in capture and handling procedures during abdominal implantation on subsequent survival, dispersal, and reproductive effort and tested

the assumption that there were no adverse effects. I found that additional processing, surgery, and holding times associated with abdominal-transmitter implantation in this study did not affect survival, breeding propensity, or initiation date and clutch size of first detected nest attempts. As such, I was able to affirmatively state, rather than assume, that measures of breeding ecology studied here were not compromised by the capture and handling methods employed as part of this project. Nevertheless, I tested for potential deleterious effects of radiotransmitters in preceding chapters, whenever available data allowed me to do so.

Any initiative that can protect females (during nesting and non-breeding) and ducklings or enhance duckling growth and survival will have the potential to improve duck production. Managers should continue to direct efforts to enhance habitat characteristics which have been linked to improved duckling survival or abundance in NZ including: i) increasing riparian margins; ii) advocating for the retention and protection of ponds, wetlands, and other waterbodies within the landscape; iii) restoring pond and wetland abundance; iv) identifying and conserving waterbodies where pest-fish have not established; and, vi) identifying and conserving areas that are prone to ephemeral wetlands or flooding. Future research should evaluate the adaptive basis of brood selection, and duckling survival and growth should be related to variations in wetland/pond characteristics (i.e., food abundance, presence of pest-fish, cover type). Additionally, managing and controlling duckling and female predators may also improve duck production, but additional research is required to determine the most cost-effective methods.

Mallards were introduced to NZ but today they are a favoured game bird and the most predominate waterfowl species in the country. Their tolerance and adaptability to fluctuating environments and agricultural expansion has allowed them to expand and thrive in a foreign environment. Predator communities, agricultural land-use, landscape composition, and climatic conditions differ between NZ and the areas within the Northern Hemisphere where mallards are abundant and have been widely studied. But the underlying mechanisms that regulate population growth are similar: i) predation risks are high; ii) the landscapes are highly fragmented, creating effective foraging opportunities for mammalian and avian predators; iii) wetland drainage and the channelization of streams and creeks threatened water retention and wetland abundance; iv) birds exhibit selection during nesting and brood-rearing, but the adaptive significance of selection is not always clear-cut (i.e., birds favour one vital rate over another, stage-specific habitat-selection trade-offs are difficult to detect), which creates difficulties for habitat managers; v) competition by heterospecific organisms likely

limit food availability and the selection of adaptive nest-sites and brood-rearing habitats; and iv) populations are hunted on an annual basis. Currently, populations are regulated based on perceived population size and not on adaptable harvest-management strategies derived from mallard ecology. Further, bag limits and season lengths vary among regions and change frequently, which leads to non-compliance within the hunting community. Female non-breeding survival may improve if hunting seasons were structured differently, but the feasibility and outcomes of such approaches must first be evaluated. Ultimately, the future of mallards in NZ is reliant on the desires and actions of the hunting community. Continuing to support conservation programs by purchasing an annual hunting license, remaining compliant, and following regulations, will continue to benefit duck populations for many years to come.

In summary, results from this study represent the first comprehensive analysis of breeding ecology and productivity of mallards in NZ. The results I presented on nesting ecology provide updated and new information which may be used by wildlife managers, should they wish to conserve breeding habitats or direct management efforts during this critical stage of the annual cycle. I have also provided the most comprehensive estimates of duckling survival in NZ, and have highlighted how important the survival of broods and ducklings are to the regulation of mallard populations. I have presented the first estimates of demographic-based population growth rates. I have related variation in vital rates to productivity and have provided numerous management options which may aid in promoting population growth rates. Finally, my research on the effects of transmitters adds to existing knowledge of marker effects and supports the conclusions of other researchers that the marking techniques used in this study are a valuable tool that is suitable in a well-designed study for investigating breeding ecology of waterbirds.

APPENDIX 1: HABITAT

A1.1 Vegetation Substrate of Nests

Vegetation measurements (density and composition) were collected at 428 nest-sites (SOU_{2014} = 141; SOU_{2015} = 113; WAI_{2014} = 74; WAI_{2015} = 100). While collecting vegetation measurements, the dominant nesting substrate was classified as 1 of 11 categories based on commonly observed nest vegetation (Table A1.1). If a nest was comprised of 2 types of vegetation, for instance in grass but within a gorse bush, it was classified as the dominant substrate. Mallards in this study nested in a vast array of vegetation types and locations including: along walls, in boxes, 4 m high in trees, at the base of trees with no cover, under netting and other man-made material left in the middle of paddocks, on silage bales, in brush piles, on pine needles with no other cover, in thick pampas/toetoe hedges, on floating islands of rāupo, and within thick shrubs such as gorse, blackberry, and hawthorn. However, the main nesting substrate was grass (Table A1.1). The definition of grass included rank grass and pasture grass, but these two types were not differentiated during the course of field work; however, from personal observations, I can affirm that most nests were in rank grass.

For the purposes of nest-habitat classification, these vegetation types were grouped into 1 of 5 main nest-vegetation categories: i) grass and tall tussock grass; ii) sedges, forbs, and flax; iii) forbs; iv) blackberry, gorse, tree ferns, other shrubs, and trees; and, v) ground vegetation (Chapter 3 – Table 3.1). As illustrated in Table A1.1, nesting substrate of 89% of nests was comprised of grass (including tall tussock grass), sedges or rushes (including flax), and shrubs or trees (including blackberry, gorse, and ferns).

Table A1.1 – Definition and proportion of the nesting substrate used by female mallards in Southland and Waikato, 2014–2015.

Nest substrate	Definition	Proportion[1]
Grass	Included rank grass and pasture grasses, but excluded tall tussock grass.	0.45
Tall tussock grass	Toetoe (*Austroderia sp.*) or pampas (*Cortaderia sp.*).	0.04
Sedge or rush	Included species within the Cyperaceae, Juncaceae, Tyhaceae families such as *Carex secta, Carex geminata*, and raupō (*Typha orientalis*).	0.11
Flax	*Phomium sp.*	0.04
Forbs	Herbaceous flowering plants (primarily non-woody dicots) such as clover (*Trifolium sp.)* and other legumes, chicory (*Cichorium intybus*), plantains (*Plantago sp.*), other non-woody angiosperms, and small ground ferns (Polypodiopsdia) such as button fern (*Pellaea rotundifolia*) or maidenhair (*Adiantum cunnghamii*).	0.04
Blackberry	*Rubus fruticosus.*	0.02
Gorse	*Ulex europaeus.*	0.08
Tree Ferns	Tree ferns (Cyatheales) such as kiokio (*Blechnum novae-zelandiae*) and whekï (*Dicksonia squarrosa*).	0.04
Other Shrubs	Included hawthorn (*Crataegus monogyna*), elderberry (*Sambucus nigra*), vines, willows (*Salix sp.*), hedgerows, and other woody-stemmed dicots; but excluded blackberry and gorse.	0.05
Trees	Included Monterey cypress (*Cupressus macrocarpa*), blue gum (*Eucalyptus saligna*), radiata pine (*Pinus radiata*), and shelterbelts or treelines.	0.06

Table A1.1 continued

Nest substrate	Definition	Proportion[1]
Other	Included nests in/on bare ground, leaf litter, pine needles, dead branches, brush pile, silage bales, or in artificial habitats such as nests in nest boxes, or under man-made materials within yards.	0.07

[1] The proportion of nests that were predominately comprised of each nesting substrate.

A1.2 Width of Nest Patch

The width of the habitat patch was measured for 185 nests. For instance, if a nest was located along a roadside that was bordered by a hedgerow, the distance from the edge of the road to the hedgerow was measured. Similarly, if the nest was in a drain along a paddock edge, the width of the riparian area of the drain (distance from the paddock to the water) was measured. Average width of the nest patch was 5.62 m (SD = 11.81 m; range = 0.2–100 m). Approximately 95% of all nests were contained within a habitat patch that was < 15 m wide, and 50% of nests occurred in patches < 2.5 m wide. Within the 5 main nest habitats, distance form nest to habitat edge differed significantly (*ANOVA*: $F = 3.64$, $p = 0.007$), such that habitat patches were widest along waterbodies ($\bar{x} = 11.79$, SD = 19.38, $n = 60$), non-linear habitats ($\bar{x} = 8.35$, SD = 18.75, $n = 42$), and roads ($\bar{x} = 5.21$, SD = 3.40, $n = 27$), but narrowest along drains ($\bar{x} = 2.92$, SD = 2.21, $n = 60$) and hedge/tree rows ($\bar{x} = 2.81$, SD = 1.97, $n = 32$), yet these measures were largely driven by extreme outliers. Thus, when I removed 5% of the observations from the right tail of the distribution so that relationships would not be driven by extreme outliers (Arnold et al. 2012), mean width patch was 3.19 m (SD = 3.22) and widest habitats were roads as opposed to waterbodies (Figure A1.1).

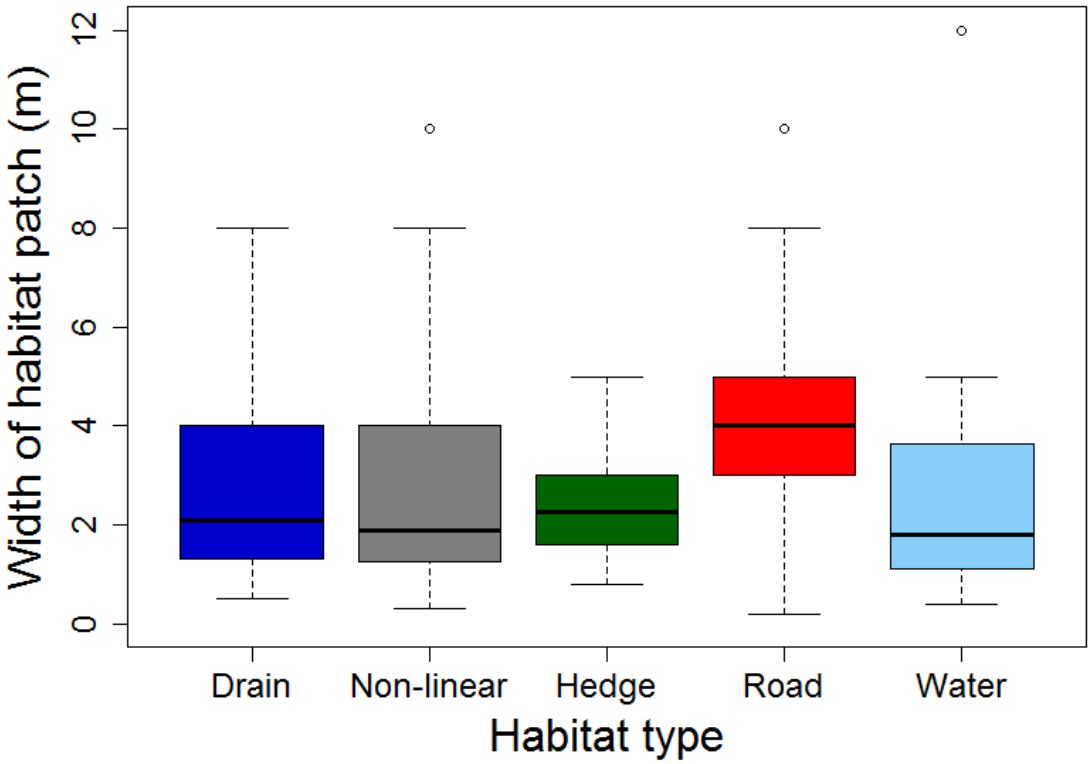

Figure A1.1 – Box and whisker plot illustrating the width of the nest patch in each habitat type, for female mallards in Southland and Waikato, 2014–2015. Black lines = the median of the data, boxes = 25th–75th quartile, dotted lines = 95% range of values (dotted lines), and dots = outlying measurements.

A1.3 Habitat Composition of Nest Buffers

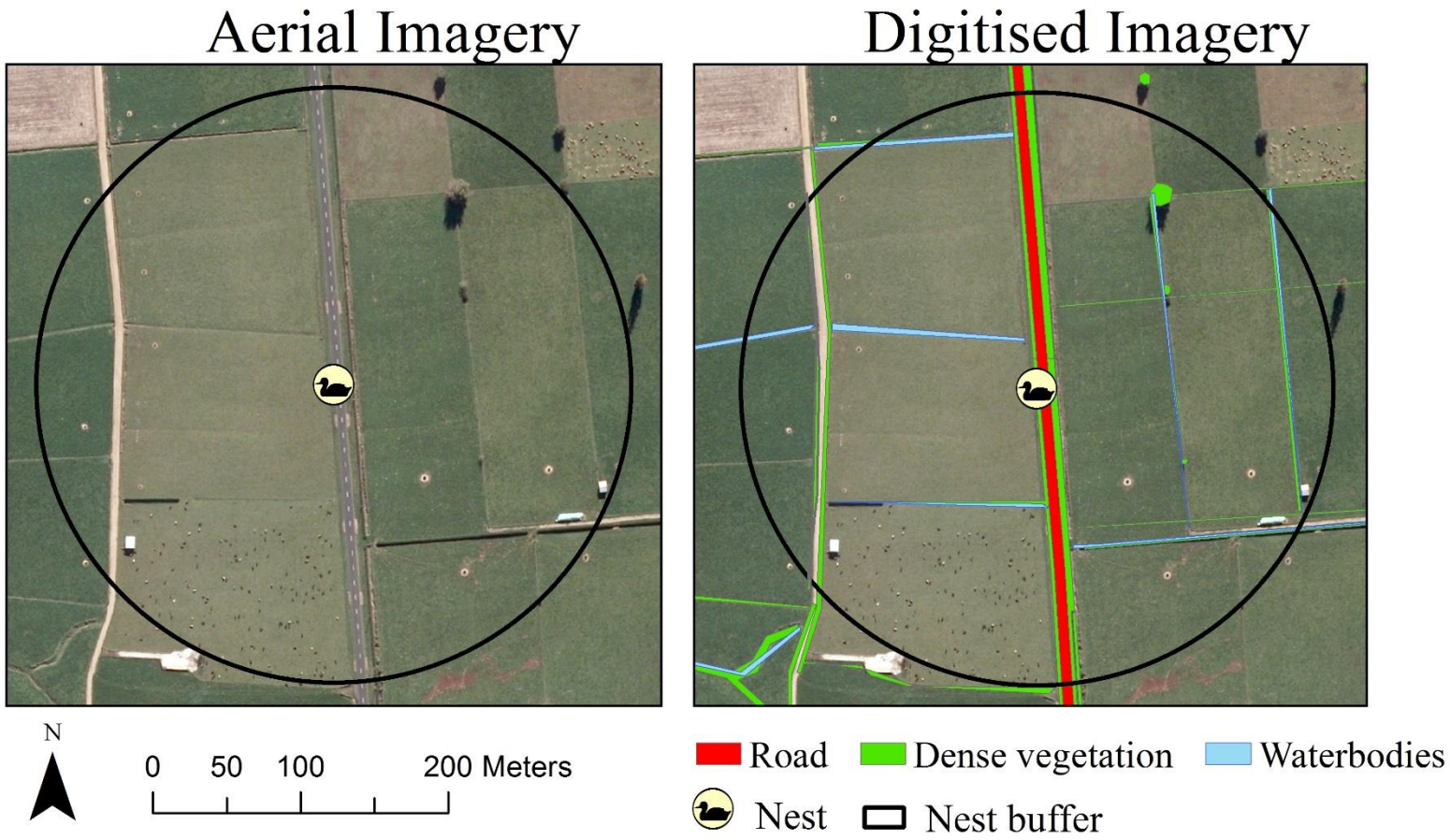

Figure A1.2 – Example of aerial imagery (left map) used to digitise the study areas (right map) and determine the proportion of primary roads, dense vegetation, and waterbodies within a 200 m radius buffer of mallard nests in Southland and Waikato, 2014–2015.

A1.4 Height above Water

The height of the nest above water was collected for 104 nests in 2015 (SOU = 55; WAI = 49) and 3 nests in Waikato in 2014. This included 63 nests along drains, 3 nests within a hedgerow, 2 within a lake on floating islands, 15 on the edge of a pond or lake (including 1 near an effluent pond), 18 along the riparian margin of a stream, creek, or river, and 6 along the roadside. Average height of the nest above nearby water was 127.9 cm (SD = 147.04). The height of the nest above water did not differ between study sites (t = 0.65, df = 670, p = 0.52), but differed by habitat type (ANOVA: F = 5.75, p = 0.0001); height of nest above water varied from 40–1000 cm if the nest was located along the riparian margin of a river, stream or creek, but ranged from 25–40 cm if the bird nested on a floating island in a lake or pond. I have illustrated these differences in Figure A1.3, but have excluded 5% of observations from the right tail of the distribution (i.e., > 600 m) so that relationships would not be driven by extreme outliers (Arnold et al. 2012).

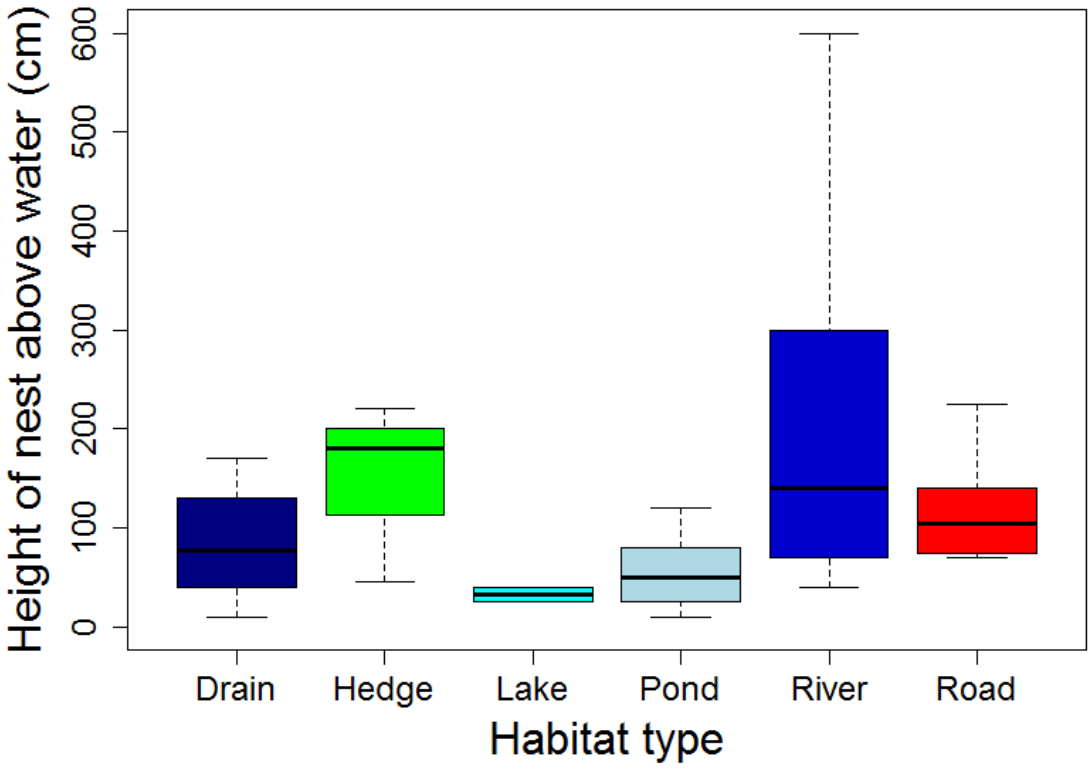

Figure A1.3 – Boxplot diagram of the height of nest above water for each habitat type used by nesting females in 2014. Black lines = the median of the data, boxes = 25th–75th quartile, dotted lines = 95% range of values.

Nest-loss due to flooding was not recorded during the course of field work, but increases in water levels of 1 m would have resulted in the loss of approximately 55% of nests, whereas an increase of 45 cm would have destroyed 25% of nests. Birds were most at risk of flooding when they nested within or near lakes or ponds or along drains, as this was when the nest was nearest to water and an increase in water levels of 10 cm would have flooded the lowest lying nests within these habitats.

A1.5 Habitat Use by Broods

During each brood observation, detailed information on upland and wetland characterises, including the type of habitat the brood was in when the observation started, was recorded as: i) Drainage ditch, which included modified streams or creeks which function primarily as drainage ditches; ii) Effluent pond; iii) Pastureland, including pastureland located within dairy, sheep, or deer farms, and fields designated for short-rotation or perennial crops; iv) Pond, including lakes, peat-lakes, and natural or man-made stock ponds, but excluding effluent ponds; v) River, including natural streams and creeks; and, vi) Other upland habitat, including hedgerow, treelines, shelterbelts, forest stands, scrubland, rural yards, farmyards, and backyards.

Table A1.2 – Proportion of habitat types used by broods during brood observations of radiomarked female mallards in Southland and Waikato, 2014–2015.

Habitat type	Proportion of observations
Drainage ditch	0.30
Effluent pond	0.22
Pastureland	0.20
Pond	0.19
River	0.005
Upland habitat	0.004

APPENDIX 2: ANALYTICAL METHODS

A2.1 Imputation and Estimation of Missing Values

A2.1.1 Female Attributes

Because wing or bursal characteristics were not recorded or were indeterminate, I did not know the age of 14 females (~3.3%). Rather than remove these birds from analyses, I followed methods of Arnold et al. (2010) and classified age of ASY birds as 2, SY birds as 1, and unknown age as 1.44 (mean value of ASY and SY birds). I imputed missing wing lengths for two birds using regression equations ($F = 13.63$, $df = 297$, $p < 0.001$) derived from morphometric measurements (i.e., wing, head, culmen, keel, and tarsus lengths) of the remaining females.

A2.1.2 Initiation Date and Clutch Size

Initiation date and clutch size were unknown for 17 nests of implant females that were left undisturbed following initial discovery (e.g., did not flush the female from the nest) but failed before eggs could be counted or candled, and 2 nests that were partially depredated prior to nest discovery but found during incubation. Further, I did not know clutch size of an additional 31 nests which failed before clutch completion, but after initiation date had been determined. Rather than censor missing records of these variables when they were included as covariates in vital rate analyses, I estimated nest initiation date and clutch size using 1 of 2 methods:

1) in cases where $\geq$ 1 remnant fresh egg remained following nest failure ($n = 8$) or partial clutch predation was evident upon nest discovery ($n = 2$), I calculated the initiation as the day found minus the predicted clutch size (CS'), derived from the top model explaining clutch size of implant females only, and the number of eggs remaining in the nest and incubation stage (incu) of the eggs upon discovery:

$$(IDATE' = Day\ Found - \frac{CS' - Eggs\ Remaining}{2} + Eggs\ Remaining + incu),$$

where, $CS' = 8.93 + -0.03 * Day\ Found + 0.33 * SIZE + 0.65 * AGE; R^2 = 0.28.$

Because initiation date was correlated with day found ($r^2 = 0.98$, $p < 0.001$, $n = 224$) and nest attempt number ($r^2 = 0.60$, $p < 0.001$, $n = 224$), using day found as a predictor allowed me to effectively estimate clutch size when initiation date was unknown, despite nest attempt;

2) or, in cases where all eggs were completely destroyed (n = 9), I determined the average age at which nests of implant birds were found (AF_i), which differed by each site-year (ANOVA: F = 3.00, df = 465, p = 0.030; SOU_{2014}: $\bar{x}$ = 14.56, SD = 7.13; SOU_{2015}: $\bar{x}$ = 10.61, SD = 4.81; WAI_{2014}: $\bar{x}$ = 12.18; SD = 5.22; WAI_{2015}: $\bar{x}$ = 11.71, SD = 4.89), and estimated initiation date by back-dating from the averages obtained for each site-year (Claassen et al. 2014). That is, a nest that failed before eggs were counted and candled would be assigned to the average AF_i for each site-year(i) and the initiation date would be calculated as:

$$IDATE'' = Day\ Found - Mean\ AF_i$$

For these nests and the remaining 31 nests with unknown clutch sizes, I imputed clutch size using a regression equation based on the top model from the analysis of clutch size:

$$CS'' = 9.20 - (0.03 * IDATE) + (0.81 * Trans_{P\&S}) + (3.42 * Cond) + (0.50 * Age) + (0.30 * Size);\ R^2 = 0.31$$

A2.1.3 Egg Measurements

I imputed missing egg volume measurements of 17 nests using regression equation based on the top model from the analysis of egg volume:

$$Vol = 55.25 - (0.32 * Clutch) + (1.92 * Trans_{P\&S}) - (0.82 * Year_{2015});\ R^2 = 0.09$$

A2.2 Covariates and Full Model Sets Used in the Evaluation of Nest Ecology

Tables A2.2–A2.14 details the full model sets that I considered in each analysis. To save space, I explain the meaning of column headings and variables here, and provide rudimentary table titles throughout. Models are ranked by differences in Akaike's Information Criterion, corrected for small sample size (AIC_c). Number of parameters (*K*) includes the intercept. Differences in AIC_c relative to the model with the lowest values are indicated by (ΔAIC_c). Model weight (w_i) is determined from the full candidate set that I considered once models containing uninformative parameters were removed. Deviance is -2*log likelihood. Intercept only model (null) is highlighted for comparative purposes.

Table A2.1 – List and definition of covariates used to explore all possible variations of model sets in the separate analysis of nesting ecology.

Covariate	Definition
Age	Female age (after-second year, second-year, or unknown).
Condition	Female body condition at time of marking.
Size	Female body size.
Initiation date	Initiation date (relative to day 1 of the nesting season); the day the first egg was laid.
Clutch	Clutch size; number of eggs per nest.
Pre-Nest age	Age of previous nest attempt.
Pre-IDATE	Initiation date of the previous nest attempt.
Pre-Clutch	Clutch size of the previous nest attempt.
Pre-Attempt	Number of previously known nest attempts.
Pre-Fate	Fate of the previous nest attempt (successful, abandoned, or destroyed).

Table A2.1 continued

Covariate	Definition
Transmitter type	Abdominal implant vs. prong-and-suture back-mounted. Or, implant vs. non-implant (prong-and-suture and unmarked birds combined).
Volume	Egg volume averaged over the entire clutch.
Nest age	Number of days since nest initiation.
Dist_Road	Distance from nest to nearest primary (paved) road.
Dist_Water	Distance from nest to nearest waterbody (e.g., pond, lake, river, effluent pond, or drainage ditch).
Water	Proportion of waterbodies within a 200 m nest buffer.
Road	Proportion of primary roads within a 200 m nest buffer.
Dense_Veg	Proportion of dense habitat within a 200 m nest buffer.
Veg_Density	Vegetation density; visual obstruction of the nest-site.
Grass	Proportion of grass in 1 m^2 quadrant centred on the nest-site.
Sedge	Proportion of sedge or rush in 1 m^2 quadrant centred on the nest-site.
Shrub	Proportion of shrubs or trees in 1 m^2 quadrant centred on the nest-site.
Hab_Type	Habitat type the nest was located in (drain, roadside, waterbody, non-linear, or hegderow/shelterbelt).

Breeding Incidence

Only implant females were considered in analysis of breeding incidence. Covariates included: female age, body condition (at time of marking), condition*site, condition*age, size, site, and year.

Table A2.2 – Results and full model set considered in analysis of breeding incidence.

Model	***K***	**AIC_c**	**ΔAIC_c**	**w_i**	**Deviance**
Age + Size	3	119.65	0.00	0.38	113.53
Size	2	119.69	0.04	0.37	115.63
Age	2	122.48	2.83	0.09	118.42
Null	**1**	**123.22**	**3.57**	**0.06**	**121.20**
Site	2	125.20	5.55	0.02	121.14
Year	2	125.20	5.55	0.02	121.14
Condition	2	125.23	5.58	0.02	121.17
Age*Condition	4	124.92	5.26	0.03	116.71
Site*Condition	4	128.26	8.60	0.01	120.05

Renesting Propensity

Only implant females were considered in analysis of renesting propensity. Covariates included: female age, body condition (at time of marking), condition*site, condition*age, size, Pre-Nest age, Pre-IDATE, Pre-Clutch, Pre-Attempt, Pre-Fate, site, year, and random effect of female ID (band number).

Table A2.3 – Results and full model set considered in analysis of renesting propensity.

Model	*K*	AIC_c	ΔAIC_c	w_i	Deviance
Pre-Clutch + Pre-IDATE +Pre-Nest age + Condition	6	149.80	0.00	0.38	137.31
Pre-Clutch + Pre-IDATE + Pre-Nest age	5	149.82	0.02	0.37	139.47
Pre-IDATE + Pre-Nest age + Condition	5	152.65	2.85	0.09	142.30
Age + Pre-IDATE + Pre-Nest age	5	153.02	3.22	0.08	142.67
Pre-IDATE + Pre-Nest age + Condition	4	153.45	3.65	0.06	145.21
Pre-Clutch + Pre-IDATE + Condition + Pre-Fate	7	157.82	8.02	0.01	143.16
Pre-Clutch + Pre-IDATE + Pre-Fate	6	158.18	8.38	0.01	145.68
Pre-IDATE + Condition + Pre-Fate	6	159.00	9.20	0.00	146.51
Pre-IDATE + Pre-Fate	5	160.11	10.31	0.00	149.76
Age + Pre-Clutch + Pre-Nest age + Pre-Attempt	7	176.36	26.56	0.00	161.69
Pre-Clutch + Pre-Nest age + Pre-Attempt	6	178.31	28.51	0.00	165.81
Age + Pre-Clutch + Pre-Attempt + Pre-Fate	8	182.94	33.13	0.00	166.08
Pre-Clutch + Pre-Attempt + Pre-Fate	7	184.62	34.82	0.00	169.96
Age + Pre-Clutch + Pre-Nest age	5	186.55	36.75	0.00	176.20
Pre-Clutch + Pre-Nest age	4	186.59	36.79	0.00	178.36
Age + Pre-Nest age + Pre-Attempt + Year	7	189.28	39.48	0.00	174.62
Age + Pre-Nest age + Pre-Attempt	6	190.27	40.46	0.00	177.77
Age + Pre-Attempt + Pre-Fate	7	193.85	44.05	0.00	179.19
Pre-Clutch + Pre-Fate	5	194.10	44.30	0.00	183.75
Age + Pre-IDATE	4	194.88	45.07	0.00	186.64
Pre-Nest age + Condition + Pre-Attempt + Year	7	194.96	45.16	0.00	180.30
Pre-Nest age + Pre-Attempt + Year	6	195.67	45.87	0.00	183.18

Table A2.3 continued

Model	**K**	**AIC_c**	**ΔAIC_c**	**w_i**	**Deviance**
Pre-Nest age + Condition + Pre-Attempt	6	195.91	46.11	0.00	183.42
Pre-Nest age + Pre-Attempt	5	196.46	46.66	0.00	186.11
Pre-IDATE	3	196.63	46.83	0.00	190.49
Condition + Pre-Attempt +Pre-Fate	7	199.15	49.35	0.00	184.49
Pre-Attempt + Pre-Fate	6	199.73	49.93	0.00	187.24
Age + Pre-Nest age + Year	5	213.92	64.12	0.00	203.57
Age + Pre-Nest age	4	215.34	65.54	0.00	207.11
Pre-Nest age + Year	4	217.12	67.32	0.00	208.88
Pre-Nest age	3	218.48	68.68	0.00	212.35
Age + Pre-Clutch + Pre-Attempt	6	218.99	69.19	0.00	206.49
Age + Pre-Fate	5	220.04	70.24	0.00	209.69
Pre-Clutch + Pre-Attempt	5	222.65	72.85	0.00	212.30
Pre-Fate	4	223.35	73.54	0.00	215.11
Age + Pre-Attempt	5	225.76	75.96	0.00	215.41
Age + Pre-Clutch	4	227.36	77.56	0.00	219.13
Pre-Clutch	3	228.51	78.71	0.00	222.37
Pre-Attempt	4	233.16	83.36	0.00	224.93
Age	3	245.06	95.26	0.00	238.93
Age*Condition	5	249.09	99.29	0.00	238.74
Null	**2**	**249.44**	**99.64**	**0.00**	**245.37**
Year	3	250.56	100.76	0.00	244.42
Condition	3	250.87	101.07	0.00	244.73
Site	3	251.04	101.24	0.00	244.90
Size	3	251.50	101.69	0.00	245.36
Condition*Site	5	254.23	104.43	0.00	243.88

Egg Hatchability

Only marked females (implant and P&S females) were considered in analysis of egg hatchability. Covariates included: female age, transmitter type, mean egg volume, clutch size, initiation date, site, and year.

Table A2.4 – Results and full model set considered in analysis of egg hatchability.

Model	*K*	AIC_c	ΔAIC_c	w_i	Deviance
Volume	2	55.76	0.00	0.26	51.69
Null	**2**	**56.39**	**0.63**	**0.19**	**54.37**
Clutch size	1	56.48	0.73	0.18	52.42
Initiation date	2	57.67	1.92	0.10	53.61
Site	2	58.11	2.35	0.08	54.05
Age	2	58.21	2.45	0.08	54.14
Transmitter type	2	58.54	2.78	0.06	54.48
Year	2	58.57	2.91	0.06	54.61

Partial Depredation

Only marked females (implant and P&S females) were considered in analysis of egg hatchability. Covariates included: female age, transmitter type, clutch size, initiation date, site, and year.

Table A2.5 – Results and full model set considered in analysis of partial depredation.

Model	*K*	AIC_c	ΔAIC_c	w_i	Deviance
Null	**1**	**251.33**	**0.00**	**0.29**	**249.32**
Initiation date	2	252.16	0.82	0.19	248.12
Transmitter type	2	252.44	1.11	0.17	248.40
Year	2	252.92	1.59	0.13	248.88
Age	2	253.21	1.87	0.11	249.17
Site	2	253.34	2.01	0.11	249.30

Daily Nest Survival – Stage 1 (landscape scale)

Analysis of nest survival at the landscape scale included all nest attempts (including marked and unmarked females). Covariates included: Nest age, transmitter type, water, Dense_Veg, Dist_Water, initiation date, Dist_Road, road, site, and year. Dist_Road and Road were correlated and treated as competing models.

Table A2.6 – Results and full model set considered in stage 1 analysis of nest survival.

Model	*K*	AIC_c	ΔAIC_c	w_i	Deviance
Nest age + Dist_Road + Site	4	956.60	0.00	0.45	948.58
Nest age + Dist_Road	3	957.56	0.96	0.28	951.55
Nest age + Road + Site	4	959.69	3.09	0.10	951.66
Nest age + Water	3	960.38	3.78	0.07	954.36
Nest age + Site	3	961.07	4.47	0.05	955.05
Nest age + Road	3	962.00	5.39	0.03	955.98
Nest age	2	962.20	5.59	0.03	958.19
Dist_Road + Site + Marker	5	975.17	18.56	0.00	965.13
Dist_Road + Site	3	975.78	19.18	0.00	969.77
Dist_Road + Water	3	976.65	20.05	0.00	970.64
Dist_Road + Marker	4	976.86	20.26	0.00	968.83
Dist_Road	2	977.02	20.42	0.00	973.01
Water + Site + Marker	5	978.03	21.43	0.00	967.99
Water + Marker	4	978.11	21.51	0.00	970.09
Road + Site + Marker	5	978.31	21.71	0.00	968.27
Site + Marker	4	979.01	22.41	0.00	970.98
Road + Site	3	979.27	22.67	0.00	973.26
Water	2	979.95	23.35	0.00	975.94
Marker	3	980.65	24.05	0.00	974.64
Site	2	981.42	24.82	0.00	977.41
Road	2	982.19	25.59	0.00	978.18
Null	**1**	**982.90**	**26.30**	**0.00**	**980.90**
Dense_Veg	2	984.10	27.50	0.00	980.09
Dist_Water	2	984.63	28.02	0.00	980.62
Year	2	984.74	28.14	0.00	980.73

Daily Nest Survival – Stage 2 (local scale)

Analysis of nest survival at the local scale included 60 nests for which local habitat information was collected. Covariates included: Nest age, Dist_Road, Veg_Density, sedge, grass, shrub, site, and year.

Table A2.7 – Results and full model set considered in stage 2 analysis of nest survival.

Model	*K*	AIC_c	ΔAIC_c	w_i	Deviance
Dist_Road + Nest age + Grass + Hab_Type + Veg_Density + Site	10	825.16	0.00	0.10	805.00
Dist_Road + Nest age + Grass + Hab_Type + Site	9	825.20	0.03	0.09	807.06
Dist_Road + Nest age + Grass + Hab_Type + Veg_Density	9	825.36	0.20	0.09	807.23
Dist_Road + Nest age + Hab_Type + Veg_Density	8	825.43	0.27	0.08	809.32
Dist_Road + Nest age + Grass + Hab_Type	8	825.85	0.69	0.07	809.75
Dist_Road + Nest age + Veg_Density	4	826.13	0.97	0.06	818.10
Dist_Road + Nest age + Grass + Site	5	826.17	1.00	0.06	816.12
Nest age + Grass + Hab_Type + Site	8	826.34	1.18	0.05	810.23
Dist_Road + Nest age + Hab_Type + Site	8	826.44	1.27	0.05	810.33
Dist_Road + Nest age + Grass	4	826.59	1.43	0.05	818.56
Dist_Road + Nest age + Hab_Type	7	826.73	1.57	0.04	812.65
Dist_Road + Nest age + Site	4	826.76	1.60	0.04	818.73
Dist_Road + Nest age	3	826.98	1.82	0.04	820.96
Nest age + Hab_Type + Veg_Density + Site	8	826.98	1.82	0.04	810.88
Nest age + Grass + Hab_Type + Veg_Density	8	827.30	2.13	0.03	811.19
Nest age + Hab_Type + Veg_Density	7	827.46	2.29	0.03	813.37
Nest age + Grass + Hab_Type	7	827.74	2.58	0.03	813.66
Nest age + Hab_Type + Site	7	827.83	2.67	0.03	813.75
Nest age + Hab_Type	6	828.76	3.60	0.02	816.70
Nest age + Site	3	832.75	7.58	0.00	826.73

Table A2.7 continued

Model	***K***	**AIC_c**	**ΔAIC_c**	**w_i**	**Deviance**
Nest age + Veg_Density	3	833.12	7.96	0.00	827.10
Nest age	2	833.26	8.10	0.00	829.25
Dist_Road + Grass + Hab_Type + Site	8	840.80	15.63	0.00	824.69
Dist_Road + Grass + Hab_Type + Veg_Density	8	841.62	16.46	0.00	825.51
Nest age	2	833.26	8.10	0.00	829.25
Dist_Road + Grass + Hab_Type	7	841.81	16.65	0.00	827.73
Dist_Road + Hab_Type + Veg_Density + Site	8	842.01	16.85	0.00	825.90
Dist_Road + Hab_Type + Veg_Density	7	842.08	16.92	0.00	828.00
Dist_Road + Hab_Type + Site	7	842.53	17.36	0.00	828.45
Grass + Hab_Type + Site	7	842.69	17.52	0.00	828.60
Dist_Road + Grass + Site	4	842.97	17.81	0.00	834.94
Dist_Road + Hab_Type	6	843.08	17.92	0.00	831.02
Dist_Road + Grass	3	843.52	18.35	0.00	837.50
Dist_Road + Veg_Density	3	843.95	18.78	0.00	837.93
Hab_Type + Veg_Density + Site	7	844.04	18.88	0.00	829.96
Dist_Road + Site	3	844.16	19.00	0.00	838.15
Dist_Road	2	844.47	19.30	0.00	840.46
Hab_Type + Site	6	844.55	19.38	0.00	832.48
Grass + Hab_Type + Veg_Density	7	844.57	19.41	0.00	830.49
Grass + Hab_Type	6	844.70	19.53	0.00	832.64
Veg_Density + Hab_Type	6	844.96	19.79	0.00	832.90
Hab_Type	5	845.92	20.76	0.00	835.88
Site	2	851.79	26.62	0.00	847.78
Null	**1**	**852.38**	**27.22**	**0.00**	**850.38**
Grass	2	852.60	27.43	0.00	848.59
Veg_Density	2	852.71	27.55	0.00	848.70
Shrub	2	854.32	29.15	0.00	850.31
Sedge	2	854.32	29.15	0.00	850.31

Daily Nest Survival – Stage 3 (female attributes)

Nest survival in stage 3 of the analysis included habitat information brought forth from stage 2 and only considered implant females. Covariates included: female age, body condition (at time of marking), condition*site, condition*age, size, nest age, Dist_Road, Veg_Density, grass, Hab_Type, site, and year.

Table A2.8 – Results and full model set considered in stage 3 analysis of nest survival.

Model	*K*	AIC_c	ΔAIC_c	w_i	Deviance
Dist_Road + Nest age + Veg_Density	4	531.80	0.00	0.23	523.76
Dist_Road + Nest age + Grass + Site	5	532.75	0.95	0.14	522.68
Nest age + Grass + Hab_Type + Veg_Density	8	532.97	1.17	0.13	516.80
Dist_Road + Nest age + Site	4	533.46	1.66	0.10	525.41
Dist_Road + Nest age + Grass	4	533.85	2.05	0.08	525.81
Dist_Road + Nest age	3	534.33	2.53	0.06	528.31
Nest age + Hab_Type + Veg_Density	7	534.39	2.59	0.06	520.26
Nest age + Grass + Hab_Type	7	534.73	2.93	0.05	520.60
Nest age + Veg_Density + Site	4	536.41	4.60	0.02	528.36
Nest age + Veg_Density	3	536.59	4.79	0.02	530.56
Nest age + Grass + Site	4	537.03	5.22	0.02	528.98
Nest age + Hab_Type	6	537.17	5.37	0.02	525.08
Nest age + Site	3	537.33	5.52	0.01	531.30
Nest age	2	538.53	6.73	0.01	534.52
Grass + Hab_Type + Veg_Density	7	539.12	7.32	0.01	524.99
Dist_Road + Grass + Veg_Density + Site	5	539.42	7.62	0.01	529.35
Dist_Road + Grass + Veg_Density	4	539.56	7.76	0.00	531.51
Dist_Road + Grass + Hab_Type	7	539.72	7.91	0.00	525.58
Dist_Road + Grass + Site	4	540.17	8.37	0.00	532.12
Condition + Grass + Hab_Type + Site + Condition*Site	9	540.58	8.78	0.00	522.37
Grass + Hab_Type	6	540.60	8.80	0.00	528.50
Dist_Road + Veg_Density	3	540.75	8.95	0.00	534.72

Table A2.8 continued

Model	***K***	**AIC_c**	**ΔAIC_c**	**w_i**	**Deviance**
Dist_Road + Grass	3	541.53	9.73	0.00	535.50
Hab_Type + Veg_Density	6	541.97	10.17	0.00	529.87
Dist_Road + Site	3	542.22	10.42	0.00	536.19
Dist_Road	2	543.25	11.45	0.00	539.23
Hab_Type	5	544.49	12.68	0.00	534.42
Grass + Veg_Density + Site	4	545.08	13.28	0.00	537.03
Grass + Site	3	545.22	13.42	0.00	539.19
Grass + Veg_Density	3	545.79	13.99	0.00	539.76
Veg_Density + Site	3	545.86	14.06	0.00	539.83
Veg_Density	2	546.17	14.37	0.00	542.16
Site	2	546.55	14.75	0.00	542.54
Grass	2	547.01	15.21	0.00	543.00
Null	**1**	**547.93**	**16.13**	**0.00**	**545.93**
Condition*Site	5	548.00	16.20	0.00	537.93
Condition	2	548.67	16.87	0.00	544.65
Size	2	548.74	16.94	0.00	544.72
Age	2	549.87	18.07	0.00	545.86
Age*Condition	4	551.70	19.90	0.00	543.65

Nest Initiation Date

Only implant females were considered in analysis of nest initiation date. Covariates included: female age, body condition (at time of marking), condition*site, condition*age, size, site, year, and variance.

Table A2.9– Results and full model set considered in analysis of nest initiation date.

Model	*K*	AIC_c	ΔAIC_c	w_i	Deviance
Age + Condition + Size + Site + Year	7	1425.45	0.00	0.43	1410.73
Age + Condition + Site + Year	6	1426.30	0.85	0.28	1413.77
Age + Condition *Site + Year	7	1428.38	2.93	0.10	1413.67
Age* Condition + Site + Year	7	1428.40	2.95	0.10	1413.68
Age + Size + Site + Year	6	1430.13	4.68	0.04	1417.59
Age + Site + Year	5	1430.63	5.18	0.03	1420.25
Age + Condition + Size +Site	6	1433.98	8.53	0.01	1421.45
Age + Condition + Site	5	1434.71	9.26	0.00	1424.33
Age + Size + Site	5	1436.44	10.99	0.00	1426.06
Age + Site	4	1436.91	11.46	0.00	1428.66
Condition + Size + Site + Year	6	1438.25	12.81	0.00	1425.72
Condition + Site + Year	5	1440.29	14.84	0.00	1429.91
Age + Size + Year	5	1443.30	17.86	0.00	1432.93
Age + Year	4	1445.08	19.63	0.00	1436.83
Size + Site + Year	5	1446.62	21.17	0.00	1436.24
Site + Year	4	1448.28	22.83	0.00	1440.03
Age + Size	4	1448.46	23.01	0.00	1440.21
Condition + Size + Site	5	1448.98	23.53	0.00	1438.60
Age	3	1450.15	24.70	0.00	1444.00
Condition *Site + Size	6	1450.29	24.84	0.00	1437.75
Condition + Site	4	1450.95	25.50	0.00	1442.70
Condition + Size + Year	5	1451.82	26.38	0.00	1441.45
Size + Year	4	1453.97	28.52	0.00	1445.72
Size + Site	4	1454.51	29.07	0.00	1446.26
Condition + Year	4	1454.92	29.48	0.00	1446.67
Site	3	1456.18	30.74	0.00	1450.03

Table A2.9 continued

Model	*K*	AIC_c	ΔAIC_c	w_i	Deviance
Year	3	1456.62	31.18	0.00	1450.47
Condition + Size	4	1459.78	34.33	0.00	1451.53
Size	3	1460.66	35.21	0.00	1454.51
Condition	3	1462.74	37.29	0.00	1456.59
Null	**2**	**1463.26**	**37.82**	**0.00**	**1459.19**

Incubation Length

Analysis of incubation length included nests of both marked and unmarked birds for which initiation and hatch dates were confirmed during the course of fieldwork. Covariates included: Initiation date, clutch, site, year and variance.

Table A2.10 – Results and full model set considered in analysis of incubation length.

Model	*K*	AIC_c	ΔAIC_c	w_i	Deviance
Site	3	155.05	0.00	0.75	148.32
Year	3	159.31	4.26	0.09	152.59
Null	**2**	**159.42**	**4.37**	**0.08**	**155.07**
Clutch size	3	160.88	5.83	0.04	154.16
Initiation date	3	160.92	5.87	0.04	154.19

Clutch Size

Analysis of clutch size included only marked females (implant and P&S birds). Covariates included: female age, transmitter type, initiation date, site, year and variance.

Table A2.11 – Results and full model set considered in analysis of clutch size.

Model	***K***	**AIC_c**	**ΔAIC_c**	**w_i**	**Deviance**
Initiation date + Age + Transmitter type	5	1254.11	0.00	0.76	1243.91
Initiation date + Age	4	1256.90	2.79	0.19	1248.77
Initiation date + Transmitter type	4	1259.87	5.75	0.04	1251.73
Initiation date	4	1264.04	9.93	0.01	1257.96
Age + Transmitter type	4	1335.42	81.31	0.00	1327.29
Age	3	1339.42	85.31	0.00	1333.34
Transmitter type	3	1344.04	89.93	0.00	1337.96
Null	**2**	**1349.91**	**95.80**	**0.00**	**1345.87**
Site	3	1351.72	97.61	0.00	1345.65
Year	3	1351.85	97.73	0.00	1345.77

Egg Volume

Analysis of egg volume included all nests (included marked and unmarked females). Covariates included: clutch size, initiation date, transmitter type, site, year and variance.

Table A2.12 – Results and full model set considered in analysis of mean egg volume

Model	***K***	**AIC_c**	**ΔAIC_c**	**w_i**	**Deviance**
Clutch size + Transmitter type + Year	5	1649.04	0.00	0.31	1638.83
Initiation date + Transmitter type + Year	5	1649.12	0.08	0.29	1638.91
Initiation + Transmitter type	4	1649.61	0.56	0.23	1641.47
Clutch size + Transmitter type	4	1650.46	1.41	0.15	1642.32
Initiation date + Year	4	1656.79	7.75	0.01	1648.65
Initiation date	3	1657.50	8.46	0.00	1651.41
Clutch size + Year	5	1657.94	8.89	0.00	1649.80
Transmitter type + Year	4	1659.27	10.23	0.00	1651.13
Clutch size	3	1659.81	10.77	0.00	1653.72
Transmitter type	3	1660.83	11.79	0.00	1654.75
Year	3	1671.83	22.79	0.00	1665.74
Null	**2**	**1673.96**	**24.92**	**0.00**	**1669.92**
Site	3	1675.06	26.02	0.00	1668.97

Nest-site Selection – Local scale

Analysis of nest-site selection at the local scale included nests and non-nest locations. Covariates included: Veg_Density, grass, shrub, sedge, and random effect of nest ID (nest number). Grass and shrub were correlated and treated in competing models.

Table A2.13 – Results and full model set considered in analysis of local scale nest-site selection.

Model	*K*	AIC_c	ΔAIC_c	w_i	Deviance
Veg_Density + Sedge + Shrub	4	1571.68	0.00	0.98	1561.64
Veg_Density + Shrub	3	1579.92	8.24	0.02	1571.89
Veg_Density + Grass	3	1581.53	9.85	0.01	1573.50
Veg_Density + Sedge	3	1586.89	15.21	0.00	1578.86
Veg_Density	2	1590.53	18.85	0.00	1584.52
Sedge + Shrub	3	1609.69	38.00	0.00	1601.66
Shrub	2	1631.19	59.51	0.00	1625.17
Sedge + Grass	3	1649.36	77.68	0.00	1641.33
Grass	2	1653.86	82.18	0.00	1647.84
Null	**1**	**1673.65**	**101.97**	**0.00**	**1669.65**
Hab_Type	5	1677.54	105.85	0.00	1665.47

Nest-site Selection – Landscape scale

Analysis of nest-site selection at the landscape scale included all nests and 1000 randomly generated points. Covariates included: Dist_Road, Dist_Water, water, road, and Dense_Veg. Dist_Road and road was correlated and treated in competing models.

Table A2.14 – Results and full model set considered in analysis of nest-site selection at the landscape scale (200 m radius buffer of nest-site).

Model	*K*	AIC_c	ΔAIC_c	w_i	Deviance
Dist_Road + Dist_Water + Dense_Veg	4	1665.70	0.00	0.99	1657.67
Dist_Road + Dist_Water + Water	4	1676.01	10.32	0.01	1667.99
Dist_Road + Dist_Water	3	1680.56	14.86	0.00	1674.54
Dist_Water + Road + Dense_Veg	4	1693.49	27.79	0.00	1685.46
Dist_Water + Dense_Veg	3	1696.50	30.81	0.00	1690.49
Dist_Water + Road + Water	4	1704.16	38.46	0.00	1696.13
Dist_Water + Road	3	1705.45	39.75	0.00	1699.43
Dist_Water + Water	3	1708.80	43.10	0.00	1702.78
Dist_Water	2	1709.32	43.63	0.00	1705.31
Dist_Road + Water + Dense_Veg	4	1815.81	150.11	0.00	1807.78
Dist_Road + Dense_Veg	3	1827.52	161.83	0.00	1821.51
Dist_Road + Water	3	1834.31	168.62	0.00	1828.30
Water + Dense_Veg	3	1840.78	175.09	0.00	1834.77
Dense_Veg	2	1846.77	181.07	0.00	1842.76
Water + Road	3	1859.65	193.96	0.00	1853.64
Water	2	1860.47	194.77	0.00	1856.46
Dist_Road	2	1871.16	205.46	0.00	1867.15
Null	**1**	**1887.21**	**221.52**	**0.00**	**1885.21**
Road	2	1888.03	222.33	0.00	1884.02

APPENDIX 3: WEATHER

A3.1 Weather Preceding Nesting

I summarised monthly weather information for the 6 month period preceding nesting (Table A3.1). Data were obtained from the National Climate Database (cliflo.niwa.co.nz), using data collected from the nearest weather station for each study site (SOU: Winton2, Agent no. 5768; WAI: Hamilton Aws, Agent No. 2112).

Table A3.1 – Mean monthly weather characteristics for the 6 month period preceding the nesting period (February–July) of female mallards, for each site in 2014 and 2015.

	Southland		**Waikato**	
	2014	**2015**	**2014**	**2015**
Total precipitation[1] (mm)	464.7	551.1	458.6	650.4
Number of wet days[2]	11.5 ± 4.0	14.3 ± 3.5	7.3 ± 6.6	11.2 ± 1.9
Temperature[3] (°C)	10.5 ± 3.4	10.2 ± 3.7	13.8 ± 4.1	13.5 ± 4.2
Soil moisture deficit[4] (mm)	41.2 ± 44.7	27.4 ± 34.3	61.4 ± 67.3	49.3 ± 58.1

[1] Cumulative amount of rainfall throughout the 6 month period.

[2] Mean number of days per month with ≥1 mm of rain.

[3] Mean monthly temperature.

[4] Mean monthly deficit of soil moisture (calculated based on incoming daily rainfall, outgoing potential daily evapotranspiration, and fixed available water capacity of 150 mm).

A3.2 Weather During Brood-rearing

During the brood-rearing period (1 September – 31 December) mean lowest air temperature (°C) and rainfall (mm) were measured on a daily basis and summarised (Table A3.2). Data were obtained from the National Climate Database (cliflo.niwa.co.nz), using data collected from the nearest weather station for each study site (SOU: Winton2, Agent no. 5768; WAI: Hamilton Aws, Agent No. 2112). Lowest daily air temperature was 2.8°C colder in Southland than Waikato ($t = -8.3$, $df = 481.3$, $p < 0.001$), but yearly differences within site were not detected ($t = 0.63$, $df = 485.6$, $p = 0.54$). Also, mean daily rainfall did not differ by site or year (Site: $t = -0.08$, $df = 455.4$, $p = 0.94$; Year: $t = 0.65$, $df = 470.5$, $p = 0.52$).

Table A3.2 – Mean minimum temperature (°C) and rainfall (mm; ± standard deviation) measured over each day of the brood-rearing period (1st September–31st December), for each site in 2014 and 2015.

	Southland		Waikato	
	2014	**2015**	**2014**	**2015**
Mean minimum temperature	6.1 ± 3.6	5.9 ± 3.4	8.9 ± 3.8	8.6 ± 3.9
Mean rainfall	3.2 ± 4.7	2.7 ± 5.4	3.1 ± 5.9	2.9 ± 7.3

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