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**The triumphs, challenges and failures of young
North Island brown kiwi (*Apteryx mantelli*): a study of
behaviour, growth, dispersal and mortality**



A thesis in partial fulfilment of the requirements for the degree of

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Abstract

North Island brown kiwi (NIBK, *Apteryx mantelli*), an endemic New Zealand species, are estimated to have declined by 90% from pre-human colonisation numbers. Currently, at least 60% of mortality is attributed to introduced mammalian predators, namely stoats (*Mustela erminea*) preying on chicks. Therefore, conservation effort focuses on predator trapping/killing, and hatching and rearing NIBK chicks in captivity and releasing them back into the wild. These efforts are resulting in increased recruitment of chicks into populations. However, little is known about the biology and behaviour of NIBK chicks in the wild and how this may affect management of these populations. Consequently, the aim of this study was to examine the ecology of young wild NIBK in a natural high density population with reduced predator diversity on Ponui Island. More specifically, the goal was to determine their growth rates, behaviour around the natal nest, dispersal and mortality, and how these factors may be influenced by environmental variables. During the 2010 - 2011 and 2011 - 2012 breeding seasons 29 young NIBK were observed from hatching until mortality or the end of 2012. Remote video cameras were set up outside nests to record behaviour. Juveniles were located daily as often as possible and location, habitat type, roost type and visibility were recorded. Growth measurements of weight, bill and tarsus lengths were taken monthly in the first season and weekly in the second. Invertebrate abundance and availability were also measured using pitfall traps and soil penetrability. Lastly, young NIBK found dead were preserved in formalin and sent for autopsy to accurately determine the cause of death.

NIBK on Ponui Island were found to grow slower $K_g = 0.0052$ than a NIBK population measured previously at Lake Waikaremoana ($K_g = 0.006$) and 296 other bird species measured to date using the Gompertz growth curve. Females grew faster than males for the first 90 days after hatching. Sample size was too small to do further comparisons after this age. The rate of growth for body mass increased with age whereas the rate of growth for bill length and tarsus length decreased with increasing age, until at least 90 days of age. On a monthly scale, with increasing temperature food abundance significantly increased and soil penetrability declined; on a weekly scale temperature significantly affected growth rates with NIBK growing fastest between 19 - 22°C. I hypothesised that this was because with

increasing temperature, food abundance increased, until a point where the soil became too hard for NIBK to probe for food resulting in the optimum growth rate between 19 - 22°C.

In 161 nights of nest observation I observed seven interactions between a chick and the adults at the nest. These observations are interesting because NIBK were not previously known to interact with their young outside the nest. The behaviours are ambiguous and therefore I was unable to be sure of the context. Juveniles changed roost location most days and the movements between roost sites of individuals were highly variable. Daily dispersal distance was significantly affected by temperature and season, juveniles moved further in the warmer seasons and there was a positive relationship between dispersal distance and temperatures.

Lastly, the mortality rate of NIBK in this population was high at 87.5% with most young NIBK dying from natural causes such as starvation and disease before 90 days of age. Cat predation was found to be higher at 30% relative to mainland populations where cat predation contributes to 5 - 9% of mortalities.

This study highlights that population density, temperature, food availability and causes of mortality other than predation are important factors to consider when researching, conserving and translocating NIBK.

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Chapter 1: Literature Review and Introduction

General Biology and Ecology of Kiwi

Birds belong to two major groups, the Neognathae and the Palaeognathae clade. The word Palaeognathae is derived from ancient Greek and means 'old jaws', this refers to the palate of these birds which is more primitive than that of the Neognathae (Houde 1986). Species in this group are flightless or weak fliers, with pectoral muscles that are under developed, have no keeled sternum, with the exception of Tinamidae, and furculae are mostly absent. Their wings are small in both musculature and skeleton relative to body size, legs are strong and only the femur has air chambers. Many of these characteristics are a consequence of being flightless (Bruning 2003). The Palaeognathae clade consists of weak flying tinamidae (Tinamiformes) and flightless: kiwi (*Apteryx* spp.), ostrich (*Struthio camelus*), emu (*Dromaius novaehollandiae*), cassowary (*Casuarius* spp.) and rhea (*Rhea* spp.) as well as the extinct elephant bird from Madagascar (*Aepyornithidae* spp.) and moa species (*Dinornithiformes* spp.) from New Zealand (Cracraft 1974). All other bird species belong to the Neognathae clade which is a more recent group; these species tend to be smaller and flighted relative to the ratites. From this point onwards in this section I will focus on Palaeognathae because kiwi are the focus of this study. Kiwi is a Maori word and as such is the same in singular as it is in plural and that is how I use the word throughout this thesis.

Kiwi (*Apteryx* spp.) are some of the smallest ratites. Kiwi are nocturnal and flightless with small vestigial wings, they lack a tail, and have whiskers protruding from the base of their long bill (Reid and Williams 1975). Kiwi have an excellent sense of smell (Bang and Cobb 1968, Wenzel 1965, 1968 and 1971, Martin et al. 2007) and touch (Cunningham et al. 2007). Their nostrils are located at the end of their bill; near a bill tip organ that is specialised to detect vibrations of prey moving under the ground (Cunningham et al. 2007). Kiwi spp. are long-lived, surviving an average of 18.7 years in the absence of mammalian predators (McLennan et al. 1996, Bassett et al. 2005). Their call is sexually dimorphic with females producing a low croaky hoarse call and males a piercing shrill whistle (Digby et al. 2013).

Kiwi are also physically sexually dimorphic; females weigh approximately 20% more, and have longer bills by approximately 25 - 30% (Reid and Williams 1975).

It was previously believed that all brown kiwi were the same species (*Apteryx australis*), with three subspecies as follows: North Island brown kiwi, *A. australis mantelli* (Bartlett 1851); South Island brown kiwi (tokoeka), *A. australis australis* (Shaw & Nodder 1813) and Stewart Island brown kiwi (tokoeka), *A. australis lawryi* (Rothschild 1893). Based on the molecular genetic work of Burbidge et al. (2003) there are now five recognised kiwi species: North Island brown kiwi (*A. mantelli*); rowi (or Okarito brown kiwi; *A. rowi*); tokoeka (or Southern brown kiwi; *A. australis*); little spotted kiwi (*A. owenii*); and great spotted kiwi (*A. haastii*) (Gill et al. 2010). Because brown kiwi were considered one species in the past it was common to make generalisations. However, it has come to light in the past few decades that there are large differences between the mating systems, parental care and foraging strategies of different species (Sales 2005). For this reason we must take great care to distinguish between species and locations. This study focuses on North Island brown kiwi (NIBK, *A. mantelli*).

Conservation

Prior to human colonisation, New Zealand was characterised by a number of large endemic flightless birds that evolved in the absence of land mammals. New Zealand was home to only three bat species and marine mammals. With the arrival of Polynesian people a thousand years ago came the Polynesian rat 'Kiore' (*Rattus exulans*) and domestic dogs "Kurī" (*Canis familiaris*; Reid and Williams 1975). European settlers came after, bringing an array of mammals including Norway (*R. norvegicus*) and Ship (*R. rattus*) rats, cats (*Felis catus*), stoats (*Mustela erminea*), weasels (*M. nivalis*), ferrets (*M. furo*), dogs, pigs (*Sus scrofa*) and possums (*Trichosurus vulpecula*; McLennan et al. 1996). New Zealand birds suffered greatly from these introductions because many had limited flight capabilities and had evolved behaviours and characteristics that were ill-adapted to surviving these novel predators. They nest in vulnerable habitats such as holes and cavities making it difficult to easily escape from these predators. New Zealand birds also have a tendency to be curious and less aware of the risks associated with introduced mammals they have not evolved with. Additionally, a number of bird species, including NIBK, have a strong odour that may

be used for communication or signalling (Buller 1888, McLennan et al. 1996, Castro et al. 2010). It is likely that the odour of New Zealand birds became a disadvantage because mammalian predators use olfaction, in conjunction with other senses, to find their prey. Predation by introduced mammals has resulted in a high level of mortality across all life stages of many native bird species (Moors 1983), including NIBK (McLennan et al. 1996, McLennan et al. 2004, Holzapfel et al. 2008).

NIBK are the most abundant kiwi species today (ca. 25,000 individuals left) and are found throughout the North Island in small pockets of protected native bush. However, historic accounts would suggest they have declined by as much as 90% in the last century and populations are still declining by at least 2% per annum (McLennan et al. 1996, Holzapfel et al. 2008). Predation is the main cause of decline for all kiwi species. Mustelids and Possums depredate the eggs, stoats and cats kill chicks, and ferrets and dogs are responsible for the death of adults (McLennan et al. 1996). An estimated 94% of all kiwi species' chicks do not reach adulthood due to predation mainly by stoats (although accidental deaths i.e., falling down hills also occur; McLennan et al. 1996). For this reason there are two main focuses of kiwi conservation. Firstly, to reduce the potential for predation events many of the pockets of native bush where NIBK survive are: trapped for introduced mammalian predators; exist within mainland islands with predator-proof fences; or are found on offshore islands that are completely or mostly predator free (Colbourne et al. 2005). The second focus of kiwi conservation is Operation Nest Egg (BNZONE™). In this program eggs are removed from the wild, and then hatched and reared safely in captivity or in a predator proof crèche until they reach 1000g, a weight at which they are considered to be safe from stoat predation (Colbourne et al. 2005). This program has had high success with NIBK and is now being extended rowi, tokoeka and great spotted kiwi. BNZONE™ is valuable for restoring populations, establishing new populations and supplementing declining populations (Colbourne et al. 2005).

Although a large number of advances have been made in NIBK conservation, resulting in increased recruitment of chicks into the wild; with populations still declining there is a necessity for further research. In this thesis I concentrate on young NIBK: specifically their behaviour around the natal nest, growth, dispersal and mortality. I hope that this information will provide a greater insight both for conservation managers and contribute to

the greater wealth of knowledge in each of these fields. For the remainder of this introduction I will discuss the general theory of each of these topics followed by a segment highlighting the details of what is known about NIBK in these particular areas.

Growth

It is necessary for young animals to grow and develop so they can reach adult size and reproduce. Growth rates are variable between species and there are many hurdles which must be overcome to reach adulthood. Animals grow by the differentiation and proliferation of cells; the energy required is obtained from the intake of food and is balanced between growth and other physiological requirements such as locomotion and thermogenesis (Ricklefs 1973). Although adults grow and cell replacement is continuous, growth and development is fastest and most prevalent in young animals (Ricklefs et al. 1998).

Sigmoidal growth curves relating growth to age, such as the Gompertz, Logistic and von Bertalanffy curves, are often used to describe avian growth and development (Ricklefs 1967, 1968). The curve that fits the growth rates best depends on the species, however, curves generally show that the rate of growth increases to a point, the inflection point, then slows until the chicks reach adult weight, or the asymptote (Ricklefs 1968). Although, there are exceptions, including many passerine species such as the cliff swallow (*Petrochelidon pyrrhonota*), where the weight of chicks peaks above the average adult weight before fledging and then decreases to adult weight after fledging (Ricklefs 1968). A growth rate constant (K) can be used to compare the growth rates of different species and populations; this constant takes into account the weight of the adult animals (Ricklefs 1967).

There are four main factors that can affect growth rate on a broad scale. Firstly, the developmental mode of a species largely affects postnatal growth, and causes the most variation in growth rates between species (Ricklefs 1973). Altricial chicks that are fed by their parents, are less developmentally mature at hatching and tend to have higher rates of cell proliferation than precocial chicks (Ricklefs 1968, Ricklefs and Weremiuk 1977, Ricklefs 1979). Tissue growth in precocial chicks is restricted due to a trade-off between growth and function (Ricklefs 1982). This is because precocial chicks have more physiological requirements with higher energetic costs to balance, particularly as they have greater movement capabilities (Ricklefs 1982). For example, a comparison of the growth rates of

altricial budgerigars (*Melopsittacus undulatus*) and precocial barred button quail (*Turnix suscitator*) showed compartmentalisation of growth rates. Quail had larger bony areas that supported movement, and small cartilaginous areas that had low growth rates. The opposite was true for the Budgerigars, they had small bony areas, no locomotion and large cartilaginous areas with fast growth rates (Starck 1994). Interestingly, cockatiel nestlings (*Nymphicus hollandicus*) although altricial, were found to develop endothermy earlier than other species of similar size. They subsequently grew slower and had lower growth rate constants than other altricial land birds (Pearson 1998). The more precocial and active a species is from a young age the slower their growth rates are likely to be because more energy must be allocated to movement, thermoregulation and finding food and less energy is available for growth.

The second factor that can affect growth rate is body size. There is a tendency for the young of larger species to take longer to reach adult size relative to smaller species (Ricklefs 1968). This is because a higher feeding rate is necessary to maintain the physiological costs of a larger body. For example, Ricklefs (1968) compared two groups of altricial land birds: temperate zone passerines and raptors. Both of these groups have similar breeding ecology and behaviour, rear three or more young a season, and include some of the most rapidly growing bird species, the exception being that adult raptors are much larger than temperate zone passerines (Ricklefs 1968). Raptorial species grew at a much lower rate in comparison to passerine species and 89% of the variation in the growth rates was dependent on the asymptote. The wood stork (*Mycteria americana*) and marabou stork (*Leptoptilos crumeniferus*) are both large birds weighing 2 - 3.3kg and 9kg respectively. It takes wood stork young 58.6 days and marabou stork young 61.3 days to grow from 10 to 90% of the asymptote. In comparison it usually takes most small land birds less than 15 days (Ricklefs 1968).

Species tend to have longer periods of growth when they live on oceanic islands or in areas that protect them from predation (Ricklefs 1968). This is because the length of the nestling period is correlated with the likely success of a nest (Lack 1948). Species that have fewer ground predators and are protected from harsh weather conditions are able to remain in the nest longer with reduced risk and subsequently can have slower growth rates. For example, ascension frigate birds (*Fregata aquila*) that live on a tiny island in the Atlantic

Ocean, take 91.7 days to grow from 10 to 90% of asymptote (Ricklefs 1968). Similar sized mainland species such as crows, ravens and magpies take between 16.7 and 32.9 days (Ricklefs 1968).

Slow growth rates and long nestling periods of seabirds and swifts (Apodidae) may be an adaptation for periods when resources are reduced or there is high competition for resources. This adaptation may decrease the adverse effects that are associated with fast growth such as susceptibility to disease and starvation. By lowering the energetic requirements for growth, energy can be allocated to necessary physiological functions other than growth such as immune function (Lack 1968, Bryant and Gardiner 1979, Griffiths 1992). In black backed gulls (*Larus marinus*) starvation is a common cause of death; males grow faster and subsequently have lower survival rates than females (Griffiths 1992). Similarly, in yellow-eyed penguins (*Megadyptes antipodes*), chicks with the fastest skull, tail and flipper growth had lower survival rates (van Heezik and Davis 1990).

The term growth rate is often used when referring to the growth rate of body mass; however, the growth of other body parts such as the wing chord, bill length and tarsus should also be considered. For example, the growth rates of Hawaiian stilts (*Himantopus mexicanus knudseni*) and scarlet macaws (*Ara macao*) differed between body parts. The growth of the tarsus and wing chord in Hawaiian stilt chicks is sigmoidal, while the growth of the bill length is linear (Reed et al. 1999). The growth rate of the macaws tarsus length was faster than the growth rate of both the bill length and wing chord (Vigo et al. 2011). Growth rates of different areas of the body may be prioritised based on their importance for survival. For example, faster growth of macaws tarsus or feet may allow for quick development of strong feet, allowing them to grasp and manipulate food easier. This is important for a species that has high competition with siblings for food (Vigo et al. 2011).

Environmental factors that affect growth rates

Growth rates are largely affected by an individual's ability to find and consume food. There are three main factors that affect food availability, 1) fluctuations in prey populations, which may be annual or seasonal, 2) prey detectability, and 3) prey accessibility (Arlettaz 2010). Environmental factors such as rainfall and temperature may have significant effects on all three. For example, survival increased with temperature for grey (*Perdix perdix*) and red-

legged partridges (*Alectoris rufa*) although the authors were uncertain if this was a direct effect of temperature on chick activity or an indirect effect via food abundance on growth (Green 1984). Western capercaillie (*Tetrao urogallus*) chicks survive better at low rainfall; however there was no effect of rainfall on the survival of their close relative the black grouse (*Tetrao tetrix*). This was speculated to be due to the final size of the adult (Cluttonbrock et al. 1985). Capercaillie adults are larger, and the chicks grow at a faster rate than black grouse, regardless of environmental effects, and therefore need more food. Foraging is thought to be limited by rainfall which is why the capercaillie chicks with greater energy requirements are more susceptible to mortality at higher levels of rainfall relative to the black grouse (Moss 1986). Conversely, Northern lapwings (*Vanellus vanellus*) that feed on soil invertebrates were found to have increased survival with higher rainfall (Beintema 1994).

Precocial species may be more susceptible to environmental conditions because they are independent from their parents. They are not brooded to the same extent as altricial species; therefore there is a high cost of thermoregulation in wet conditions and a greater surface to volume ratio compared to adults leads to faster heat loss and a higher energetic cost to keep warm (Nagy 2005). If energy requirements increase for thermoregulation, less energy may be available for growth. For example, corncrakes (*Crex crex*) are precocial rails that leave the nest within days of hatching. The growth rate of corncrake chick's increased with temperature, and survival decreased with higher rainfall (Tyler and Green 2004). Cool weather may also reduce the length of time chicks are able to forage (Tyler and Green 2004) and young are not likely to be as proficient foragers as adults (McKean 1990), particularly precocial chicks that receive little or no help and teaching from their parents. For this reason they are more likely to be negatively affected by food shortages and adverse weather conditions than adults and altricial chicks. There are many studies that highlight both the negative and positive effects of weather variables on growth (For example, Siikamaki 1996, Reed et al. 1999, Ashton and Armstrong 2002, Pearce-Higgins and Yalden 2002, Brown et al. 2007, Kosicki and Indykiewicz 2011).

Additional factors that influence Growth

Immune responses in NIBK and hormonal effects of stress on growth is beyond the scope of this study. However, it is a topic to bear in mind whilst considering both growth rates and also factors that influence mortality; because these are underlying mechanisms that also play a role.

Hormonal effects of stress on growth

Hormones are control mechanisms that allow growth rates to be adapted to variable environmental conditions. Stressors such as food deprivation can cause a rise in corticosterone in the body via the hypothalamic-pituitary-adrenal axis (Wall and Cockrem 2009). Corticosterone negatively affects a number of hormones that are important for growth, including: the growth hormone (GH), Insulin-like growth factor 1 (IGF-1) and thyroid hormones (T_3 and T_4). For example, when a chronic stressor was applied to young American kestrels (*Falco sparverius*), a small increase in baseline corticosterone occurred. This resulted in a decrease in feather growth until the treatment was stopped (Butler et al. 2010). Schew et al. (1996) found a decrease in T_3 and IGF-I when food was restricted in both altricial European starlings (*Sturnus vulgaris*) and precocial Japanese quails (*Coturnix japonica*). Chicken chicks that were implanted with corticosterone grew slower than those without the implant (Hayward 2004). Hens implanted with corticosterone that could be passed into the egg and embryo tended to hatch lighter chicks that grew significantly slower than chicks from mothers that had not been implanted (Hayward 2004). Additionally, higher levels of corticosterone can increase movement (Breuner et al. 1998), foraging activity and food intake (Angelier et al. 2007). This may be an important mechanism that reduces the risk of starvation although it may also make young animals more susceptible to predators because foraging and movement is increased to the detriment of vigilance (Lima 1986).

Immune response

Life history theory predicts that if resources are limited animals will favour energetic requirements for growth over immune response (Brzek and Konarzewski 2007). In sand martin nestlings (*Riparia riparia*) there was a positive correlation between the immune response to phytohaemagglutinin (PHA; measured as a swelling response) and body mass increase; a lower immune response occurred when the birds had lower body mass (Brzek

and Konarzewski 2007). Brzek and Konarzewski (2007) also noted that the cost of immune function in juvenile sand martins may be modified by external factors such as weather. In studies where a trade-off between immune function and growth has been observed (Horak et al. 2000, Merino et al. 2000, Soler et al. 2003), it is thought that resources are preferentially allocated to functions and structures that are necessary for young to fledge and survive (Schew and Ricklefs 1998). However, this trade-off did not occur in all studies (Horak et al. 2000, Whitaker and Fair 2002). Great tit nestlings (*Parus major*) that were injected with PHA did not show suppressed growth relative to control nestlings (Horak et al. 2000). Nor did the growth of body mass and tarsus length, and survival differ between control nestling mountain chickadees (*Poecile gambeli*) and those that were immunologically challenged with non-pathogenic antigens (Newcastle disease virus vaccine or sheep red blood cells) (Whitaker and Fair 2002). If the immune response of young animals is compromised in favour of growth rates, this is likely to make them more susceptible to parasites and disease.

NIBK Growth

Food availability and abundance is important to the growth of an individual and a large number of studies have looked at the diet and abundance of food in the environment of NIBK. The diet of NIBK was originally determined by looking at the stomach contents of adult dead birds (Gurr 1952, Bull 1959, Watt 1971, Reid et al. 1982, Chan 1999). A number of studies have gone on to analyse the relationship between the invertebrates found in NIBK faeces and the invertebrates found in their environment (Gurr 1952, Miles 1995, Shapiro 2005). These studies have shown that adult NIBK diet includes invertebrates and plant material such as seeds and berries, and in some cases rocks and wood. The invertebrates eaten appear to vary widely and may include: slugs, spiders, earthworms, beetles and larvae. Colbourne and Powlesland (1988) found that Lepidoptera (36%), Coleoptera (21%), Arachnida (19%) and Hemiptera (10%) contribute the most to the diet of Stewart Island kiwi (*Apteryx australis*), and Bull (1959), Reid et al. (1982), and Miles (1995) found that NIBK seemed to be particularly fond of cicada nymphs (*Amphisalta*) and scarabaeid larvae. Reid et al. (1982) found plant material in 93% of 50 NIBK gizzards that were examined. Although, some plant material is thought to be incidentally eaten, hard material such as rocks and the hard kernels of some berries such as hinau berries (*Elaeocarpus dentatus*) are thought to be

ingested intentionally to aid the grinding of food (Gurr 1952, Reid et al. 1982). Watt (1971) found quite a number of pasture invertebrates in the gizzard of two NIBK, including: black field crickets (*Teloegryllus cornmodus*), black beetles (*Heteronychus arator*) and rove beetles (*Thyreocephalus chloropterus*).

Less is known about the diet of young NIBK. The few studies have shown that faecal samples mirror the environmental abundance of invertebrates closely (Shapiro 2005) and that young NIBK diet is similar to the diet of little spotted kiwi on Kapiti Island (Colbourne et al. 1990). Gizzard examination of dead young NIBK showed a high number of litter dwelling invertebrates which indicate mainly surface-feeding (Chan, 1999). The most common invertebrate found in the faecal samples of NIBK chicks studied on Ponui Island between November and December 2004 was scarabaeid larvae (Shapiro 2005), which matches adult preferences in other studies (Bull 1959, Reid et al. 1982, Miles 1995).

McLennan et al. (2004) examined the growth of young NIBK in a low density NIBK population around Lake Waikaremoana and developed a body mass growth curve. Chicks hatched weighing between 320 and 390g, and then lost weight in the first 10 - 15 days after hatching while they used residual yolk stores. Weight increased until birds reached an adult weight, averaging 2038g (SE = 16g) for males and 2662g (SE = 32g) for females. NIBK in this population grew very slowly relative to most other birds and at one quarter the rate that is allometrically predicted, taking 511 days to grow from 10 to 90% of asymptote weight.

Based on the four main factors I described above that affect growth rates, NIBK which are highly precocial, large, evolved in the absence of mammals and had high competition for food pre-human colonisation, are predicted to grow slowly. While this is generally true, there are some interesting deviations from this expectation. NIBK grow three times slower than the highly precocial megapodes (*Alectura lathamii*, *Leipoa ocellata* and *Macrocephalon maleo*) that receive no parental care after they hatch (Ricklefs 1973). The first two megapode species listed are similar in size to NIBK (1.5 - 2.1kg and 1.6kg, respectively) whilst the last is much smaller (0.2 - 0.3kg). NIBK at 2 - 2.8kg; NIBK grow much slower than their relatives the emu (adult weight of 30 - 45 kg; O'Brien, 1990) and ostrich (100 - 150 kg; Folch 1992), although both weigh significantly more than NIBK. Two hypotheses have been suggested as to why NIBK may grow so slowly. McLennan et al. (2004) suggested that NIBK

grow slowly because they had a reduced selection pressure for growing fast during their evolution. Fast growth may be beneficial if it results in a lower predation risk; however, it is energetically costly. Because NIBK evolved in an environment without mammalian predators, and in dense undergrowth in which they could avoid large, diurnal predators, there were no selective pressures for NIBK to grow quickly to avoid predators. We cannot determine the relationship between extinct predators and the growth of NIBK, because the fauna and flora of New Zealand has changed greatly in the last few hundred years. Predators that may have preyed on NIBK are now extinct or greatly reduced in numbers and introduced mammalian predators, that are probably much more destructive than native predators would have been, have taken their place.

Alternatively, Isabel Castro, Lee Shapiro and Rogan Colbourne (Unpublished manuscript, pers. comm.) hypothesised that slow growth rates have evolved in NIBK due to the large amount of competition for food resources with other native New Zealand ground feeding insectivores such as, saddlebacks (*Philesturnus carunculatus*), wrens (*family Acanthisittidae*), piopio (*Turnagra capensis*), snipe (*Coenocorypha spp.*) and snipe rail (*Capellirallus karamul*); before human colonisation. The adaptation of slow growth rates would have increased the likelihood of survival because physiological demands for growth would be lower relative to other species. Energy obtained from food could have been allocated to other necessary physiological processes such as thermoregulation. If the first hypothesis proposed by McLennan et al. (2004) is true, I would expect that growth rates would be similar between seasons and populations. However, if growth rates in NIBK are slow as proposed by Castro, Shapiro and Colbourne, due to competition for resources, we would expect that growth rates may vary between populations dependent on both the density of NIBK populations and the number of inter-specific competitors for food resources that are currently present in the New Zealand environment.

Behaviour and learning of young animals

Parental Care

Parents take their young to areas where food and shelter are available and young animals either learn actively, copy or get imprinted on such areas; contributing to their learning of how to forage and navigate in their environment (Gonzalez-Voyer and Kolm 2010)(Beach

1945). Parental care may be uniparental, solely by the mother (maternal care) or father (paternal care), or biparental whereby both parents exhibit parental care behaviours. It can have significant impacts on the growth, dispersal, and behaviour of offspring. In species that demonstrate little or no parental care, young need to fend for themselves without protection, provision of food, warmth or other aspects of parental care. These species are precocial, they hatch with feathers or down, their eyes are open and they ready to move and begin foraging soon after hatching (McNabb et al. 1984). Members of the family Megapodiidae exhibit no direct parental care. For example, the Australian brush-turkey (*Alectura lathami*) male builds a nest by piling vegetation into a mound, the female lays eggs inside the mound which are incubated by the heat produced when the vegetation decomposes (Birks 1997). After hatching the chicks dig themselves out and are completely independent, learning to move, forage, hide and communicate with Brush-turkeys without any parental help (Goth 2002).

Altricial species hatch in a state more closely resembling an embryo in which they lack feathers, their eyes are closed and they cannot thermoregulate (Starck 1998). Altricial chicks are entirely dependent on parental care for warmth, food and protection; and they do not leave the nest for some time after hatching. Most passerine species and parrots are altricial (Starck and Ricklefs 1998b). For example, cockatiels (*Nymphicus hollandicus*) are blind and have poor insulation when they hatch (Pearson 1998). Incubation is one form of parental care that at least one parent in all bird species must provide (exception Megapodiidae; Goth 2008) whereby the parent cares for the egg(s) by sitting on or near them. They warm and turn the egg(s) so that the embryos can develop correctly and are able to successfully hatch.

Although beyond the scope of this study is important to note that the level of parental care is often linked to mating behaviours (Wittenberger and Tilson 1980, Webster 1991). For example, one hypothesis for the evolution of social monogamy is that male care in addition to female care is necessary for the survival of the offspring (Emlen and Oring 1977, Wittenberger and Tilson 1980). When monogamous male snow buntings (*Plectrophenax nivalis*) were experimentally removed, food delivery to the young was greatly reduced and fewer offspring survived (Lyon 1987). Monogamy is more likely to be seen when the fitness cost is too high if male care is not given. This tends to occur when there are fluctuations in environmental suitability and/or extreme predation takes place (Webster 1991).

In a polygynous mating system, males provide significantly less parental care than females. Emlen and Oring (1991) suggested that there is a trade-off between parental care and mating effort which is due to the demands on time and energy. Polygyny will persist if females can successfully raise offspring alone. In contrast, polyandry is a mating system in which a female mates with a number of males during a breeding season. There are three main hypotheses regarding why male only care is generally seen in this system with little care exhibited by the females (this is referred to as sex-role reversal). Firstly, if a species has a low rate of fecundity they will benefit if the female is able to mate more than once in a season producing more than one clutch of eggs (Maclean 1969). Secondly, the egg size is large comparative to the female, thus the egg(s) require a great deal of energy to produce, and consequently less energy is used to care for the young after laying (Graul et al. 1977). Lastly, if the female has a greater opportunity for re-mating, they will benefit from increased fitness due to a larger number of offspring (Wittenberger 1981). Polyandry is seen in black coucals (*Centropus grilli*), whereby males take sole responsibility for parental care (Goymann and Wingfield 2004). In black coucals high nest predation and small territory sizes are important factors contributing to the evolution of a sex-role-reversal (Goymann 2004b). In cooperatively breeding bird systems young are cared for by both the genetic parents and other individuals. This generally results in a higher number of viable offspring or more young in each brood because there is a decreased risk of depredation and starvation (Brown 1987). Cooperative breeders tend to have prolonged parental care as multiple carers reduce the cost to each individual (Langen 2000). They also have high adult survivorship, a greater number of broods relative to non-cooperative breeders and smaller clutch sizes (Brown 1987, Arnold and Owens 1998). Interestingly, male birds with altricial young are more likely to bring food to the female and young, but do not incubate the eggs. On the other hand, males that have precocial young are more likely to incubate and care for the young, but not provide food for them or the female. This is thought to be related to differences in motor mechanisms for feeding and incubation (Ketterson and Nolan 1994).

NIBK Parental care

NIBK have traditionally been reported as a monogamous species with long term pair bonds, although divorces occur and individuals usually re-pair after losing a mate (Bassett et al. 2005, Holzapfel et al. 2008). However, research by Ziesemann et al. (2011) reported NIBK

breeding in trios of two males and one female and suggested that the mating system was facultative polyandry. More recent observations however have described quartets of two males and two females and a quintet of three males and two females (Isabel Castro and Sarah Jamieson pers. comm.) suggesting that the mating system is more flexible than previously thought. Copulation events begin in the winter months (June-August) and eggs are laid from July to February (Reid and Williams 1975). Females take approximately 20 - 25 days to form each egg and can lay one, two or occasionally three eggs per clutch, (Burbidge et al. 2003). Eggs are laid in a dug hole in the ground, tree root system or fallen tree (Calder 1979, McLennan et al. 1987). The NIBK egg weighs 14 - 20% of the females pre-laying weight, is one of the largest of all bird species and represents a significant parental investment (Calder et al. 1978). Normally one, but occasionally two (Ziesemann et al. 2011) or three males (pers. Obs.) incubate the eggs for 75 - 84 days (Reid and Williams 1975), leaving the nest to forage at night for 3 - 6 hours (Colbourne 2002; Jamieson et al. unpub. data). However, because females take a long time to produce each egg, if two eggs are laid in a clutch, males usually incubate for longer than 84 days at a time (Colbourne 2002). Due to the large size of the egg, and the significant amount of yolk, NIBK chicks hatch with a large internal yolk sac, approximately 34% of the body mass at hatching (Calder 1979). The yolk is absorbed over the first 10 – 15 days after the chicks hatch, supplying them with the energy required for growth and other physiological processes (Robertson et al. 2003). Because of the significant investment both in the egg size and the length of incubation, when NIBK chicks hatch they are extremely precocial, fully developed, miniature versions of adults (Robertson et al. 2003). They spend approximately five days in the nest, then start venturing out at night by themselves to explore and forage in the surrounding habitat (Colbourne 2002). NIBK chicks initially return to the nest with the male to roost during the day, and then fledge the nest at an average of 25 days of age ($\pm 14d$) (McLennan et al. 1996, Colbourne 2002). NIBK have a low rate of fecundity with pairs successfully producing 0.85 chicks per year (McLennan et al. 1996).

Although this has not been studied in any detail NIBK are not thought to provide any parental care to their young aside from laying and incubating the egg, and brooding chicks. Parents have not been observed teaching their young in any aspect, which suggests that they have innate behaviours, or learn to forage and find food by practising. In summary,

NIBK invest heavily in their young in egg production and incubation resulting in highly precocial young that have little or no parental care after hatching.

Natal and Juvenile dispersal

Dispersal movements of young individuals have important consequences on population dynamics by influencing species evolution (Greenwood 1980, Johnson and Gaines 1990), local adaptation (Lenormand 2002) and the survival of metapopulations (Hansson et al. 2002). There are four main non-mutually exclusive hypotheses explaining why individuals disperse: economic thresholds, conflict over resources, mating systems and inbreeding avoidance. It must be noted that although these factors are thought to affect the dispersal movements of young individuals by influencing how far they move, some of these factors will also affect the movements of adults after they have dispersed from their natal area and have begun breeding. The aim of this section is to give a general overview and background about why animals disperse, so that the dispersal movements of NIBK in both past studies and in this thesis may be better understood.

The economic thresholds hypothesis suggests that young individuals disperse from an area when resources are below a sustainable level (Lidicker 1962, Grant 1978). High natal dispersal rates may be an ultimate adaptation to resource limitation (Lomnicki 1988). This is seen in young red-cockaded woodpeckers (*Picoides borealis*), whereby males were more likely to stay in their natal territory as helpers if the territory was good. These individuals exhibit natal philopatry- the tendency to remain in or close to the parent's home range (Massot and Clobert 2000). In contrast, if resources in the territory were poor, individuals were more likely to disperse (Pasinelli and Walters 2002).

This hypothesis links with the second hypothesis that conflict over resources and competition with conspecifics affects dispersal (Andreassen and Ims 2001, Serrano et al. 2003, Wauters et al. 2004). If resources are limited there is likely to be a greater conflict over resources and inferior and/or young individuals may be forced to disperse further because they cannot compete for resources with stronger individuals. In North American pikas (*Ochotona princeps*) dispersal of juveniles was related to competition for territories, with juvenile pikas being forced to settle in vacant territories near their natal territory (Peacock 1997). Conflict over resources is also greatly affected by ecological and population

constraints i.e., density and population saturation (Delestrade et al. 1996, Negro et al. 1997). Resources are not limited to food, and may include conflict over shelter sites, territory and mates. If young individuals are considered a threat they may be required to disperse to find a new territory to occupy, resulting in a greater natal dispersal distance. For example, Juvenile guanacos (*Lama guanicoe*) are expelled from family groups by aggressive territorial males, this expulsion is believed to be driven by competition for food in these territories (Sarno et al. 2003). If young animals are not a threat to breeding adults they may not need to disperse from the territory resulting in a smaller natal dispersal distance. This was the case for the male red-cockaded woodpeckers mentioned previously. Juvenile males were tolerated in their parents territory and were helpers in the following season (Pasinelli and Walters 2002).

Some studies suggest that individuals prefer to move to areas with unoccupied territories and that fitness will decline with increasing conspecific density (Rosenzweig and Abramsky 1985, Parker and Sutherland 1986). Other studies report examples of the attraction hypothesis where individuals may settle in the same area because it gives a number of advantages. For example, the number of conspecifics may reflect resource quality (McPeck and Holt 1992) and juveniles may use adults as an indicator of quality, protection in numbers from predators or more opportunities for mating when settling in a group (Muller et al. 1997). After translocation, the hihi or stitchbird (*Notiomystis cincta*), a species endemic to New Zealand, prefers to settle in areas where there are conspecifics (Castro et al. 1994).

Additionally, the conflict over resources hypothesis may be linked to the mating system hypothesis that has been proposed to explain differences in dispersal between sexes (Greenwood 1980). In this hypothesis, dispersal distance is related to the amount of time and energy each sex devotes to defending a territory or mate as adults. In monogamous bird species, where males tend to defend territories and females select mates; juvenile females disperse further than juvenile males in 49 - 59% of studies (Greenwood 1980). There is an advantage to males being familiar with their natal area when they need to defend their territory. Female laysan albatrosses (*Diomedea immutabilis*), for example, were found to disperse further from the natal nest than males (Fisher 1971). A comprehensive list of sex biased dispersal can be found in Greenwood (1980).

The final hypothesis, suggests that inbreeding avoidance is an ultimate explanation for the distance individuals disperse from their natal area. This hypothesis also aims to explain the differences in dispersal between sexes (Dobson and Jones 1985), stating that dispersal differences between sexes and/or related individuals will reduce the chance of inbreeding (Dobson and Jones 1985, Pusey 1987, Pusey and Wolf 1996). Szulkin and Sheldon (2008) found that individual great tits (*Parus major*) that dispersed shorter distances had higher levels of inbreeding than those that dispersed further. Inbreeding and the resulting inbreeding depression can significantly affect population growth and viability, therefore it is beneficial to avoid inbreeding (Amos and Balmford 2001, O'Grady et al. 2006).

A large number of studies have centred on hypotheses that explain general patterns regarding how and why individuals disperse (i.e., Lidicker 1962, Greenwood 1980). Fewer studies have explored dispersal in the wild, however this now appears to be an increasing focus of dispersal research (Negro et al. 1997, Verhulst et al. 1997, Alonso et al. 1998, Spear et al. 1998, Forero et al. 2002, Serrano and Tella 2003, Serrano et al. 2003). The relatedness of individuals, social hierarchies, relative dominance status, habitat and individual quality are being examined because they are believed to cause variation in dispersal distances. This highlights the need for studies aimed at understanding the dispersal distances of individuals and populations alongside factors that may influence dispersal such as rainfall and food abundance, and population variables; to determine if these factors do indeed influence dispersal.

NIBK Dispersal and Habitat selectivity

Birds that cannot fly or swim are restricted in terms of the distance they can disperse, particularly, those that live on islands or in areas that have barriers such as large rivers or lakes. Members of the ratite group are either poor fliers or completely flightless as is the case with NIBK (Reid and Williams 1975). However, NIBK possess strong legs which provide a means for dispersal. NIBK are also nocturnal and have poor eye sight, therefore they are thought to rely heavily on tactile and olfactory information to navigate within their environment (Cunningham et al. 2007, Martin et al. 2007, Castro et al. 2010).

Young NIBK can disperse some distance after leaving the nest (700-2000m; McLennan 1997, Forbes 2009). Although most long distance dispersal so far reported, occurs during the sub-

adult stage, from nine months of age when birds are not yet breeding (Robertson 2004). Studies have shown that sub-adult NIBK are capable of dispersing 1 - 50km from their natal area (see Table 1.1). However, comparisons among these studies is difficult for two reasons, firstly ages are classified differently; in some cases young are considered chicks until they fledge at which time they become juveniles and do not become adults until sexual maturity (McLennan et al. 1996). In other case NIBK are considered chicks until they reach 1000g, at which point they are considered sub-adults until they reach 4.5 years of age, are breeding, or their bill grows <1.5mm in a six month period (Forbes 2009). Secondly, the number of times NIBK were located varied between studies, is sometimes not stated, and is not at regular intervals. For example, if an individual NIBK is found one kilometre from the natal nest at two years of age and has not been found since it was a chick, the authors assumed it had only dispersed a distance of one kilometre. However, this individual is not likely to stay in the same location for this duration and may have moved variable distances from the natal nest before being found at its given location. Therefore, unless this final measurement is taken at the same age for all individuals comparisons between populations are impossible.

Table 1.1. A summary of published studies examining dispersal distances of North Island brown kiwi from other studies and locations. Listed is the location of the study, the North Island brown kiwi taxa, the age or age-class of the North Island brown kiwi studied, how the authors reported dispersal distance and the number of individuals in the study.

Location	Taxa	Age (d)	Source	Number	Sex	Class	Distance	Authors
Tongariro	Western	163-1018	BNZONE™	21	F>M	Sub-adult	1-12km from release site	Grant 2003
Lake Waikaremoana	Eastern	120-180	Wild	58	M=F	Juveniles	Move up to 2km then settle in area for 4-6months with small home range <3ha. Sometimes in parent territory.	McLennan 1997
Lake Waikaremoana	Eastern	300-390	Wild	11	F>M	Sub-adult	Average minimum 5.24km ± 0.97 (SE)	Basse and McLennan 2003
Trounson	Northland	U	Wild	U	M=F	Juvenile	Some recruited in park others move >25km to neighbouring Waipoua forest	T. Herbert & N. Coad in Forbes 2009
Trounson	Northland	U	Wild	U	U	Juvenile	'many kilometres from natal area'	Chan 1999
Moehau	Coromandel	average age 149 (95% CI 14.3)	Wild	60	F>M	Chick	834m ±131 (SE)	Forbes 2009
Moehau	Coromandel	see above	BNZONE™	10	F>M	Chick	See above	Forbes 2009
Moehau	Coromandel	average age 682 (95% CI 85.8)	Wild	77	F>M	Sub-adult	Females (7215m) males (4226m)	Forbes 2009
Moehau	Coromandel	U	Wild	U	U	U	20-50km	P. de Monchy pers. comm. In Forbes 2009

*if one sex was found to disperse further than the other this was demarcated by the greater than symbol (>), if dispersal distances were found to be the same between sexes this was demarcated by an equal symbol (=). U = if the information is unknown or could not be obtained.

There are four main factors that are thought to influence NIBK dispersal, these are: barriers to dispersal, population density, sex, and habitat selection. Chan (1999) suggested that rivers may be barriers to dispersing NIBK, because juveniles appeared to be following the Waima River, Northland (approximately 20m across) and also fence lines. However, Gibbs (2000) and Robertson (2004) noted that both rivers and fence lines (exemption predator

proof fences in mainland islands) were not significant barriers to dispersal. It was also speculated that habitat fragmentation of native forest negatively influenced dispersal patterns and affected the survival of NIBK because birds avoided walking over large open areas such as pasture (Diamond 1984, Forbes 2009). However, NIBK in Northland populations dispersed over pasture, (Chan 1999, Forbes 2009) and on Ponui Island have been found foraging in pasture (Cunningham and Castro 2011). Additionally, juveniles are thought to survive better in some modified habitats relative to native forest because there is a reduction in predation pressures (Robertson 2004).

The density of NIBK populations may be an important factor affecting the dispersal rate of individuals, although the relationship appears uncertain. NIBK sub-adults that were reared in captivity and released into areas in the Tongariro region, without resident birds, were found to disperse further than when resident NIBK were present (Grant 2003). In contrast to Grant (2003), based on population models from kiwi Sanctuaries, Robertson (2004), hypothesised that the rate of emigration (kiwi leaving an area) is density dependent, with increasing density there are fewer gaps for new individuals to establish territories therefore emigration rates and hence dispersal distances will increase once a population reaches carrying capacity. In the instance of NIBK, attraction of conspecifics may occur at lower densities, however, at higher densities dispersal may increase as territories or areas become saturated with individuals. This type of dispersal behaviour was seen in young Lesser Kestrel colonies (*Falco naumann*); the probability of young staying in the natal colony increased with the number of philopatric adults, up until a point, past this point recruitment was prevented by more dominant adults (Serrano et al. 2003).

Sex differences in dispersal were also found in NIBK (Grant 2003, Forbes 2009). Both Grant (2003) and Forbes (2009) found that average dispersal distance per month was greater for sub-adult females (750m 95% CI \pm 227m) than for males (545m 95% CI \pm 193; Forbes, 2009). It should be noted that Grant followed NIBK that were hatched and reared in captivity until they reached 1000g, while Forbes followed wild young as well as young reared in captivity. Differences in dispersal were additionally found between NIBK that were reared in captivity (BNZONE™) and those that hatched in the wild; those that were reared in captivity were found to disperse shorter distances than wild chicks (Grant 2003, Forbes 2009).

Habitat selection may also play an important role in the movement and dispersal of NIBK. A large amount of research has taken place looking at roosting sites of NIBK during the day (Taborsky and Taborsky 1995, Chan 1999, Gibbs 2000, Forbes 2009), and what their habitat use is at night (Colbourne and Kleinpaste 1983, Taborsky and Taborsky 1992, 1995, Chan 1999). NIBK have been found roosting in a number of habitats including: all forest types, coastal sand dunes, high mountain tussock land and exotic pine forest plantations (Colbourne and Kleinpaste 1983, Taborsky and Taborsky 1992, 1995). Studies have found that roost type is highly dependent on the habitat type (Taborsky and Taborsky 1995, Miles et al. 1997, Forbes 2009). Miles et al. (1997) found that surface roosts were used more in native toe toe (*Austroderia* spp.) and exotic pampas grass (*Cortaderia* spp.) and less in logged forests relative to unlogged and broadleaf/scrub forests in the Tongariro region. Forbes (2009) observed that NIBK in the Coromandel were more likely to be on the surface in manuka (*Leptospermum scoparium*) and kanuka (*Kunzea ericoides*) forest relative to other forest types (69%) and that broadleaf forest was the only forest type in which hole roosts were used more than surface roosts. Additionally, roost sites have been found to differ significantly between sexes (McLennan et al. 1987), elevations, age classes (Forbes 2009) and seasons (Miles et al. 1997). Forbes (2009) found that females in the Coromandel used surface more often than holes to roost and males used each roost type a similar amount. McLennan et al. (1987) did not differentiate between sexes but noted that adult NIBK in the Hawkes Bay were found 36% of times located in hole roosts and the rest of the time under vegetation or in hollow logs. Sub-adults in the Coromandel used holes more with increasing elevation and selected sub-alpine forest over broadleaf forest (Forbes 2009). The roost site was also dependent on the season, in the summer surface roosts tended to be used more whilst dug roosts were used more during spring and winter (Miles et al. 1997). NIBK showed a tendency to roost in a different location each day but occasionally returned to sites used previously (McLennan et al. 1987, Ziesemann 2011).

It was suggested that the location of the nest site is selected by the adult for the benefit of the chick (Taborsky and Taborsky 1995) and that the location would bias the habitat choice of juvenile NIBK (Chan 1999, Gibbs 2000). However, this hypothesis was dismissed because whilst some young NIBK were found close to the nest, others were found to move large distances indicating that they were not limited to the habitat in their natal area (Chan 1999,

Gibbs 2000). In the Coromandel, young NIBK tended to roost on the surface (rather than in holes) and under debris such as dead fern fronds rather than other ground cover types (Forbes 2009). In other studies at Lake Waikaremoana (habitat consisted of: native forest, with mixed beech (*Nothofagus* spp.)/podocarp on lower slopes with almost pure beech at higher levels) and Trounson Kauri Park (Northland; mixed podocarp/angiosperm forest, and 100ha of leased farmland), young NIBK show a preference for seral habitat relative to mature forests particularly in the winter months (McLennan 1997, Chan 1999, Gibbs and Clout 2003). Gibbs (2000) found over a period of one year (1998-1999) at Trounson Kauri Park that young NIBK that used three habitat types (mature forest, seral and mature vegetation), versus just one or two, had a greater chance of survival. Use of different habitats may be important as each can play a different role in protection from weather and provision of warmth and food, which may ultimately affect survival. The habitat use of young NIBK at Trounson Kauri Park was different to adult NIBK with adults selecting more for podocarp/broadleaf forests (Gibbs 2000). This difference was hypothesised to be caused by increased bill length with age, resulting in a difference in food availability for young and adult NIBK (Gibbs 2000). The difference may also be due to a greater density of ground cover in seral vegetation (Taborsky and Taborsky 1995, Chan 1999) that allows young NIBK to avoid native aerial predators such as the Australian harrier (*Circus approximans*) and New Zealand falcon (*Falco novaeseelandiae*).

NIBK live in a range of habitats from: regenerating native bush, exotic pine, mature native forest and pastures, and in areas that range from no predator trapping regime to intensive management such as that found on pest free islands or mainland islands with predator-proof fences. It is important to understand the dispersal of NIBK in a range of conditions to ensure conservation areas are large enough to contain dispersing NIBK.

Mortality

In most species the juvenile life stage is the most vulnerable with the survival of young birds lower relative to adults (Lack 1946). Altricial chicks are often completely vulnerable in the nest with no feathers to provide warmth or the ability to move and find food. They are completely reliant on their parents to provide these resources and are at high risk of being depredated, dying from starvation and/or hypothermia if their parents are not vigilant and

able carers. Young of species that hatch more highly developed face another set of issues; they must warm, feed and protect themselves from predation, with little or no help from their parents (Starck and Ricklefs 1998b). There are a number of interacting factors that greatly affect the survival of young chicks these include yolk related infections, climate factors, food availability, parasite load, and predation.

Yolk sac

In birds, a number of health related problems may occur during hatching and shortly after. Just before the chick hatches the remaining yolk sac in the egg is pulled into the abdominal cavity. This yolk is absorbed shortly after hatching and provides nourishment before the chicks are fed or can feed themselves (Khan et al. 2004). Yolk related mortality can be difficult to find in wild populations therefore most studies have used domestic reared animals from the poultry industry. In some instances the yolk sac is not completely internalised before the chick hatches. This may be caused by low temperature or high humidity during development (Harrison and Harrison 1986). In other instances yolk retention, where the yolk is not completely absorbed once the yolk sac is internalised and the chick has hatched, is caused by bacterial infection of the yolk sac or infection in the umbilicus (Kenny and Cambre 1992, Deeming 1995). Infection tends to occur because yolk sacs provide ideal conditions for bacterial growth (Khan, 2004). *Escherichia coli* is the most common bacteria in the yolk sac of domestic chicken chicks (*Gallus gallus domesticus*; Sharada et al. 1999). *Salmonella* (Alisantosa et al. 2000), *Staphylococcus*, *Streptococcus*, *Proteus* and *Bacillus* (Anonymous 2000) can also cause infection. In addition, ostrich chicks (*Struthio camelus*) that did not have enough oxygen in the last week before hatching had a greater prevalence of retained yolk sacs (Tully and Shane 1996). Yolk related factors cause 13% of mortalities in domestic ducks (*Anas platyrhynchos domesticus*; Sharma and Kaushik 1986b), 20% in domesticated turkeys (*Meleagris gallopavo*; Sharma and Kaushik 1986a, Thyagarajan et al. 1987), 7.3% in domesticated geese (*Anser anser domesticus*; Boado and Rojas 1990) and 30% in domesticated ostriches (Aslan et al. 2008). Precocial chicks tend to have a much larger yolk sacs weighing 12 - 34% of their body weight, in comparison to altricial chicks whose yolk sac only weighs 5 - 10% of their body weight, making precocial chicks are more prone to infection (Calder 1979, Schmidt et al. 1985, Welty and Baptista 1988).

Environmental factors

Birds are endothermic and maintain a body temperature between 38 and 44°C (Prinzinger et al. 1991). Continuous energy is required to maintain thermogenesis and other physiological functions (Peters 1983). Without adequate energy input starvation can take place resulting in a number of negative thermoregulatory, behavioural and metabolic consequences (McCue 2010). Temperature may have a negative influence on birds in two ways, firstly temperature may affect the abundance of food in a bird's habitat by reducing the food available (e.g., invertebrates) and subsequently energy input. Secondly, low or indeed extremely high temperatures may cause an increased need for thermoregulation, resulting in higher energy requirements. Rainfall can influence energy intake and survival as well, however its effects can be positive or negative, depending on the species (Moss 1986, Beintema 1994, Arlettaz 2010). Rainfall can also cause thermoregulatory challenges, whereby when animals are wet and/or cold resulting in ambient temperatures below their thermo-neutral zone they require a greater amount of energy to keep warm. Because young birds have higher energy demands while they are growing and a greater surface area to volume ratio (causing faster heat loss or gain) they are more likely to be negatively affected by these factors and suffer mortality

Parasite load

Heavy parasite loads, both internal and external can significantly affect the health of an animal, lowering the effectiveness of their immune system and in some instances causing death (Toft 1991). For example, purple martin (*Progne subis*) nests without acarine nest parasites produced heavier young than those with the parasite (Moss and Camin 1970). A similar result is also seen in cliff swallows (Chapman and George 1991). Other parasites that also affect young birds include: nest mites (Burt et al. 1991), dipterous fly larvae (Delannoy and Cruz 1991, Rogers et al. 1991) and ticks, which are also vectors for a number of blood borne pathogens (Pruett-Jones and Pruett-Jones 1991).

Predation

Young animals are more vulnerable to predation because they tend to be smaller relative to adults and/or have limited means of defending themselves. If a species is highly precocial,

young may have little or no parental protection from predators. For example, the mortality rate of Australian brush turkey chicks (*Alectura lathami*), that were released into two small rainforest patches, was found to be between 88 - 100% due to predation by cats and birds of prey. The survival rate of those released into thickets was higher than those that were released into rainforests; the author thought this was because chicks were better protected from predators in thickets (Goth 2002). Young altricial species can be vulnerable in the nest if the parents leave to find food or other resources.

Additionally, animals are more vulnerable to predation when they have a negative energy balance or parasite infection. Hudson (1986) found that red grouse chicks (*Lagopus lagopus scotica*) were more susceptible to predation when their body condition was lowered due to the presence of endo-parasites, and those more heavily infected with parasites had a higher rate of mortality. There is evidence that some predators may selectively catch heavily infected birds (Dobson and Hudson 1995). Interestingly, Dobson and Hudson (1995) observed that female red grouse emit a scent for most of the year by producing caecal faeces, with the exception of when they are incubating. The parasite *Trichostrongylus tenuis* is known to burrow into the caecal mucosa and this is thought to affect the ability of birds to control scent emission. As a result incubating birds with heavy parasite loads were more susceptible to mammalian predators that hunt by scent, such as dogs that were experimentally used to find the birds.

Mortality in NIBK

A study of 12 populations of NIBK, great spotted kiwi and rowi, estimated that the mortality rate of young kiwi in mainland populations is 94% during the first 100 days of age (McLennan et al. 1996). Natural causes of death accounted for 18.4% of these deaths and included incidents such as falling out of nests, down steep slopes into streams or entangled in vegetation (McLennan et al. 1996). Predators killed at least 60% of young kiwi, with stoats mainly responsible for these deaths (McLennan et al. 1996); other predators included feral cats, Australasian harriers and potentially weasels. Forbes (2009) similarly found that predation was responsible for 60% of deaths of young NIBK on the Coromandel, with stoats being the main predator. In Forbes (2009), conservation management techniques were also responsible for 20% of deaths, mostly through transmitters becoming entangled in

mangemange (*Lygodium articulatu*), a ground creeping vine. This mortality figure may be much lower in other areas, for example, Pim de Monchy reported 26 deaths due to entanglement in mangemange, from a total of 2,491 transmitter years using data from 12 sites (unpub data 2006 in Forbes 2009). An additional 20% of deaths in the Forbes study (2009) were due to natural or unknown causes. NIBK evolved in an environment free from mammalian predators. The predators present in pre-human time included birds of prey and, sit and wait predators such as the tuatara (*Sphenodon* spp.). With these predators there is an advantage to the chicks being small and able to freeze or run away quickly through the undergrowth, however, this advantage does not work with small and sinuous scent orientated mammalian predators (McLennan et al. 1996).

Although NIBK deaths have not been directly attributed to external parasite infestations, NIBK often carry a large number of parasites especially ticks, which may disadvantage those that have diseases or inadequate energy intake (Castro 2006). NIBK ticks (*Ixodes anatis*) are the most common tick found on NIBK and tend to be present at high number in burrows (Peirce et al. 2003). Numerous NIBK may inhabit each burrow but they also move between a number of burrows (Ziesemann 2011), allowing transmission of ticks and diseases between birds. Ixodid ticks are primary vectors for avian piroplasmas (*Babesia* spp.), therefore it is likely that *I. anatis* is a vector for *Babesia kiwiensis* and *Heptozoon kiwii* (Peirce et al. 2003). The effect of *B. kiwiensis* and *H. kiwii* on NIBK are not known and both genera are not usually associated with death or disease in their hosts. For example, only one *Babesia* of 13 recognised species was found to be pathogenic to its host (*B. shortii*) (Peirce et al. 2003). However, clinical observation of NIBK chicks with *Babesia* indicate that parasitism may lower chick viability when they are most vulnerable, i.e., when suffering for negative energy balance (Jakob-Hoff et al. 2000). Further research is needed to identify the extent of this parasite in NIBK populations, if there is a negative effect of *B. kiwiensis* and *H. kiwii* on the survival of NIBK, and if there is potential for ticks to carry other pathogens such as avian malaria.

Determining the cause of mortality in NIBK appears to be limited to physical signs i.e., teeth marks, remains, entanglement, cliffs, road kill. Most studies list a number of cases with unknown causes of death (i.e. McLennan et al. 1996, McLennan et al. 2004, Forbes 2009, Reid et al. 1982, Pierce 1997). It is important to understand what causes the mortality in

these 'unknown' cases by accurately autopsying the bird, so if possible, the proportion of these unknown cases can be reduced and contribute to slowing the rate of NIBK population decline.

Aims, Contribution and Study Site

Purpose of this study

NIBK are unusual birds in many aspects of their biology. In particular, their breeding biology is unparalleled with the exception perhaps of other species in its own genus. I have been particularly impressed by their incredibly precocial chicks and the huge challenges they face for survival. NIBK as a species continues to decline, with this decline centred on low chick recruitment. This is despite success with BNZONE™, predator control, and translocation to mainland islands with predator-proof fences or predator-free islands. This decline highlights the importance of learning more about NIBK biology. The aim of this thesis was to collect information on the growth rates, behaviour, movements and survival of North Island Brown kiwi in a high density population with low mammalian predator community.

Aims

1. Present the growth rate of young NIBK and determine and report if any environmental factors influence growth rate.
2. Determine the behaviour of young NIBK around the natal nest, presenting information of vigilance, learning behaviours and interactions between adults and/or chicks.
3. Intensively follow young NIBK to determine dispersal movement, habitat choice and variables that influence movement.
4. Intensively follow young NIBK to ascertain the causes of mortality.

Importance of Thesis

- The conditions at this study site were assumed to be closer to the conditions in which NIBK may have lived prior to the arrival introduced mammalian predators. NIBK in this study population persist at a high density in the presence of a low number of predators.
- The overall aim of NIBK conservation is to increase population numbers so they reach high 'natural' densities such as this population. Therefore, it is important to

understand how interactions take place in this type of population i.e., are there any large risks to survival that can be remedied and benefit the survival of the species? How large of a reserve is required for an increasing population? What type of food, level of food or habitat influence movement and survival? Whilst this thesis does not answer all of these questions it aims to be a building block with which further research can expand on and benefit from.

- To my knowledge an in-depth study on the weekly growth rates (with the exception of Shapiro 2005), daily dispersal, and causes of mortality has not been carried out. Nor has a study taken place describing the behaviour of young NIBK around their nest. Furthermore, in this study I aim to look at the interactions between the behaviour of NIBK and the environment; how rainfall, temperature, food abundance and availability affect the growth, dispersal and survival of NIBK.
- Due to their distinct biology and behaviour, NIBK are also a very interesting species to study and represent extreme examples in many fields. Understanding species such as this is important to understanding evolutionary patterns in nature. For example, NIBK are highly precocial and grow incredibly slowly; why might this be and how do they compare to other species? Are there species with similar ecological traits that grow just as slow though are yet to be studied?

History of NIBK at the Study site

Ponui Island (or Chamberlin's Island; 36°50'S, 175°10'E) has an area of 1770 ha and is located in the Hauraki Gulf of New Zealand (Figure 1.1a). Approximately two thirds of the island (1180 ha) is covered by exotic pasture and is farmed for beef, wool, lamb and a range of horticultural products such as stone fruit; the remaining area is native forest (Figure 1.1b; Miles and Castro 1999). In June 1964 on request from the owners, the New Zealand Wildlife Service released six NIBK that originated from Little Barrier Island. Later that same year a further eight NIBK were released from Waipoua, Northland (Colbourne et al. 2005). The density of NIBK is now estimated at one bird per ha (Cunningham et al. 2007). The primary study site is approximately 200 ha and consists of three neighbouring forested catchments and neighbouring pastureland (Figure 1.1c). The vegetation at the study site is a mixture of broadleaf forest, regenerating kauri forest (*Agathis australis*), scrub (primarily *Kunzea ericoides*, *Pseudopanax crassifolius* and *Coprosma* spp.), and swamp (*Typha orientalis*)

bordered and/or mixed with pasture (Shapiro 2005). In addition to cattle and sheep which are farmed, and feral donkeys, the only introduced resident mammals on the island are farm dogs (*Canis domesticus*), rats (*Rattus rattus* and *R. norvegicus*) and both feral and domestic cats (*Felis catus*). Feral cats and dogs are thus the only potential introduced predators of NIBK, with feral cats being the only introduced predator that could have an impact on NIBK numbers because the farm dogs are contained. Potential native predators of NIBK on the island are Australasian harriers (*Circus approximans*) and morepork (*Ninox novaeseelandiae*).

Study site and subjects

As part of an on-going study programme, between July 2010 and March 2012, 48 adult NIBK were fitted with either 'Activity' radio transmitters (Kiwitrack Ltd., Havelock North, NZ) or 'Chick Timer' radio transmitters (WildTech Ltd., Havelock North, NZ). Pulse rates from transmitters were detected using a Telonics TR4 receiver and Yagi three element antennae. Each bird had an individual radio frequency so they could be individually identified. Activity transmitters change the pulse rate of the signal from 30 pulses per minute to 60 when the bird moves allowing the observer to detect and follow their movement. If the transmitter did not move for 48 hours the pulse rate changed to 90ppm indicating possible mortality. When male NIBK are incubating their nightly activity outside the nest significantly reduces and the night a chick hatches the male often does not leave the nest (Jamieson et al., unpub. data). Chick timer transmitters have a data logger which records daily the total active period of the bird (when they are outside their burrow at night) and uses this information to tell the observer via the receiver whether the bird is incubating/brooding, has deserted a nest, or has died. This activity information can also be downloaded from the transmitter after it is removed from the bird. Therefore 'chick timers' allowed the estimation of the most likely laying and hatching dates. Unlike activity transmitters, 'Chick timers' do not inform of immediate activity therefore birds must be located via their individual frequencies to determine whether they are moving. Adults were located daily for at least two weeks of each month, with monitoring increasing during incubation particularly when approaching the estimated hatch date.



Figure 1.1. Ponui Island, New Zealand where the ecology of young North Island brown kiwi was studied. a) Aerial photograph of New Zealand with the general location of Ponui Island indicated by the white circle. b) Aerial photograph of Ponui Island, landmass visible in the top left hand corner is Waiheke Island, lower left hand corner is Pakahi Island, study site is highlighted within the white rectangle. c) Study site with three main gullies demarcated in white. Maps are orientated north and were sourced from Google Earth 19 November 2012.

Hatching date was confirmed by either visualising the chick outside the nest with a remote video camera (Sony Handicams -DCR-HC40E & DCR-HC42 with NightShot™ function) and infrared lights (IRLamp 6, Bat Conservation and Management Inc), or by visiting the nest at

night while the nesting male was away. Females do not incubate or provide brood care. Chicks were considered 0 days old on the day of hatching. Chicks were fitted with a Sirtrack® V1L118A chick transmitter, weighing ~7g, including the band, with a maximum life of 273 days (Miles and McLennan 1998). Attachment and management of the transmitter followed the Kiwi Best Practise Manual; in summary chicks were banded when they were older than five days or when they weighed >250g (Robertson et al. 2003). Transmitters are placed on the tibiotarsus of the bird, and shifted from one leg to the other monthly to prevent injury to the leg and ensure the size of the band is corrected as the young NIBK grows. I used feathers that naturally fell out or dropped during handling to sex each chick using DNA techniques at the Massey University Equine Parentage and Animal Genetics Services (Huynen et al. 2006).

Permits and Animal Ethics:

This project was conducted under DoC permit AK-28039-FAU and under Massey University Animal Ethics 10/30. Permission to work on South Ponui Farm was granted by the owners Peter and Pat Chamberlin and Ros and David Chamberlin.

Chapter 2: Factors influencing growth rates of an extreme precocial species: North Island brown kiwi



Introduction

Young animals grow and develop through the proliferation of cells that forms tissues and organs. Birds initiate growth inside the egg at the start of incubation and continue to grow after hatching. Some chicks hatch more developed, or functionally mature, than others and the degree of development can be located along a spectrum that varies from altricial to precocial (Starck and Ricklefs 1998b). Altricial species hatch in a state of very low functional maturity; they have closed eyes, no feathers and are incapable of thermoregulation (Starck and Ricklefs 1998b). These chicks are dependent on parental care for warmth, food and

protection. This parental investment frees up energy that chicks would otherwise need to invest in these processes and as a result they are able to allocate a large amount of energy to growth (Ricklefs 1969b, Ricklefs and Cullen 1973). In contrast, precocial species are very functionally mature at hatching. They have open eyes, are feathered and capable of thermoregulation, and receive less parental care (Starck and Ricklefs 1998b). Therefore, they need to invest more energy in locomotion, foraging and thermoregulation, resulting in less energy available for growth (Ricklefs 1969b, Ricklefs and Cullen 1973).

There are a number of general characteristics shared by precocial species; for example, adults have the tendency to be large, ground-dwelling birds that feed on slow moving prey on the ground or surface of the water (Ricklefs and Starck 1998). Furthermore, basal metabolic rates tend to be lower in precocial birds as rates decrease with increasing body size (Schmidt-Nielsen 1984). Altricial adults are smaller, more active and tend to use flight for foraging (Ricklefs and Starck 1998). There are advantages and disadvantages to both developmental modes, such as precocial chicks being able to move about and avoid predation from a young age, while altricial birds grow quickly and have shorter incubation periods (Starck and Ricklefs 1998b).

Whilst the developmental mode and type of growth rate are species specific, there are many elements that contribute to the growth rates of individuals such as environmental factors, and physiological and anatomical constraints (Konarzewski et al. 1998). Environmental factors can influence a birds' growth rate. For example, high rainfall may increase food abundance and hence the rate of growth (Beintema 1994), however it may also cause a thermoregulatory challenge, limiting energy that can be allocated to growth and thus decreasing survival (Green 1984). There are three levels of physiological and anatomical constraints that act on the growth of birds (Ricklefs et al. 1998). Firstly, growth can be limited by the availability of a resource, primarily food. Secondly, growth may be limited by the ability of an individual to utilise resources. For example, the digestive tract in altricial species may not be fully developed, restricting the rate of food digestion and the extraction of energy needed for growth. Thirdly, there is a trade-off between mature functioning tissues, and cell growth and proliferation. This trade-off is why growth rates of precocial chicks tend to be slower in comparison to altricial chicks.

There is a large knowledge gap regarding the study of individual species growth rates and developmental modes. This gap makes it difficult to generalise and categorise growth rates amongst species. By looking at individual species we can understand more about the specific strategies used to grow and develop, how this relates to fitness, and how the different strategies may have evolved. It is particularly important to examine those species at the extremes of the spectrum as they provide the strongest points for comparison. We can then fit other species along the altricial - precocial spectrum and predict what their growth rates might be. Additionally, we can hypothesise how other life history traits may relate to developmental mode.

Here I have used a population of North Island brown kiwi (NIBK, *Apteryx mantelli*) as a case study to examine growth rates at the precocial end of the spectrum. NIBK are the classic extreme precocial species, they have a long incubation period of 75 - 84 days (Calder et al. 1978). When chicks hatch they are developmentally mature, fully feathered and able to thermoregulate shortly after hatching. Chicks also hatch with an extremely large yolk sac, that is 34% of the neonatal mass (Calder 1979) this sustains them for up to 17 days after hatching; allowing them to be independent from parental food provision from a very young age (Calder et al. 1978). They have full locomotory function within five days of hatching when they leave the nest at night to forage by themselves and are almost entirely independent of their parents after hatching (Chapter 3). The only form of parental care known to date is brooding by the father when the chick roosts in the nest during the day before fledging. Chicks fledge from the nest at an average of 24 days of age (± 3 days, Chapter 3). Other features that are shared with other precocial species include: medium-sized adults, weighing between 2.0 - 2.8kg (Castro and Morris 2011), ground dwelling, and feeding on slow moving prey such as scarabaeid larvae (Shapiro 2005).

Understanding more about an extreme precocial species, the North Island brown kiwi, will contribute significantly to the field of developmental biology. One other study has looked at the growth rates of NIBK, the authors considered the effect of sex on growth rates but no other variables (McLennan et al. 2004). In this study I examine the effect of sex, season, weather and food resources on the growth rates of NIBK.

Methods

Monitoring

General information regarding the study site, the species and monitoring is given in the Introduction, section: Aims, Contribution and Study Site. In addition to the data I collected between 2010 and 2012, this chapter uses data collected by Lee Shapiro (2005) in the 2004-2005 season on Ponui Island. Young NIBK were located and captured monthly in the 2010 - 2011 summer (November to February; herein referred to as 2010), and weekly in the 2004 - 2005 (December to February; Shapiro 2005) and 2011 - 2012 seasons (September to March; herein referred to as 2004, and 2011, respectively). The reason for the discrepancy in the data collection occurred because data were collected as part of a summer research project I carried out which was later developed into an in depth study in 2011 - 2012 similar to that of Shapiro (2005). Each time a NIBK was captured their bill length, tarsus length, tarsus width, tarsus depth (Vernier® callipers $\pm 0.01\text{cm}$), and body weight (Pesola® scales $\pm 1\text{g}$) were recorded. The weight included the transmitter and band that weighed approximately 7g. Measurements were taken as described in the Kiwi Best Practise Manual (Robertson et al. 2003) with the exception of tarsus length, which was measured from the first scale on the middle toe to the back of the intertarsal joint rather than the lump at the outside of the joint. It was measured this way, because from past experience our team found it resulted in less variation among measurements and observers.

Seasonal measures

Pitfall traps

Soil invertebrates were sampled each month from November 2010 to March 2012. Invertebrates were collected at 25 sites established in three habitat types in 2005 each containing five pitfall traps (Figure 2.1; Shapiro 2005). The number of pitfall traps per habitat followed the perceived availability of each habitat for the study birds in 2005 as follows: forest $n = 10$, scrub $n = 10$ and pasture $n = 5$. Within each habitat type the location of the pitfalls was assigned randomly (Shapiro 2005). During my study a new site (Figure 2.1; Kauri Bush) was used; I did not set up additional pitfall sites in this area because I considered that the existing sites were representative of the habitats at the new location. After collection, invertebrates were preserved in 70% ethanol and stored to be identified at a

later date. Identification took place at a gross level, with only large groups identified (spiders, beetles, cockroaches, worms, isopods, amphipods, gastropods, crickets, weta, ants, flies, centipedes and millipedes, bees and wasps, and larva). Invertebrates less than eight millimeters were not found in the diet of little spotted kiwi (*A. owenii*), the smallest extant kiwi species (Colbourne et al. 1990); therefore, only invertebrates larger than seven mm, to account for any uncertainty, were recorded in this study. The number of individual invertebrates in each group was recorded for each pitfall site sample; the sample was then weighed and dried (Sunbeam Food Dehydrator DT5600, Appendix 2.1). During dehydration, the samples were weighed at two hour intervals until a constant mass was reached and the final dry biomass weight was recorded. All invertebrate groups were included in this sample to give an overall indicator of invertebrate abundance rather than selecting for groups that NIBK are thought to prefer. In some months, individual pitfall traps flooded or were interfered with by livestock, therefore, to account for the missing pitfall samples, the average dry weight biomass per pitfall trap each month was used in the analysis rather than the total biomass per month.

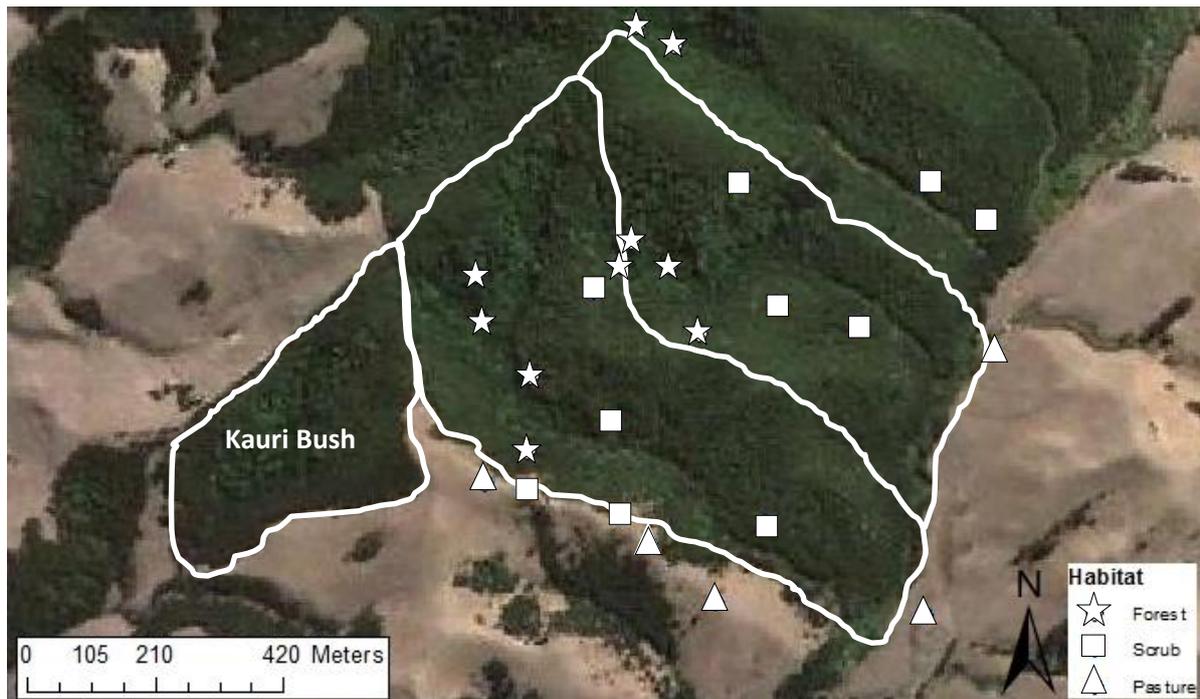


Figure 2.1. Map of the study site. The three catchments on Ponui Island, New Zealand where growth rates of North Island brown kiwi were studied are demarcated in white. Plotted are the locations of pitfall traps.

Soil penetrability

Soil penetrability was measured at each of the 20 forest and scrub pitfall trap sites, and an additional five penetrability sites were established using selected points on a grid map in forest (n=3) and scrub (n=2) in Kauri Bush (Figure 2.1). These additional points were added to ensure that penetrability did not differ across the three main bush sites particularly because the third bush site, Kauri Bush was NE-SW facing compared to the other two sites that faced NW-SE. At the pitfall sites, the centre pitfall at each site marked the central point of a 20m transect line with five points each five metres apart. The transect line lay in the direction of greatest slope within the gully of each of the three bush sites. At each of these points penetrability was measured four times using a penetrometer (Ground Engineering WF 24950 soil pocket penetrometer, Wykham Farrance Eng. Ltd) at each corner in a 20 x 20cm square. This resulted in 500 measurements of penetrability per month, the average penetrability per month was used to analyse the effect of soil penetrability on growth rate. In some instances (n=37, 0.6% of measurements) penetrability was beyond the measuring capabilities of the penetrometer, i.e., >5kg/cm², in such cases I assigned a score of 5.1.

Measurements of higher values indicated lower penetrability of the soil i.e., the ground was harder.

Weather

Weather data for November 2010 – March 2012 was obtained from National Institute of Water and Atmospheric Research's national climate database (<http://cliflo.niwa.co.nz/>, accessed 6th June 2012). The nearest weather station to Ponui Island was Waiheke Island, Awaroa Valley (36° 48' 25.12"S, 175° 6' 52.34"E), approximately 10.5km from the study site. To analyse the effect of weather conditions on growth rate, I used monthly rainfall and average daily rain per week (mm), monthly mean temperature and weekly maximum and minimum temperature averages (°C).

Statistical analysis

Average measurements for body mass (g day^{-1}), bill length and tarsus length, width and depth (mm day^{-1}) were calculated for each week from 1-91 days of age for all young NIBK combined, males and females separately, and each season. Average gain per day was only calculated until 91 days of age, because only four individuals lived past this age. I used a generalized linear model (GLM) to determine the effect of age, sex and season on weight and bill length. Likewise I used a GLM to determine the effect of temperature, age and fate of the chick on growth rates. I used a linear distribution for these models. The individual identity of each chick was included in the models, as an offset value, to account for individual variation. The average growth rates per day for each week of age (13 weeks or 1-91 days) were calculated using growth curves in CurveExpert Professional (Version 1.6.5). The Gompertz curve was used because this curve was used in a previous study of the growth rates of NIBK and allowed a comparison between the populations to be made (McLennan et al. 2004).

A growth rate constant (K) was also calculated for body mass growth as it is a standard measure that allows growth rates to be compared among populations and species (O'Conner 1984). I used the conversion factors for the Gompertz equation (Ricklefs 1967) that were linearly related to age (range 15-750 days), with an asymptote of 1569g (A). These conversion factors transformed the growth curve into a straight line and allowed the slopes

to be measured. The linear line was proportional to the overall growth rate. The slope of the regression was then determined (dW_i / dt) and the K_g value was calculated using the equation: $K_g = 2.72 \times dW_i / dt$ (Ricklefs 1967) and equalled 0.00192. The growth rates of the first 15 days after hatching were excluded because chicks lose weight when absorbing their yolk sac and before they begin foraging (McLennan et al. 2004). If included this would have lowered the K_g value. All individuals were included in this equation even though a significant number did not survive to the end of the season. They were included because when sampling you do not know if an animal will survive or die and in many instances an animal is not continually tracked for its entire lifetime therefore one would not know if it survived. This method gives an overall representation of the growth rates of brown kiwi on Ponui Island during this study.

The length of time it took young NIBK to grow from 10 to 90% of the asymptote was calculated using the formula:

$$t_{10 - 90} = \frac{(C_{90} - C_{10})}{dW_i / dt}$$

Where C_{90} and C_{10} are conversion factors for the Gompertz equation (Ricklefs 1967a).

The relative growth rate (RGR) was calculated for the body mass of each chick using Brody's equation (1945):

$$R = \frac{\ln g_2 - \ln g_1}{t_2 - t_1}$$

The RGR is the difference in mass between consecutive measurements, g_1 and g_2 are the values of body mass at age t_1 and t_2 , respectively.

Because there were differences in the body mass growth rate within seasons and between seasons I used a path analysis to determine factors that changed seasonally and may have affected growth rate across all seasons. Path analysis is a technique used to apply multiple regressions to a system where the causal variables are correlated and are determinates of a response variable such as growth rate (Wright 1921, Kingsolver and Schemske 1991). Path analysis gives standardised coefficients which indicate how many standard deviations a

dependent variable will change, per standard deviation increase in the independent variable. Additionally, residual variation is calculated as $\sqrt{1-r^2}$ and is attributed to dependent variables (U). r^2 is the proportion of variation in a dependent variable that is explained by all the measured independent variables (McCarty and Winkler 1999). I used path analysis to determine the level of variation in the dependent variables: RGR, invertebrate abundance and soil penetrability, which could be explained by the independent climate variables: temperature and rainfall. Path analysis was calculated with both monthly (RGR, temperature, rainfall, penetrability and invertebrate abundance) and weekly measurements (RGR, rainfall, and maximum and minimum temperature). This was done to determine at what level seasonal variables affected the growth rate of the chicks.

Critical alpha was set at 0.05 and means are presented with standard errors. Data were analysed using the statistical packages IBM SPSS® (version 20.0, 2011) and graphs were produced using IBM SPSS® and R 2.15.1 (R Development Core Team 2010).

Results

The growth rates of 29 young NIBK were measured during three breeding seasons (2004, $n = 3$; 2010, $n = 10$ and 2011, $n = 18$). The mortality rate was 87.5% with only four individuals surviving ≥ 448 days of age (Chapter 5). There were ten chicks with only one measurement taken either because they were not fitted with a transmitter ($n = 6$), or died after the first measurement ($n = 4$). The data from these chicks have been included in the generalized linear models and growth curves but not in the RGR measurements. Lastly, the weights of two birds found dead were included in the analyses because they were found < 12 hours after death and I considered that this weight would still be the same as when they were alive. The measurements of all other NIBK found > 12 hours after dying were excluded from the analysis as weight is likely to change after this point due to decomposition. Data were tested for normality using Shapiro-Wilkinson tests and data were normally distributed. Data for each brown kiwi can be found in the appendix table 2.1.

Growth rates

The growth rate constant for NIBK in this population in the 2004, 2010 and 2011 seasons was $K_g = 0.0052$ and young NIBK took 591 days to grow from 10 to 90% of the asymptote. The body mass gain increased with age from 3.0 to 3.7g day⁻¹ (1 – 91 days, Figure 2.2a). In contrast, the bill length growth rate decreased with age from 0.14 to 0.12mm day⁻¹ (1 – 91 days, Figure 2.2b) as did tarsus length growth rate, from 0.12 to 0.10mm day⁻¹ (Figure 2.2c). The rate of growth of both tarsus width and depth remained constant with age 0.01mm day⁻¹ and 0.02mm day⁻¹, respectively (Gompertz equation $R = 0.86$, $SE = 0.66$ and $R = 0.90$, $SE = 0.93$, respectively). Weight and bill length were found to be significantly affected by both the age of the chick ($P = 0.00$, $df = 1$, Wald Chi Square = 299.99, $P = 0.00$ and $df = 1$, Wald Chi Square = 858.37) and the individual identification ($P = 0.00$, $df = 27$, Wald Chi Square = 161.24 and) with weight and bill length increasing with age.

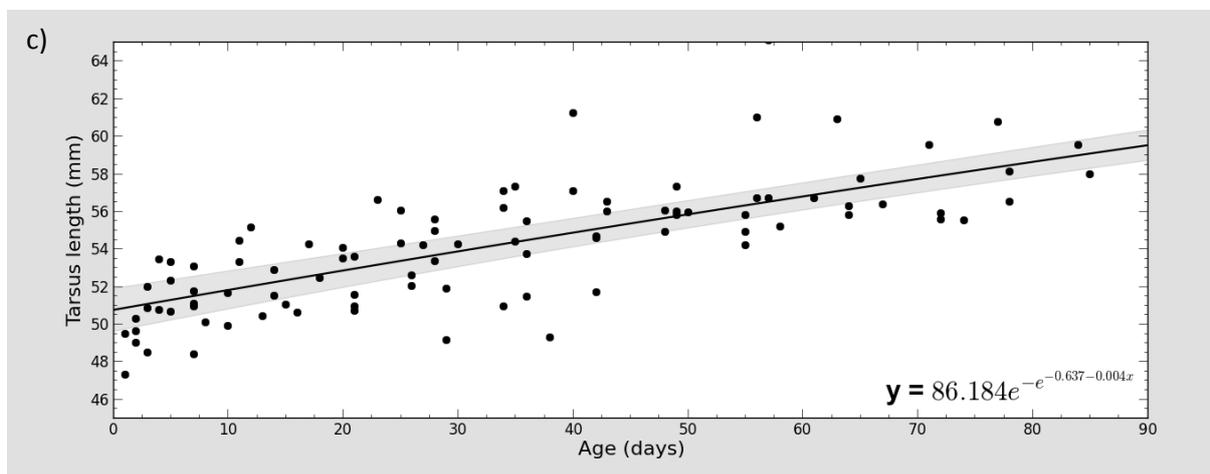
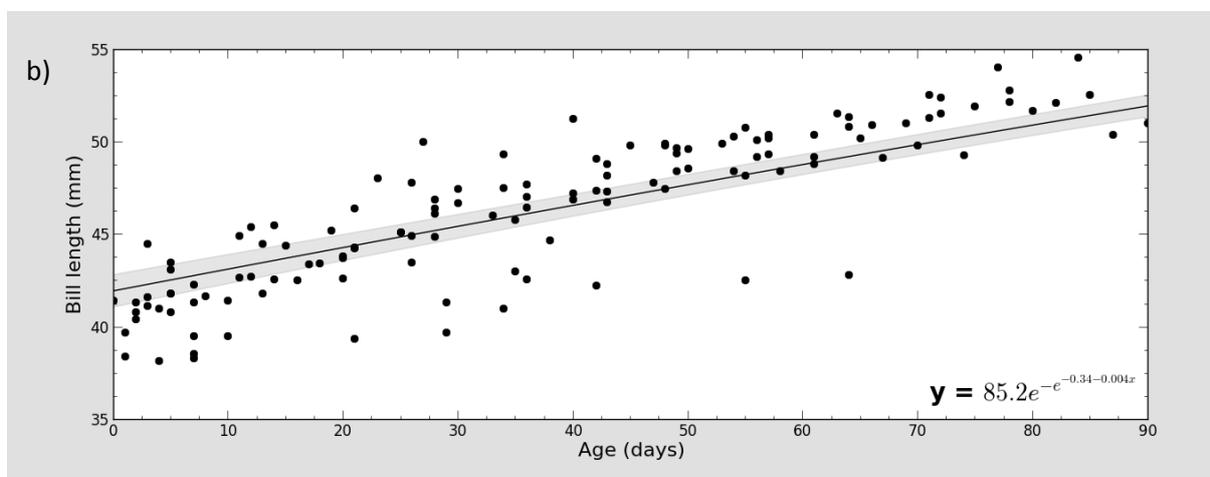
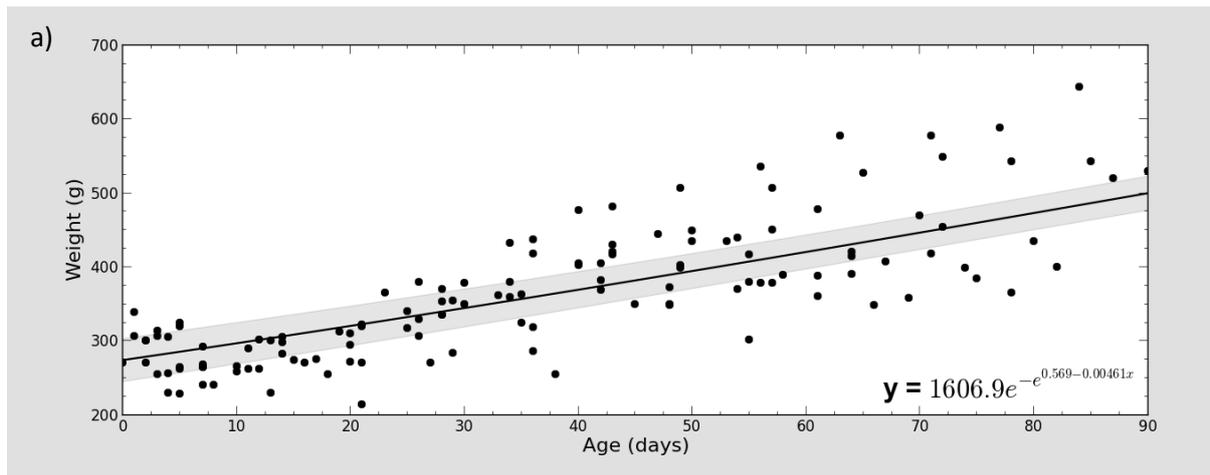


Figure 2.2. Growth rates of 29 North Island brown kiwi during three breeding seasons on Ponui Island, New Zealand. All solid lines and equations represent the Gompertz equations fitted by methods described in Ricklefs (1968). a) Body mass: $R = 0.94$, $SE = 118.7$, b) Bill length: $R = 0.95$, $SE = 3.4$, c) Tarsus length: $R = 0.92$, $SE = 4.1$. Shaded areas represent a 95% confidence interval of the curves. Only four chicks survived longer than 91 days, one in the 2004 and 2010 seasons and two in the 2011 season.

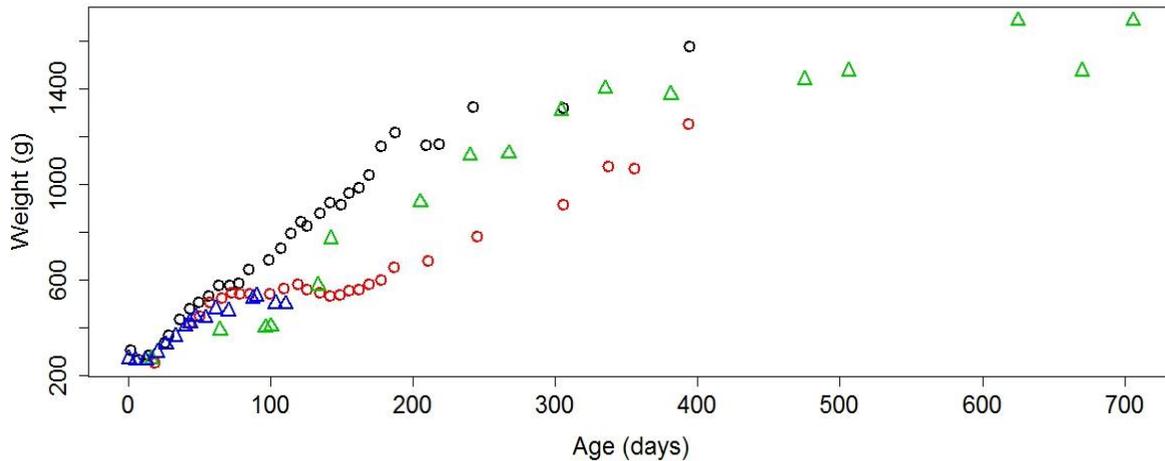


Figure 2.3. Growth rates of four North Island brown kiwi during three breeding seasons on Ponui Island that survived until March 2012. Each colour represents an individual brown kiwi, circles symbolise females and triangles, males.

Growth in relation to sex

Females weighed more than males at similar ages even when individual identity was considered ($P = 0.03$, $df = 1$, Wald Chi Square = 4.73, Figure 2.4). The rate of body mass gain per day increased from 1 - 91 days of age in both females and males from 3.2 (1 day old) to 3.7g day⁻¹ (91 days old; Gompertz relation, $R = 0.91$, $SE = 143.9$) and 2.0 to 2.3g day⁻¹ (1 and 91 days; Gompertz, $R = 0.92$, $SE = 133.2$), respectively. Similarly, the bill length growth per day was greater in females than males with females growing from 0.34 to 0.11mm day⁻¹ (1 - 91days; Gompertz, $R = 0.94$, $SE = 3.9$) compared to males whose bill length grew between 0.10 and 0.09mm day⁻¹ from 1 - 91 days of age (Gompertz, $R = 0.95$, $SE = 3.1$) although this difference was not significant when individual identity was taken into account ($P = 0.35$, $df = 1$, Wald Chi Square = 0.883).

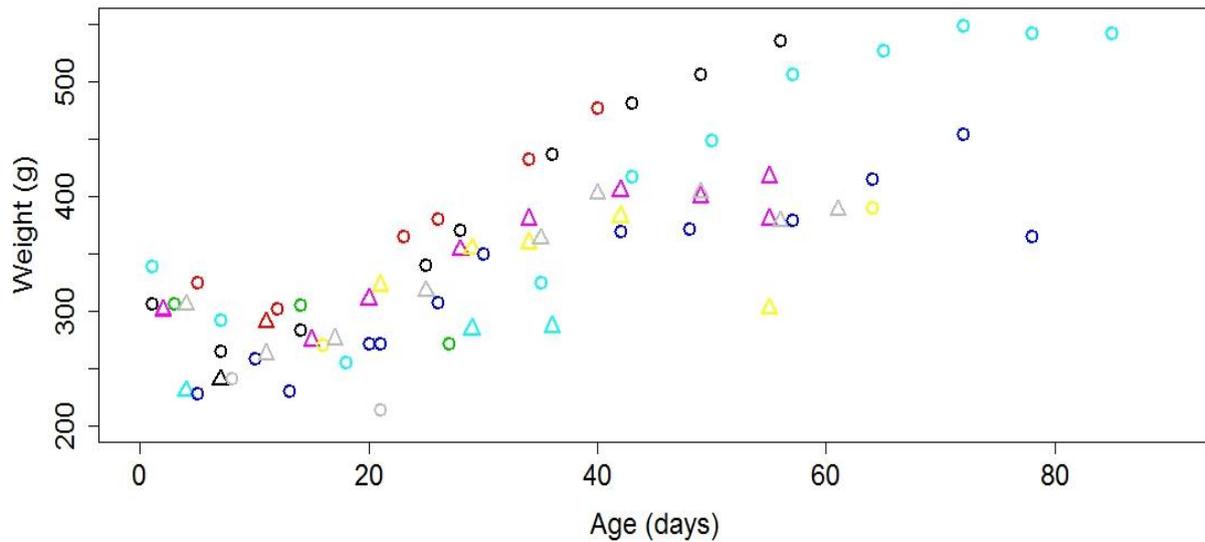


Figure 2.4. Growth rates of 29 North Island brown kiwi during three breeding seasons on Ponui Island. Each individual is represented by a different colour and female are demarcated by circles, males by triangles.

Growth between seasons

The average rate of growth (g day^{-1}) was determined for each week from 10 - 91 days of age using a Gompertz growth curve (2004: $R = 0.99$, $SE = 11.7$; 2010: $R = 0.86$, $SE = 31.9$; 2011: $R = 0.80$, $SE = 58.3$; Figure 2.3a). NIBK in 2004 grew from $1.3 - 1.4 \text{ g day}^{-1}$ (week 2 and week 13, respectively), in 2010 from $2.7 - 3.4 \text{ g day}^{-1}$ and $3.2 - 3.7 \text{ g day}^{-1}$ in 2011. I found no significant seasonal effects on RGR ($P = 0.46$, $df = 2$, Wald Chi Square = 1.54)

Weather and Resources

The invertebrate average dry weight per pitfall was greatest in January, February and March in both the 2010 and 2011 seasons (2011, range = $2.94 - 3.48 \text{g}$; 2012, range = $3.51 - 6.89$, Appendix 2.1a; Figure 2.5a). Average monthly temperature was highest in February (2011: 20.7°C and 2012: 18.8°C ; Figure 2.5b). Conversely, invertebrate abundance was lowest in July to September 2011 (range = $0.29 - 0.62 \text{g}$) and mean daily temperature was lowest in August 2011 at 9.8°C . The penetrability measure tended to be slightly higher in the summer months compared to the winter months, indicating that the ground was less penetrable in the summer (Figure 2.5c). Rainfall was unevenly distributed with a large peak in January

2011 and low rainfall, <50mm per month, in November 2010, February 2011 and November 2011 (Figure 2.5d).

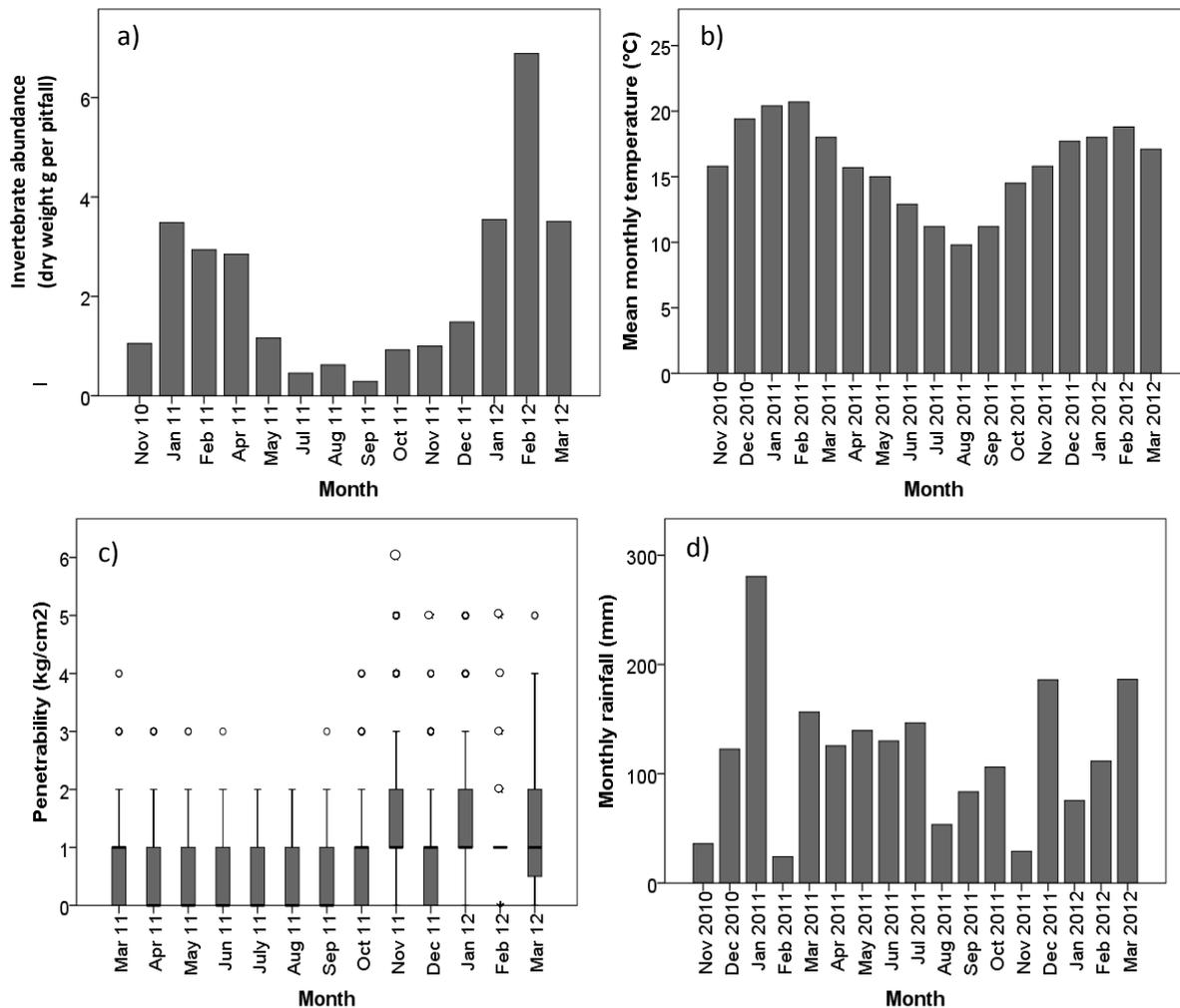


Figure 2.5. Environmental variables, food abundance and availability on Ponui Island, New Zealand from 2010 to 2012. a) Dry weight measure of invertebrate abundance from 25 random sites on Ponui Island (average weight (g) per pitfall) from November 2010 - March 2012. b) Mean monthly temperature on Waiheke Island (10.5km from study site, obtained from NIWA, 6th June 2012). c) Mean penetrability of the soil from 25 random sites (n = 500 per month) on Ponui Island from March 2011 - March 2012. Shown are: the median, 25% and 75% interquartile ranges (box length), non-outlier minimum and maximum values (whiskers) and outliers (circles). d) Monthly rainfall on Waiheke Island (obtained from NIWA, 6th June 2012).

Effect of weather and resources on weight gain

Monthly Path Analysis

The monthly path analysis showed that average monthly temperature significantly affected both invertebrate abundance and penetrability (Figure 2.6). With increasing mean monthly temperature invertebrate abundance increased (standardised coefficient = 0.666, $P < 0.01$), and the average soil penetrability measure also increased indicating that the soil became harder with increasing temperatures (standardised coefficient = 0.617, $P < 0.01$). Rainfall was found to only affect penetrability. With increasing rainfall the soil penetrability measure decreased indicating that with increasing rainfall soil penetrability increased. Monthly temperature, rainfall, invertebrate abundance and soil penetrability did not significantly affect monthly body mass growth rates, and +0.983 of residual variation in mass growth rate was not explained by these variables.

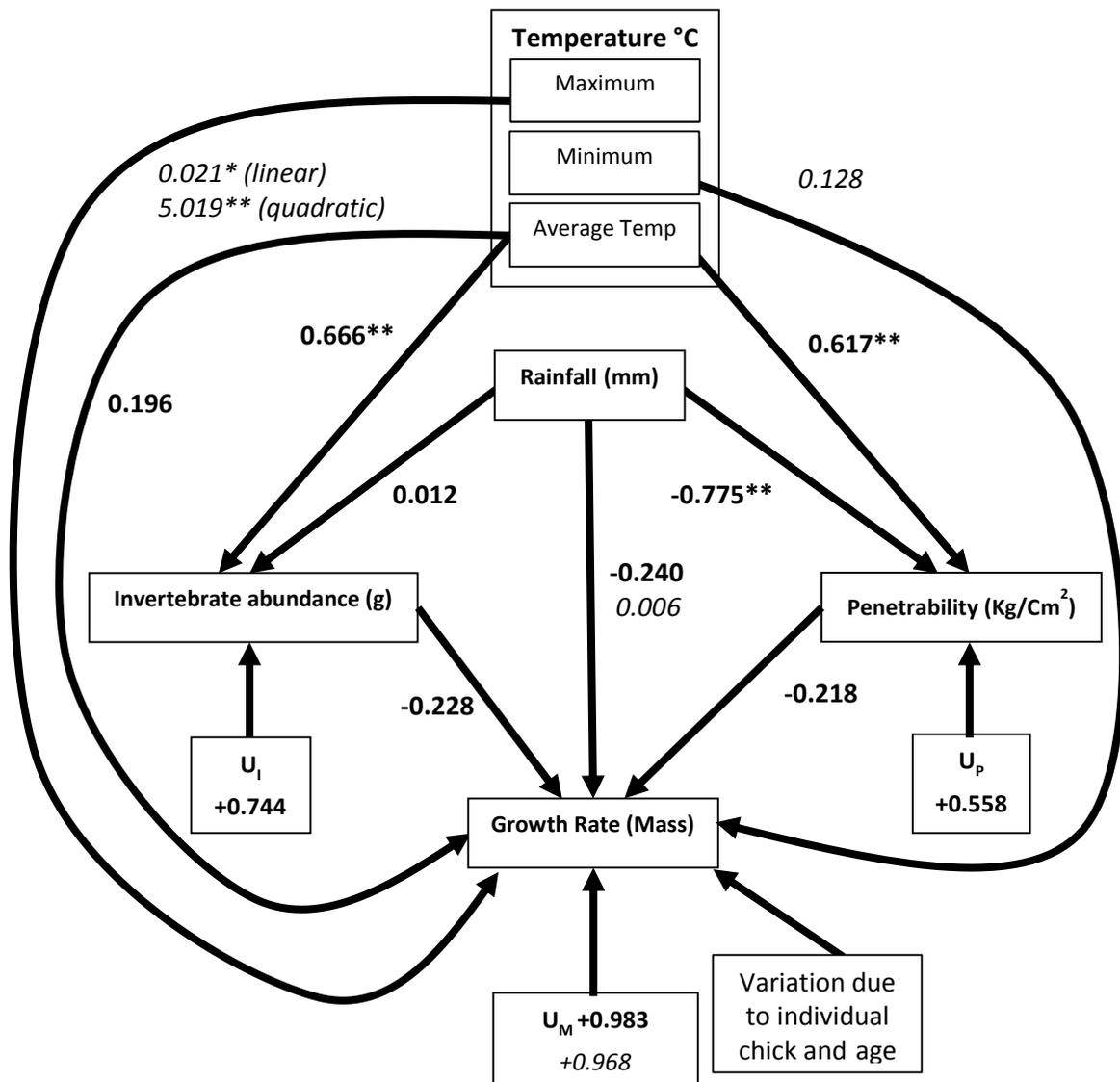


Figure 2.6. Effects of environmental variables on relative growth rate (RGR) in young North Island brown kiwi. Numbers adjacent to arrows show standardized coefficients from multiple regression analysis, where the variable at the tip of the arrow is the dependent variable and the variables at the base of the arrows are the independent variables. Results for monthly measurements are in **bold**, and results for weekly measurements are in plain *italicised* type. U_M , U_I and U_P indicate residual variation for mass growth rate, invertebrate abundance and penetrability, respectively, that is not explained by the measured variables. Statistical significance is indicated by asterisk, $*0.05 > P > 0.01$; $**P < 0.01$.

Effect of weather and resources on weight gain: Weekly path analysis

Weekly rainfall and minimum temperature did not significantly affect weekly growth rates in 2011. In contrast, weekly growth rates were affected by the average maximum weekly

temperature. A quadratic regression fitted the data best, indicating that growth was maximised between 19 and 22°C and declined at temperatures either side of this range. Although there was a relationship between maximum temperature and growth rates the quadratic regression was very weak ($R^2 = 0.077$, $F=3.55$) and +0.968 of residual variation in mass growth rate was not explained by the variables measured.

Because this path analysis showed that temperature had a significant effect on growth rate a generalized linear model was produced to look at the effect of temperature on growth rates when individual identity, age and fate of the brown kiwi were also taken into account. I found that when individual identity was considered maximum temperature still had a significant effect on growth rates ($P = 0.025$, $df = 1$, Wald Chi Square = 5.05); however, fate ($P = 0.083$, $df = 2$, Wald Chi Square = 4.98) and age ($P = 0.60$, $df = 1$, Wald Chi Square = 0.27) had no significant effect on growth rates.

Discussion

Growth rate

In this study the growth rate constant for NIBK was $K_g = 0.0052$, this is lower than the lowest growth constant of the 296 bird species listed by Ricklefs and Starck (1998a). In their paper, only 58 species from 15 families had growth constants < 0.05 indicating slow growth rates and only one other species, the Malleefowl (*Leipoa ocellata*), had a growth constant below 0.010 ($K_g = 0.007$; Appendix 2.1, Table 2.6; Starck and Ricklefs 1998a)

There are at least four reasons that are likely to contribute to the extremely slow growth rate of NIBK. Firstly, young NIBK are highly precocial and hatch with high levels of functional maturity (Table 2.3). Due to this high level of maturity there is a greater trade-off between growth and function, and less energy is available that can be allocated to growth (Ricklefs 1968, 1979). Secondly, body size can affect growth rates and the young of larger species tend to take longer to reach adult size relative to smaller species (Ricklefs 1968). This is because a higher feeding rate is necessary to maintain the physiological costs of a larger body. Although NIBK (2 - 2.8kg) are not large relative to other bird species such as emu

(37kg, *Dromaius novaehollandiae*), cassowary (up to 58kg, *Casuarius*) and wood stork (9kg, *Mycteria americana*), they are larger than most passerine species (Starck and Ricklefs 1998a). Hence, relatively we would expect them to have a slower growth rate. Interestingly, NIBK in this study grew slower taking 591 days to grow 10 - 90% of the asymptote than the much heavier wood stalk that takes 58.6 days and the marabou stalk that takes 61.3 days.

Table 2.1. General trend of life history traits in precocial species and North Island brown kiwi.

**indicates if North Island brown kiwi are an extreme example of this trait.

Precocial birds – general trend	North Island brown kiwi
Phylogeny = basal groups	Part of paleognaths – basal of all birds
Lower BMR	Lowest BMR of all known birds**
Lower T°	Low body temperature 38°C
Ground birds	Flightless, roost in burrows
Medium to large birds	Medium birds average (2-2.8kg)
Feed on ground, and or on or close to water	Feed from the ground, amongst litter or by probing in the soil, also known to feed in water.
Feed on slow moving or immobile food	Feed on a number of larvae species
Larger nutritional content of eggs	Yolk of eggs has a very high nutritional content one of the highest measured thus far**
Long incubation times	One of the longest incubation times for a bird it size (75-85 days)
Less post-hatch parental care	No parental care known, other than brooding in the nest by the father when roosting**
Thermal independence soon after hatching	Unknown exactly when begins, but thought from hatching or very soon after**
Feathered (down)	Fully feathered from hatching**
Self-feeding	No prey provided by parents, forages within first week of life
Grow slow	Slowest growth rate of all known birds**

Thirdly, species tend to have longer periods of growth when they live on oceanic islands or in areas that protect them from predation (Ricklefs 1968). This is because the length of the nestling period is correlated with the success of a nest (Lack 1948). It is beneficial to grow faster in the nest when it reduces predation risk (Remes and Martin 2002). Species that are protected from high predation rates and weather remain in the nest longer and tend to have slower growth rates. For example, the Ascension frigate bird (*Fregata aquila*) that lives on a tiny island in the Atlantic Ocean, takes 91.7 days to grow from 10 to 90% of asymptote (Ricklefs 1968). Similar sized mainland species such as crows, ravens and magpies take between 16.7 and 32.9 days (Ricklefs 1968). McLennan and colleagues (2004) hypothesised that the evolution of slow growth rates in NIBK is driven by energetic considerations and not by predator avoidance. Fast growth rates come with high energetic demands, this may increase the risk of nutrient deficiency when developing and may have long lasting effects on metabolism, life span and disease resistance (Lindstrom 1999, Metcalfe and Monaghan 2001). McLennan et al. (2004) suggest that NIBK were able to avoid diurnal avian predators because they are nocturnal, cryptic and camouflage well. Because there was no selective pressures to grow quickly and avoid predators, NIBK were able to evolve adaptations such as slow growth that minimised the energy requirements (Holdaway 1999, McLennan et al. 2004).

Lastly, slow growth rates may be an adaptation that allows for survival in an environment with variable resources or a high level of competition for resources. This adaptation is seen in some seabirds and swifts (Apodidae). For example, in black-backed gulls (*Larus marinus*) starvation is a common cause of death; males grow faster and subsequently have lower survival rates than females (Griffiths 1992). Similarly, in yellow-eyed penguins (*Megadyptes antipodes*), chicks with the fastest skull, tail and flipper growth rates had lower survival rates (van Heezik and Davis 1990). Isabel Castro, Lee Shapiro and Rogan Colbourne hypothesised that slow growth rates have evolved in NIBK due to the large amount of competition for food resources with other native New Zealand ground feeding insectivores such as, saddlebacks (*Philesturnus carunculatus*), wrens (*family Acanthisittidae*), piopio (*Turnagra capensis*), snipe (*Coenocorypha spp.*) and snipe rail (*Capellirallus karamul*); before human colonisation (Unpublished manuscript, pers. comm.). Slow growth rates would have increased the likelihood of survival because physiological demands for growth would be

2.4). This supports the first prediction, chicks that were reared in captivity grow the fastest because they had access to sufficient food and had no competitors. Young NIBK at Lake Waikaremoana had the second highest weight gain likely because population density was low, 0 - 2.8 birds/km² (McLennan 1997) and, therefore, intra-specific food competition was low. Ponui Island (est. 100 birds/km²; Cunningham et al. 2007) and Trounson Kauri Park potentially have similar population densities. However Ponui Island NIBK are likely to have higher levels of inter-specific competition because islands tend to have higher and more stable Rat densities than mainland sites (Adler and Levins 1994). Predator densities might also be indirectly influencing growth rates by influencing intra- and inter-specific competition, however such data are often lacking.

Table 2.2. Growth rates for first 100 days after hatching of young North Island brown kiwi from captive and wild populations.

	Density	Mass (g/d)	Bill (mm/d)	Tarsus length (mm/d)
Captive ^a (n=28)	-	7.6	0.2	0.2
Lake Waikaremoana ^b (n=126)	0-2.8	5.9	~0.2	-
Trounson Kauri Park^c (n=9)	Unknown*	3.4	-	-
Our study (n=29)	100	3.4	0.13	0.11

^a (Jones 2010), ^b (McLennan et al. 2004) and ^c (Gibbs 2000) *Call surveys from the Tutamoia Region, which encompasses Trounson Kauri Park from 1992 - 1993 estimated mean calls per hour per site to be 4.2 (Miller and Pierce 1995). On Ponui Island in 1999 a call survey stated 5.1 calls per hour per site (Miles and Castro 1999).

Additionally, Castro, Shapiro and Colbourne (unpublished manuscript) listed other factors that support the hypothesis that a competitive environment results in slower growth rates; female NIBK lay one of the largest eggs relative to body size (Reid 1971) and have highly precocial, developed chicks with yolk that sustains them for 7 - 10 days after hatching (Calder 1979). These large precocial chicks have an advantage when food resources are limited because a) they have a yolk sac that sustains them for an extended period of time relative to other species and b) because they hatch more developmentally mature less energy is required for growth processes. Hence, adverse effects such as susceptibility to

disease and starvation associated with fast growth due to energy insufficiency, are reduced (Lack 1968, Ricklefs 1969a, Bryant and Gardiner 1979, Griffiths 1992, Ashton 2000).

These results highlights that NIBK fit into a complex ecosystem, all of which can influence growth rates. However, the management implications for the relationship between competition for resources, growth rates and population density are: when translocating NIBK or returning young NIBK hatched in captivity to the wild we must be wary of population densities, the size of the area and Rat densities, particularly on islands as these factors may negatively affect growth and subsequent survival rates.

Growth Rate Trends

The growth rate of young NIBK in this study was similar to the rates that McLennan and colleagues (2004) found at Lake Waikaremoana, Hawke's Bay, North Island. In both studies NIBK experienced an initial drop in weight between 1 - 15 days of age. It has been suggested that during this time, energy is metabolised and used from the large reservoir of rich yolk inside the hatchling (Prinzinger and Dietz 2002, McLennan et al. 2004). This is supported by my observations that for the first few nights when outside the nest, very little foraging occurs; chicks appear to be exploring, learning and familiarising themselves with the surrounding environment during this time (Chapter 3). After this point, young kiwi begin foraging and the rate of weight gain on average steadily increases. This increase in the rate of growth is likely due to increased foraging success with age, as suggested by Shapiro (2005). Similar increases have been observed in a wide range of bird species including: bald eagles (*Haliaeetus leucocephalus*; Bennetts and McClelland 1997), bananaquits (*Coereba flaveola*; Wunderle and Lodge 1988) and king penguins (*Aptenodytes patagonicus*; Le Vaillant et al. 2012). A general increasing trend in the rate of growth could also be related to the fluctuating abundances of prey items (Bryant 1975, Blancher and Robertson 1987). However, invertebrate abundance varied within the 2011 season and chicks hatched from September to February, therefore, it is unlikely that food abundance led to the linear increase in the average weight gain with age. I found that the rate of growth of the bill and tarsus lengths decreased during the period from 1 – 91 days of age. McLennan et al. (2004) also found that bill length growth declined with age during the same period, although the rate of growth of the tarsus width or length did not change. A decline in the growth rate

with age as young animals move closer to adult weight and size is seen in most birds (Ricklefs 1968). Additionally, females were found to have faster growth rates in body mass relative to males, although there was no difference in bill length between sexes. McLennan et al. (2004) found that within age classes that ranged from 0 to > 300 days of age, growth rates of body mass of females and males were not significantly different. McLennan et al. (2004) also found that the bills of females grew significantly faster than males mainly from 200 – 1400 days. This may explain why no difference was seen in this study, because measurements were only analysed to 91 days of age. Jones (2010) found that females grew faster in body mass than males and the rate of male growth slowed at the end of 100 days of age. She also found no difference in the growth rates of the bill length between males and females, although females hatched with slightly longer bills (Jones 2010). Adult females weigh 20 - 30% more and have longer bills than males (Robertson et al. 2003), and therefore the difference in growth rates between males and females may be due to this sexual dimorphism. Differing growth rates between males and females have been seen in other species, for example, female red-winged blackbirds (*Agelaius phoeniceus*) are smaller and grow slower than males (Ricklefs 1968). The bill length of females may grow faster to reduce high competition for food by being able to feed on food deeper in the soil or leaf litter. However, I do not have a conclusive explanation as to why female NIBK may initially grow faster than males or why there are so many differences between different populations. Small sample sizes and perhaps sexing errors could account for some of the differences between studies.

The influence of climate on growth rates

Growth rates varied both within seasons and between seasons and this variability was partly due to changes in climatic variables. A significant causal relationship was found with maximum weekly temperature and weekly growth rates indicating that young NIBK grew fastest between 19 and 22°C. Although there was a large amount of variation in weekly growth rates that could not be explained some of this variation may be due to individual identity as this was found to significantly affect growth rates. Average monthly temperature significantly affected soil penetrability and invertebrate abundance. Importantly, the large increase in invertebrate abundance in the summer months was partly due to an increase in the number of black crickets (*Teleogryllus commodus*; Appendix 2.1b), this may have

benefited young NIBK with access to pasture habitats. Monthly rainfall had a significant positive effect on soil penetrability, affecting the ability of NIBK to probe and find food in the soil. This shows how these environmental factors can interact and influence growth rates of NIBK. I hypothesise that growth rates are highest between 19 and 22°C because this temperature range represents a foraging optimum for young NIBK. I found that during cold winter and spring months, invertebrate densities remained low, thus limiting food abundance for the young NIBK. This period of low food availability is likely interrupted by the cicada emergence. For much of the year cicada nymphs remain deep in the soil, however, during the cool part of early summer, they move closer to the surface just prior to emerging as adults (Colbourne and Powlesland 1988). The young NIBK opportunistically feed on the emerging insects (Colbourne and Powlesland 1988, Shapiro 2005). However, the rising temperatures of summer cause the soil to harden, which means that there is a decline in the accessibility of food because young NIBK are no longer able to penetrate the soil and are limited to foraging in the litter. This concept is supported by Shapiro's (2005) result that the concentration of soil-living prey found in the diet of juvenile NIBK was lowest in the hottest months, and Cunningham and Castro's (2011) finding that adult NIBK used the litter significantly more in the summer than the winter. Because I only considered the 2011 season in the weekly analysis I can only presume that maximum temperature had the same effect across the other seasons. I did not measure invertebrate abundance and soil penetrability on a weekly basis; however, I can hypothesise that because monthly temperature and rainfall affects these factors, they will also be influenced on a weekly scale.

The influence of life history on growth rates

In some instances precocial species are more susceptible to environmental conditions because they are independent from their parents; they have a higher chance of suffering from cold and rain as they are not brooded to the same extent as altricial species. This results in a high cost of thermoregulation, particularly in wet conditions. Additionally, precocial chicks are not likely to be as proficient at foraging as adults because they receive little to no help and teaching from their parents. For this reason they are more likely to be negatively affected in food shortages due to difficulties foraging, relative to adults and altricial chicks with their parents. Poor environmental conditions partnered with the inability to obtain prey to fuel basic physiological functions, such as thermoregulation, can

have detrimental effects on young animals and often causes high mortality rates. Corncrakes (*Crex crex*) are precocial rails that are similar to NIBK as they leave the nest within days of hatching, although in contrast, they are fed by their mother for 4 - 5 days. Corncrake chicks' growth rate increased with temperature, however, survival was decreased with rainfall (Tyler and Green 2004). Survival also increased with temperature for grey (*Perdix perdix*) and red-legged partridges (*Alectoris rufa*) although the authors were uncertain if this was a direct effect of temperature on chick activity or an indirect effect via food abundance (Green 1984), as I believe is the case with young NIBK. Western capercaillie (*Tetrao urogallus*) chicks were also found to be vulnerable to rainfall; however there was no effect of rainfall on black grouse (Moss 1986). This was speculated to be due to the final size of the adult (Cluttonbrock et al. 1985). Capercaillie adults are larger, and the chicks grow at a faster rate than black grouse, and therefore, need more food. Foraging is thought to be limited by rain which is why the capercaillie chicks with greater energy requirements were more susceptible to mortality with rainfall (Moss 1986).

NIBK do not appear to be limited directly by rainfall and cold temperatures as many other precocial species are, but indirectly via food resources. This perhaps is due to their extreme precociality and high level of development at hatching. NIBK chicks hatch with feathers similar to the adults, although slightly softer, rather than hatching with only down or no plumage as many other species. These feathers are able to repel water and cold, thus protecting them from the environment. The large relative size of NIBK chicks (and low surface to volume ratio) also may reduce the amount of thermoregulatory challenges they face. Furthermore, NIBK body temperature is relatively low at 38°C compared to a number of birds and is similar to other ground dwelling species (Prinzinger et al. 1991); therefore, maintenance of basal metabolic rate, and body temperature requires less energy than if it was maintained at a higher temperature. Lastly, NIBK are not limited by food availability in the rain, as many aerial insectivore animals are, because they prey on ground dwelling invertebrates; and some including earth worms, a very important prey item for NIBK, are more available in wet weather. All of these factors may increase young NIBK survivorship when subjected to a range of environmental conditions.

Furthermore, risk of starvation is likely reduced by growing slowly during periods when resources are reduced (Ricklefs 1969a, Griffiths 1992). I speculate that extreme precociality

and slow growth rates have been selected for in NIBK because without them the cost of mortality would be too high. If NIBK were to hatch less developed, they would likely need to grow faster to reach adult size, as with capercaille (Moss 1986); resulting in greater energy demands. In an environment where climatic variables can increase both intra- and inter-specific competition for food resources; when resource availability is low, higher energy demands would significantly reduce survival (Van Heezik and Davis 1990, Griffiths 1992).

In conclusion, North Island brown kiwi are a very slow growing, extremely precocial species. My results support that NIBK grow slower than any bird with similar life history traits because of the highly competitive environment they evolved in and following this, I hypothesised, and confirmed with published data, that differences in growth rates between populations are due to differences in both NIBK and competitor densities. Young NIBK would have a reduced chance of survival if they hatched less developed or with higher energetic demands, due to the high level of competition for resources. This is evident as growth rates differ: within seasons and among populations. Within season variation was found to be affected by maximum temperature, and temperature was found to affect both food abundance and availability. It is important to understand how individual bird species grow and what factors influence growth to ascertain where they fit along the precocial-altricial spectrum to allow us to explore how such diversity has evolved.

Appendix 2.1

Table 2.3. Measurements of 29 North Island brown kiwi that hatched on Ponui Island in the 2004, 2010 and 2011 seasons.

Chick	Hatch date	Season	Sex	Age (days)	Weight (g)	Bill length (mm)	Tarsus length (mm)	Tarsus width (mm)	Tarsus depth (mm)
1	20.09.11	2011	Female	1	306.0	40.0	50.0	7.0	7.0
				7	265.0	41.0	53.0	8.0	7.0
				14	283.0	43.0	52.0	7.0	7.0
				25	340.0	45.0	54.0	7.2	8.0
				28	370.0	46.0	56.0	7.0	7.0
				36	437.0	47.0	55.5	7.0	9.0
				43	482.0	48.0	56.0	7.0	8.0
				49	507.0	50.0	57.3	8.0	9.0
				56	536.0	50.0	61.0	8.0	10.0
				63	578.0	52.0	60.9	8.0	9.0
				71	578.0	53.0	59.6	8.0	9.0
				77	588.0	54.0	60.8	8.0	9.0
84	643.0	55.0	59.5	8.0	9.0				
2	22.09.11	2011	female	5	325.0	43.0	53.0	7.0	8.0
				12	302.0	45.0	55.0	7.0	7.0
				23	365.0	48.0	57.0	7.0	8.0
				26	380.0	48.0	52.0	7.0	8.0
				34	433.0	49.0	57.1	7.0	8.0
				40	477.0	51.0	61.3	7.0	8.0
3	23.09.11	2011	female	14	305.0	46.0	52.9	7.0	7.0
4	2.10.11	2011	female	5	228.0	40.8	52.0	7.0	7.0
				13	230.0	41.8	50.0	7.0	7.0
				20	272.0	42.6	54.0	7.0	7.0
				26	307.0	43.5	53.0	7.0	7.0
5	1.11.11	2011	male	4	230.0	38.0	51.0	7.0	7.0
				29	284.0	41.0	52.0	7.0	7.0
				36	286.0	43.0	51.0	7.0	7.0
6	18.10.11	2011	male	2	300.0	41.0	49.0	8.0	6.0
				15	274.0	44.0	51.0	6.0	7.0
				28	353.0	47.0	53.4	7.0	7.0

				34	380.0	48.0	56.2	7.0	7.0
				42	405.0	47.0	54.7	7.0	7.0
				49	399.0	49.0	55.8	7.0	7.0
				55	417.0	51.0	55.8	7.0	8.0
7	6.10.11	2011	male	21	322.0	39.0	51.0	7.0	7.0
				29	354.0	40.0	49.2	6.0	8.0
				34	359.0	41.0	51.0	7.0	8.0
				42	382.0	42.0	51.7	7.0	8.0
				55	302.0	42.0	54.2	6.0	7.0
8	11.10.11	2011	male	4	305.0	41.0	53.0	6.0	7.0
				11	262.0	43.0	54.0	6.0	7.0
				17	275.0	43.0	54.0	6.0	7.0
				25	317.0	45.0	56.0	6.0	8.0
				35	363.0	46.0	57.0	7.0	7.0
				40	402.0	47.0	57.0	7.0	8.0
				49	403.0	48.0	56.0	7.0	8.0
				56	378.0	49.0	57.0	7.0	7.0
				61	388.0	49.0	57.0	6.0	7.0
9	14.11.11	2011	unknown	7	268.0	42.0	51.0	7.0	7.0
				14	298.0				
				21	320.0	44.0	52.0	7.0	8.0
				28	335.0	45.0	55.0	7.0	7.0
				36	318.0	46.0	54.0	6.0	7.0
				48	349.0	47.0	55.0	7.0	7.0
				58	389.0	48.0	55.0	7.0	7.0
				67	407.0	49.0	56.0	7.0	8.0
				74	399.0	49.0	56.0	7.0	8.0
12	6.12.11	2011	female	10	258.0	41.0	52.0	6.0	7.0
				21	271.0	46.0	54.0	6.0	7.0
				30	350.0	47.0	54.0	7.0	7.0
				42	369.0	49.0	55.0	7.0	8.0
				48	372.0	50.0	56.0	7.0	8.0
				57	379.0	50.0	65.0	7.0	7.0
				64	415.0	51.0	56.0	7.0	8.0
				72	454.0	52.0	56.0	7.0	8.0
				78	365.0	53.0	56.0	7.0	7.0

13	20.09.11	2011	female	18	255.0	43.0	52.0	7.0	7.0
				43	417.0	47.0	56.0	8.0	8.0
				50	449.0	49.0	56.0	7.3	8.0
				57	507.0	49.0	57.0	7.7	8.4
				65	527.0	50.0	58.0	7.5	9.0
				72	549.0	52.0	56.0	7.9	8.0
				78	543.0	52.0	58.0	7.2	8.0
14	3.11.10	2010	male	2	301.0	40.4	50.3	7.0	6.3
				20	310.0	43.7	53.5	7.1	6.3
				55	380.0	48.2	54.9	7.2	8.4
15	7.11.10	2010	female	16	270.0	42.5	50.6	6.1	6.8
				64	390.0	42.8	56.3	6.2	7.3
17	25.11.10	2010	male	7	240.0	38.3	48.4	6.1	6.3
18	27.12.10	2010	male	11	290.0	44.8	53.3	7.6	7.5
19	17.01.11	2010	female	3	306.0	44.5	48.5	7.7	7.2
				27	271.0	50.0	54.2	6.6	6.4
20	1.12.10	2010	unknow n	2	270.0	40.8	49.6	7.6	7.3
				38	255.0	44.7	49.3	6.4	6.4
21	22.11.10	2010	Female	1	339.0	38.4	47.3	6.1	6.9
				7	292.0	39.5	51.1	6.3	8.2
				35	325.0	43.0	54.4	6.1	7.2
22	25.12.11	2011	unknow n	3	314.0	42.0	52.0	7.0	8.0
23	16.09.11	2011	unknow n	7	265.0	39.0	52.0	7.0	7.0
24	8.02.12	2011	female	8	241.0	42.0	50.0	6.6	7.0
				21	214.0	44.0	51.0	6.6	6.0
25	13.01.12	2011	unknow n	3	255.0	41.0	51.0	6.0	7.0
26	5.02.12	2011	unknow n	5	264.0	42.0	51.0	6.0	8.0
27	17.10.10	2011	unknow n	10	266.0	39.5	49.9	6.7	6.9
28	23.12.10	2010	unknow n	4	256.0				
29	18.10.04	2004	male	0	270.0	41.4			
				5	262.0	41.8			

				12	262.0	42.7
				20	295.0	43.8
				26	329.0	44.9
				33	362.0	46.0
				40	405.0	46.9
				43	420.0	47.3
				47	445.0	47.8
				54	440.0	48.4
				61	478.0	48.8
				70	470.0	49.8
				87	520.0	50.4
				90	530.0	51.0
30	29.11.04	2004	unknown	5	320.0	43.5
				13	300.0	44.5
				19	312.0	45.2
				28	335.0	46.4
				45	350.0	49.8
				48	350.0	49.9
				54	370.0	50.3
				61	360.0	50.4
				66	348.0	50.9
				69	358.0	51.0
				75	385.0	51.9
				82	400.0	52.1
31	8.10.04	2004	unknown	30	378.0	46.7
				36	418.0	47.7
				43	430.0	48.8
				50	435.0	49.6
				53	435.0	49.9
				57	450.0	50.4
				64	420.0	50.8
				71	418.0	51.3
				80	435.0	51.7

Table 2.4. Invertebrate abundance in grams of dry mass weight from pitfall traps on Ponui Island, New Zealand from November 2010 – March 2012. Measures of each of the 25 pitfall traps are given along with their habitat type.

Pitfall	Habitat	Nov-10	Jan-11	Feb-11	Apr-11	May-11	Jun-11	Jul-11	Aug-11	Sep-11	Oct-11	Nov-11	Dec-11	Jan-12	Feb-12	Mar-12
1	Forest	0.19	0.9	0.1	0.5	2.6	0.9	1.7	0.7	0.4	1.4	0.7	1.5	0.8		1.3
2	Forest	1.59	1	0.8	0.1	0.4	0.9	0.3	0.4	0.2	0.2	0.5	2	2.2	0.5	1.1
3	Forest	0.44	0.4	0.1	0.05	0.6	0.5	0.2	0.4	0.2	0.9	0.8	1.1	0.6		0.2
4	Forest	0.25	0.6	0.4	0.6	1.5	0.6	0.6	1.2	0.1	0.8	1.1	1.3	1.6		2.1
5	Forest	1.42	0.9	0.6	0.1	1	1.1	0.3	0.4	0.1	0.3	0.7	1.2	1.1	1.3	0.9
6	Forest	0.22	0.3	0.3	0.3	0.1	0.3	0.1	0.2	0.1	0.5	0.4	0.8	0.7	0.2	0.4
7	Forest	0.26	0.1	0.4	0.1	0.1	0.5	0.1		0.1	0.5	1.1	0.6	0.3		0.5
8	Forest	0.37	0.4	0.3	0.4	0.2	0.5	0.3	0.5	0.3	0.8	1.5	1.2	1.3	0.7	1.5
9	Forest	0.26	0.8	0.1	0.2	0.1	0.7	0.3	0.2	0.1	0.4	0.4	0.8	0.5	0.4	0.5
10	Forest	0.27	0.3	0.2	0.2	0.2	1.1	0.4	0.1	0.8	1.2	0.8	0.7	0.8	0.3	1.1
11	Scrub	0.79	1.8	0.3	0.3	0.6	0.6	0.2	0.2	0.1	0.6	0.9	0.9	1.5		1.4
12	Scrub	0.42	0.2	0.6	1.2	0.4	0.4	0.6	0.2	0.2	0.9	1.2	1.3	1.5	0.7	2.1
13	Scrub	0.23	0.6	0.3	1.6	0.5	0.4	0.3	0.7	0.2	0.7	0.5	1.3	0.6	0.2	0.9
14	Scrub	1.23	1.6	1.3	0.6	1.1	1	0.4	1.1	0.1	0.9	0.9	1.5	1.5		1.8
15	Scrub	1.03	0.9	0.6	0.1	0.1	0.9	0.9	0.3	0.4	0.6	0.7	0.8			1.3
16	Scrub	1.02	1.8	1.1	0.6	2.6	1.1	1.3	0.2	0.2	1.1	1.9	1	1.5		1.7
17	Scrub	0.95	2.1	1.4	0.5	0.8	0.8	0.2	0.5	0.1	1	0.9	1.7	2.5		4.5
18	Scrub	0.45	1.2	0.5	0.8	0.7	1.1	0.1	0.6	0.1	1.7	1.1	2.3	1.5	1.8	1.7
19	Scrub	0.96	1.2	0.6	1	1	0.3	0.4	0.1	0.1	1	2.2	1	2.8	1.3	2
20	Scrub	0.76	6.8	2.9	2	0.5	0.5	0.3	0.2	0.2	0.8	1.3	0.9	1.4		1.8
21	Pasture	2.44	4.8	7	16.4	0.9	0.8	0.3	0.5	1	1	1.2	1.7	0.5	13.3	5.2
22	Pasture	5.02	7.8	9.3	12	0.8	1.3	1	1.7	0.8	1.4	0.3	1.3	1.2	8.7	7.2
23	Pasture	0.99	14.7	11.8	4.6	3.7	0.9	0.4	1.2	0.4	0.4	0.6	3.1	19	21.6	5.9
24	Pasture	2.72	13.8	15.4	9.45	2.1	0.9	0.3	1.3	0.1	1	1.6	3.7	14.9	19.3	11.5
25	Pasture	2.00	22.1	17.1	17.5	6.5	2.3	0.4	2	0.8	3	1.7	3.4	24.8	33	29.1

Table 2.5. Invertebrate abundance in numbers of individual invertebrates from pitfall traps on Ponui Island, New Zealand from November 2010 – March 2012. Measures of each month are given as the sum of all pitfall traps.

Month	Spider	Worm	Amphipod	Isopod	Slug/ Snail	Cockroach	Cricket	Weta	Bee tle	Ant	Fly	Centipede /millipede	Caterpillar	Wasp/bee	unknown	larvae	total
Jan-11	227	11	221	617	7	100	263	92	107	306	29	23	0	0	16	16	2035
Feb-11	209	4	177	325	50	89	450	48	93	176	69	9	2	5	13	4	1723
Apr-11	169	23	139	678	128	41	464	11	50	64	62	41	4	42	8	5	1929
May-11	132	61	603	235	94	40	90	21	31	35	9	35	3	24	2	9	1424
Jun-11	102	62	295	264	147	15	8	81	14	16	22	18	5	4	2	10	1065
Jul-11	62	70	26	251	96	9	23	0	48	1	31	16	4	50	28	2	717
Aug-11	72	51	495	76	145	11	5	21	24	10	14	8	16	26	4	15	993
Sep-11	55	24	566	124	103	10	2	13	14	5	13	16	6	1	3	41	996
Oct-11	222	37	1005	371	119	8	3	18	68	21	42	100	0	14	0	78	2106
Nov-11	384	16	421	992	41	8	4	25	81	42	47	191	3	9	2	48	2314
Dec-11	513	21	1378	987	33	35	69	44	183	257	144	183	1	6	0	37	3891
Jan-12	266	10	1007	241	29	94	441	54	111	185	33	171	7	2	0	6	2657
Feb-12	308	15	625	308	93	158	311	58	115	65	34	185	5	1	0	0	2281
Total	2721	405	6958	5469	1085	618	2133	486	939	1183	549	996	56	184	78	271	

Table 2.6. Adapted from Starck and Ricklefs (1998a) showing species whose growth rates constants (K_g) are < 0.05 . Type indicates the type of developmental mode; Sup = Super precocial, P = precocial, Sa = semi altricial, Sp = semi precocial and A = altricial.

Family	Species	Type	K
Apterygidae (kiwi)	<i>Apteryx mantelli</i> (North Island brown kiwi)	P	0.005 (this study)
	<i>Apteryx mantelli</i> (North Island brown kiwi)	P	0.006 (McLennan 2004)
Tinamidae	<i>Nothura darwinii</i> (Darwin's Nothura)	P	0.047
	<i>Nothura maculosa</i> (Spotted Nothura)	P	0.037
Spheniscidae	<i>Aptendytes forsteri</i> (Emperor Penguin)	Sa	0.034
Diomededae	<i>Diomedea amsterdamensis</i> (Amsterdam Albatross)	Sp	0.013

	<i>Diomedea epomophora</i> (Southern Royal Albatross)	Sp	0.018
	<i>Diomedea exulans</i> (Wandering Albatross)	Sp	0.018
	<i>Diomedea immutabilis</i> (Laysan Albatross)	Sp	0.016
	<i>Diomedea melanophrys</i> (Black-browed Albatross)	Sp	0.042
	<i>Diomedea nigripes</i> (Black-footed Albatross)	Sp	0.022
Procellariidae	<i>Macronectes giganteus</i> (Southern Giant Petrel)	Sp	0.047
	<i>Macronectes halli</i> (Northern Giant Petrel)	Sp	0.040
	<i>Procellaria aequinoctialis</i> (White-chinned Petrel)	Sp	0.043
	<i>Procellaria cinerea</i> (Grey Petrel)	Sp	0.026
	<i>Puffinus pacificus</i> (Wedge-tailed Shearwater)	Sp	0.038
Sulidae	<i>Sula dactylatra</i> (Masked Booby)	A	0.046
	<i>Sula sula</i> (Red-footed Booby)	A	0.039
Fregatidae	<i>Fregata Aquila</i> (Ascension Frigatebird)	A	0.027
	<i>Fregata magnificans female</i> (Magnificent Frigatebi)	A	0.029
	<i>Fregata minor</i> (Great Frigatebird)	A	0.035
Anatidae	<i>Aix galericulata</i> (Mandarin Duck)	P	0.047
	<i>Anas platyrhynchos domesticus</i> (Domestic duck)	P	0.041
	<i>Anser anser domesticus</i> (Domestic geese)	P	0.040
	<i>Mergus serrator</i> (Red-breasted Merganser)	P	0.043
	<i>Somateria mollissima</i> (Common Eider)	P	0.036
Accipitridae	<i>Aquila verreauxii</i> (Verreaux's Eagle)	Sa	0.047
	<i>Gyps africanus</i> (White-backed Vulture)	Sa	0.024
Megapodiidae	<i>Alectura lathami</i> (Australian Brushturkey)	Sup	0.022
	<i>Leipoa ocellata</i> (Malleefowl)	Sup	0.007
	<i>Macrocephalon maleo</i> (Maleo)	Sup	0.027
Phasianidae	<i>Alectoris graeca</i> (Rock Partridge)	P	0.035 (male)
	<i>Bonasia umbellus</i> (Ruffed Grouse)	P	0.042
	<i>Gallus gallus</i> (Red Junglefowl)	P	0.025
	<i>Lophortyx californica</i> (California Valley Quail)	P	0.039
	<i>Meleagris gallopavo</i> (Wild Turkey)	P	0.016
	<i>Pavo cristatus</i> (Indian Peafowl)	P	0.020
	<i>Phasianus colchius</i> (Common Pheasant)	p	0.031
Opisthocomidae	<i>Opisthocomus hoazin</i> (Hoatzin)	Sa	0.047
Gruidae	<i>Anthropoides paradise</i> (Blue Crane)	P	0.040
	<i>Balearica pavonina gibbericeps</i> (Black Crowned Crane)	P	0.044
	<i>Grus Americana</i> (Whooping Crane)	P	0.049
	<i>Grus Antigone</i> (Sarus Crane)	P	0.035
	<i>Grus canadensis pratensis</i> (<u>Sandhill Crane</u>)	P	0.032
	<i>Grus grus</i> (Common Crane)	P	0.038
	<i>Grus japonensis</i> (Red-crowned Crane)	P	0.034
	<i>Grus monacha</i> (Hooded Crane)	P	0.045
Rallidae	<i>Fulica Americana</i> (American Coot)	P	0.041
Ottidae	<i>Lophotis ruficrista</i> (Red-crested Korhaan)	P	0.048
	<i>Otis tarda</i> (Great Bustard)	P	0.043
Strigidae	<i>Bubo bubo</i> (Eurasian Eagle-Owl)	A	0.041

Chapter 3: Behaviour of North Island brown kiwi chicks at the nest



Introduction

Young animals must learn to navigate and survive in their environment. In most vertebrate species young learn necessary skills from their parents and are reliant on them for their survival. Birds in particular show a wide diversity in the degree of parental reliance (Starck

and Ricklefs 1998b). Some species depend on their parents for a long period even after they have left the nest. For example, Australian magpie (*Gymnorhina tibicen*) young are fed by their parents for up to six months (Marchant et al. 2006). On the other end of the spectrum, Australian brush-turkeys (*Alectura lathami*) are from the highly precocial Megapodiidae family. Their eggs are incubated by fermenting vegetation, after hatching chicks must dig themselves out from the vegetation and learn how to forage and survive with no parental guidance (Goth and Vogel 2003).

North Island brown kiwi (*Aterpyx mantelli*, NIBK) also fall on the precocial end of the spectrum. They are medium sized (2 - 2.8kg) nocturnal, flightless birds, endemic to New Zealand (Holzapfel et al. 2008). In the wild, eggs are incubated by the male for 75 - 84 days (Reid and Williams 1975) in a nest located in hollow tree or a hole dug in the ground (Calder 1979, McLennan 1988). Young NIBK begin to leave their nest at night at 5 days of age (Holzapfel et al. 2008) and fledge leaving the nest permanently at an average of 25 days of age (McLennan et al. 1996, Colbourne 2002). It is believed that NIBK chicks receive little post-hatch parental care (Holzapfel et al. 2008); to my knowledge this had never been intensively examined, and this is likely due to the challenges of studying a nocturnal species.

NIBK are endangered (IUCN 2012) and extensive conservation efforts are being made to slow population decline. A significant cause of decline is predation of young NIBK by introduced mammalian predators, primarily stoats (*Mustela erminea*; McLennan et al. 1996). Consequently efforts mainly focus on predator control and Operation Nest Egg (BNZONE™). In BNZONE™, eggs are removed from the wild to be artificially incubated and hatched in captivity. Chicks are then reared in predator-proof enclosures or predator-free islands and parks (i.e., crèches) until they reach 1000g, a weight that is considered to be safe from stoat predation (Colbourne et al. 2005). It is important to understand the behaviour of NIBK chicks at a young age for two reasons. Firstly, to expand what is known of the behaviours of these rare and elusive birds. Secondly, understanding the behaviours of young NIBK may enable BNZONE™ practises to be improved so that chicks are reared in a way that allows them to adopt and practise natural behaviours and potentially enhance their survival when released into the wild.

Using video cameras situated outside the nests I was able to obtain information about the behaviour of NIBK chicks, gaining insight into how the chicks first learn to navigate their environment. Based on our current knowledge of NIBK I made the following predictions regarding their behaviour: a) sniffing behaviours (as defined in Castro et al. 2010) may be used for vigilance, and older chicks would sniff more than younger chicks as they become more functionally mature; b) chicks will spend less time around the nest with increasing age as they learn about the surrounding area, and c) because NIBK are highly precocial and no parental care is known (other than incubation and providing warmth to the chick in the nest), I expected to see no parental-care interactions between chicks and their parents.

Methods

Monitoring

General information regarding the study site, the species and general monitoring is given in the Introduction, section: Aims, Contribution and Study Site. While chicks were still roosting in their nests, video camera setups were used for as many nights as weather allowed to observe chick behaviour in close vicinity to their nest. The video camera setups consisted of Sony Handicams (DCR-HC40E & DCR-HC42 with NightShot™ function) and infrared lights (IRLamp 6, Bat Conservation and Management Inc.) that were attached to a tripod and then tied to surrounding trees to ensure stability in the wind and to prevent cattle and sheep damaging the camera if they found them. An umbrella was attached to the tripod so equipment did not get wet; however, video cameras were not used during heavy rainfall or strong winds. Tripods were setup 2 - 5m from the nest depending on the terrain and focused on the nest entrance giving a 2 - 5m meter radius of view subject to the nest location. Each day before dark (to ensure that the movements of the birds would be recorded) video cameras were taken to nests, set up on tripods and left recording; great care was taken around nests to ensure incubating males did not desert their nest and no desertions occurred as a result of this study. Video cameras were collected in the morning so that data could be downloaded.

Behavioural data

I used VLC media player (version 4.4.4) to extract from the videos the following data: the time of departures and arrivals of the chick and father; the number of times each chick was seen in the nest entrance per night; the number of times the chick left the vicinity of the nest; whether the chick sniffed the air when emerging from the nest or when nearby (recorded as: yes or no); the number of tumbles (i.e., lost their footing); and their level of probing behaviour (foraging or exploratory). I subjectively decided the level of probing behaviour observed from each chick in proportion to the amount of time they were visible on screen. Then used an index as follows: 1 = no probing behaviour seen, 2 = chicks probing a few times, but less than half the time they were visible on screen, 3 = chicks probed half the time they were visible on screen, 4 = chicks probed the entire time they were visible on screen. The proportion of probing behaviour given the amount of time chicks were on screen was used rather than a count of the number of times probed; this was because chicks were visible on screen for varying lengths of time and this method allowed comparisons between chicks and ages. Probing and tumbling were used as indicators of learning behaviours, and sniffing an indicator of vigilance behaviour. When both the father and the chick were observed leaving the nest, it was recorded who left first. Additionally, any interactions between birds were recorded and described. The sex of unmarked individual adults that were observed in the videos were ascribed according to the length of their bills (females have significantly longer bills, Cunningham and Castro 2011). In the rare cases when two chicks hatched from the same nest, videos were not used as the identity (and age) of each chick could not be determined.

Statistical Analyses

All statistical analysis and graphs were produced in IBM SPSS® (version 20.0, 2011). All means are presented with \pm SE and graphs with error bars show \pm 2 SE. All data were not normally distributed (Kolmogorov–Smirnov test: $P < 0.05$); namely, the number of times seen in the entrance and leaving the nest, the length of time before leaving the area, probing index, number of tumbles and sniffing behaviour. Therefore, I used generalized models to determine if there was any significant relationship between these factors and the age of the chick. I used the following distributions: poisson, poisson, linear, ordinal logistic,

poisson and binary logistic, respectively. The individual identity of each chick was included in the models to account for individual variation.

Results

In total 914 hours of video data were recorded from 21 chicks in 20 nests, six chicks were videoed for 116 hours in 2010 - 2011 with a median of 6:00:09 hours:min:sec recorded each night (range = 3:04:18 – 9:09:01 hours:min:sec) and 15 chicks for 798 hours in 2011 - 2012 with a median of 5:01:25 recorded each night (range = 1:07:49 – 10:38:47 hours:min:sec). The length of video recordings each night was dependent on the weather, daylight hours and life of the camera battery. Chicks used in this study hatched between mid-October and mid-January in the 2010 - 2011 breeding season and between late August and early February in the 2011 - 2012 breeding season. In the 2011 - 2012 season two males had two successful clutches, however, clutch number was not used as a variable because the sample size was too small. Chicks first emerged from their nest at an average age of 4.3 days of age (SE = 0.55, n = 12) and fledged at an average age of 24 days (SE = 2.8, n = 18). In this study 87.5% of young NIBK died; 20% of these had not fledged when they died, and one of these was observed on video being killed by a cat (Chapter 5).

Most chicks were not seen at the entrance of the nest (emerging) before five days of age. From five to eight days of age, the number of times chicks were seen at the entrance of their nest ranged from once for some individuals to six or more times for others. Chicks were seen less at the entrance of the nest per night with increasing age (Figure 3.1). This change in the number of times chicks were observed in the entrance of the nest was not significantly related to age ($P = 0.54$, $df = 28$, Wald Chi Square = 40.96), however there was a significant effect of chick identity ($P < 0.01$, $df = 21$, Wald Chi Square = 41.71). Similarly, the number of times the chicks left the nest, once they started coming out at approximately 5 days of age, decreased with age (Figure 3.2). However, this relationship only approached significance ($P = 0.074$, $df = 28$, Wald Chi Square = 22.78). There was no significant effect of individual chick on the number of times chicks left the nest ($P = 0.097$, $df = 21$, Wald Chi Square = 29.76).

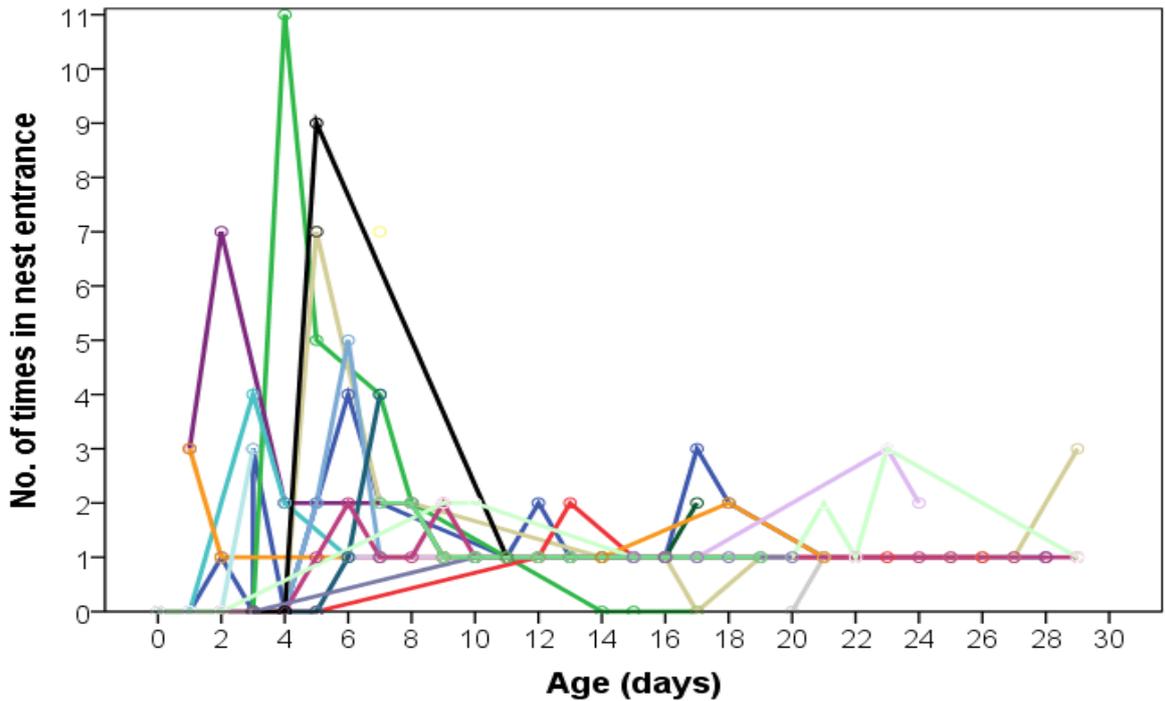


Figure 3.1. North Island brown kiwi chick behaviour at the nest on Ponui Island, New Zealand from 2010 - 2012. The number of times chicks were seen in the nest entrance each night at different ages. Each colour represents an individual chick.

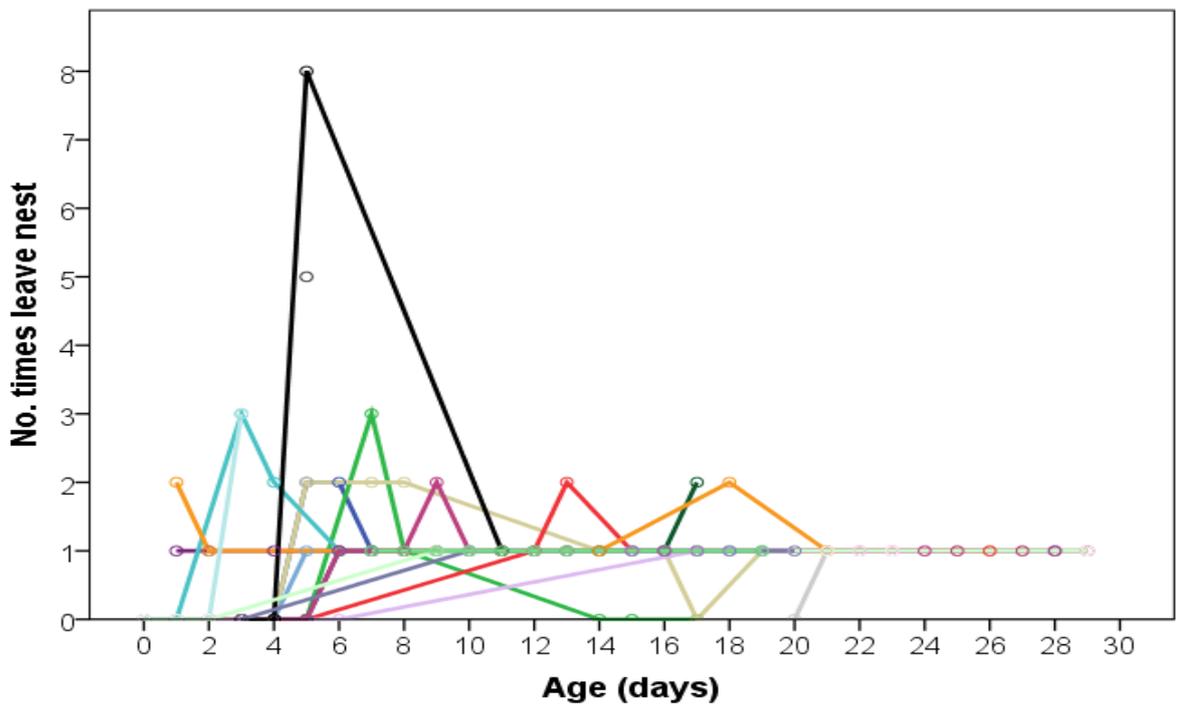


Figure 3.2. North Island brown kiwi chick behaviour at the nest on Ponui Island, New Zealand from 2010 - 2012. The number of times chicks of different ages were seen leaving the nest each night. Each colour represents an individual chick.

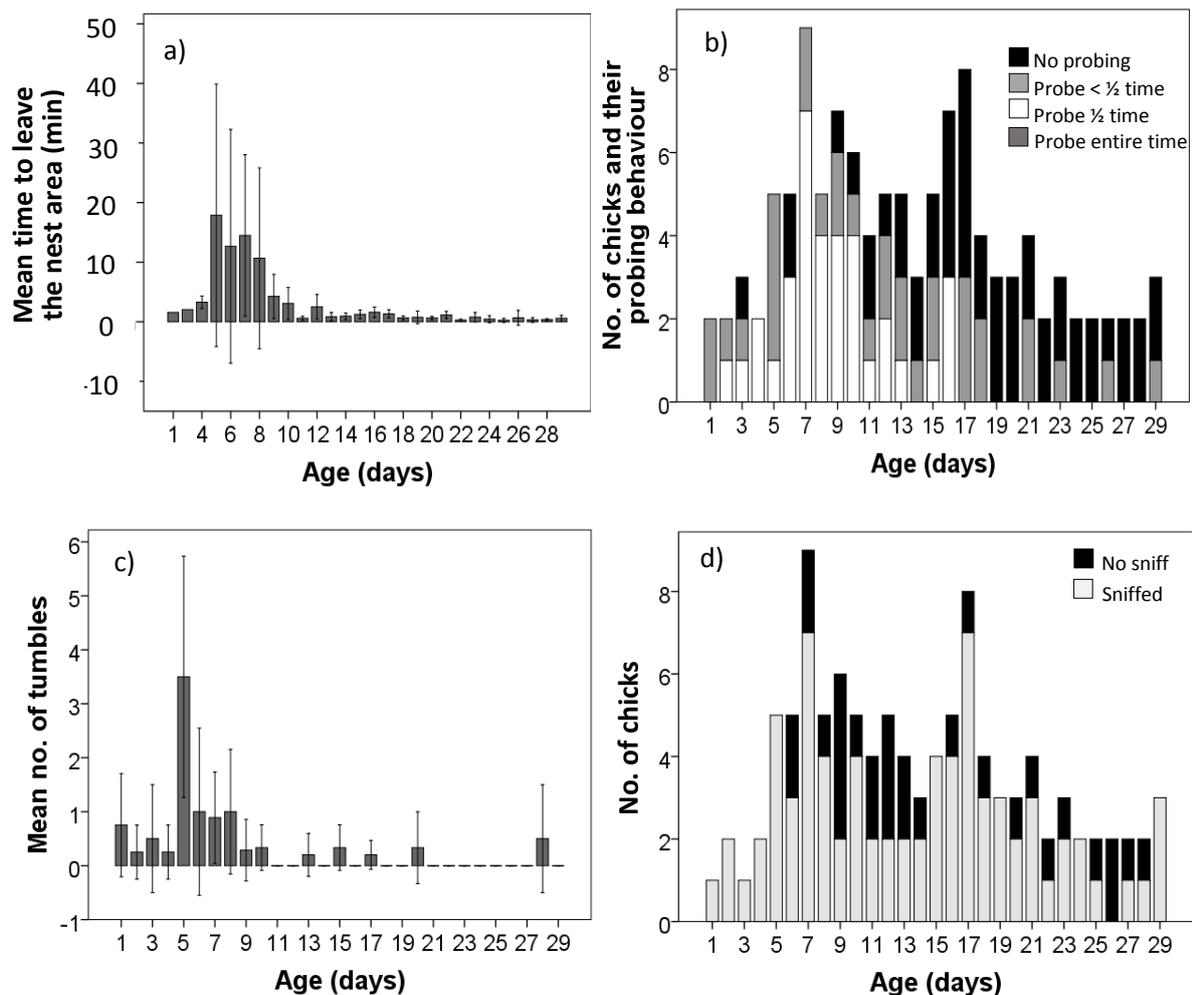


Figure 3.3. North Island brown kiwi chick behaviours at their nests on Ponui Island, 2010 - 2012. a) Mean time spent in the vicinity of the nest. Error bars ± 2 SE. b) Index of probing behaviour while in the vicinity of the nest. No chicks probed the entire time while in the vicinity of the nest. c) Mean number of times a chick tumbled at different ages (days). Error bars ± 2 SE. d) 'Sniffing' behaviour of chicks when emerging or close to their natal nest.

Chicks stayed close to the nest the longest between five and eight days of age. Age did not have a significant effect on the amount of time spent close to the nest ($P = 0.41$, $df = 29$, Wald Chi Square = 30.06, Figure 3.3), however, chick identity did ($P < 0.01$, $df = 21$, Wald Chi Square = 43.6). There was a significant difference in probing behaviour with age ($P < 0.0001$, $df = 29$, Wald Chi square = 63.4), with younger chicks probing more around the nest than older chicks. After 18 days of age, chicks probed less than half the time, if at all (Figure 3.3). There was also a significant effect of individual chicks on probing behaviour ($P < 0.05$, $df = 21$, Wald Chi Square = 38.5). Chicks between five and eight days of age were observed to tumble more than older chicks, but this was not statistically significant ($P = 0.62$, $df = 11$,

Wald Chi Squared = 9.0, Figure 3.3c). There was a significant effect of chick identity on the number of tumbling behaviours observed ($P < 0.05$, $df = 11$, Wald Chi Square = 22.9). A pairwise t-test showed that significantly more chicks sniffed than not when emerging from the nest ($P < 0.001$, $t = 4.33$, $df = 28$). Sniffing behaviour did not appear to differ with age ($P = 0.22$, $t = -1.2$, $df = 106$; Figure 3.3d). Chicks were observed leaving the nest before the incubating male 80% of nights (Figure 3.4).

It should be noted that there may be a bias in the frequency of: probing, tumbling and sniffing behaviours, due to the length of time chicks are in the vicinity of the nest. As chicks were observed close to the nest, for longer periods of time at a young age, these behaviours are more likely to be observed at a greater frequency at a younger age. However, this bias can be partly accounted for with probing behaviour because the score given is the amount of probing seen as a proportion of time visible rather than a total count of the number of probes seen. With regard to sniffing behaviour, if chicks sniffed it tended to be when emerging from the nest or immediately after, so the bias maybe limited with this behaviour. Lastly, there is likely to be a bias with the number of 'tumbles' seen in the vicinity of the nest. However from observations of the videos, chicks were less sure footed when first emerging from the nest, and improved quickly within a day or two. Additionally, when chicks initially emerge from the nest, their large yolk sac is often visible on video (it protrudes significantly from the abdominal region), and may contribute to the chicks being off balance and more likely to tumble over.

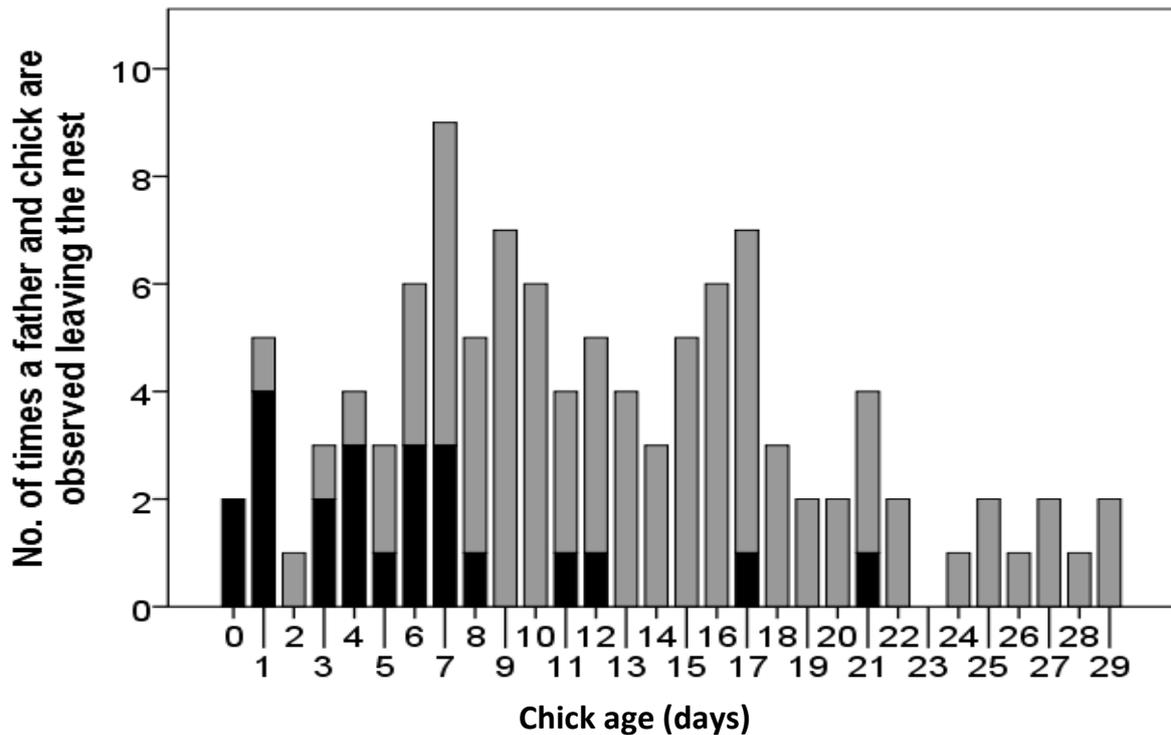


Figure 3.4. The order of nightly departure from the nest, of chicks and brooding male North Island brown kiwi on Ponui Island, 2010 - 2012. Black represents nights when the father left the nest first and grey signifies when the chick left first.

Social Interactions

Of the 161 recorded nights seven interactions between chicks and adults were observed. Of these, five interactions were filmed at the same nest. Interactions are described below. Please note: 'squeal', 'grunt' and 'squeaks' were used to explain noises that chicks made in a social context. I do not know the meaning of these interactions. Therefore, I do not imply these were negative (or positive) interactions, simply the best way to describe the noise that was made. All time measurements are given in hours: minutes: seconds format. In all seven cases the adult bird interacting with the chick (other than the father) was a female. For two of the three nest sites (Charlie and Ridley), I believe the interacting female was the mother of the chick because she was wearing a metal band or transmitter, respectively, and had been seen at the nest multiple times before.

1. **Female Devin, four days of age (22:17:10 – 22:18:30, Video 1):** chick is foraging 2m from the entrance of the nest, jumped and ran 0.5m (22:17:15) towards a tree, within 4 seconds an adult female runs into the same tree beside the chick (22:17:19). Immediately the female pushes the chick with her bill, at the same time the chick makes a repeated

high pitched noise similar to a squeal six seconds long. The chick moves slightly away from the female as she pushes her. They then begin foraging beside one another (adult seen swallowing food). The chick then runs another 0.5m away from the female (22:17:58) and continues to forage. At 22:18:20 the chick runs off screen, followed shortly after by the adult female at 22:18:30 in the same direction.

2. **Female Charlie, seven days of age (20:21:41 – 20:36:11, Video 2):** the chick emerged from the nest and an adult female with a metal band walks close by. The chick begins to move in the direction of the female (20:35:31), hears the adult crunch leaves underfoot and then sniffs in the adults' direction. Both approach each other, touching bills whilst sniffing (20:35:41). When the chick walks past the female, the adult pulls/grabs the feathers at the back of the chick with her bill and the chick makes a high pitched noise that could be likened to a squeal. The chick then runs in the opposite direction from the female (20:36:11).
3. **Male Ridley, seven days of age (21:11:05 – 21:30:05, Video 3):** the chick is heard making a high pitched noise that could be likened to a squeal (off-screen) for a 20 second period starting at 21:11:05. A short time later the chick is then seen beyond the nest with an adult female (21:11:34), the female appears to push the chick with her bill. Within 20 seconds (21:11:54) the father appears from above the nest, the chick backs away from both the male and female, and sniffs at the two adults. The male then chases the female away, and growling and squealing is heard from their direction. Nine minutes later (21:20:51) the chick is back on screen foraging around the nest. An adult female with a transmitter comes back into view and the chick makes a low, grunt like noise and then a high pitched noise that could be likened to a squeal, as both sniff one another. The chick continues to rear up, standing tall on both legs. A few minutes later (21:24:51) the female begins to forage, while the chick is still sniffing the female. The female circles the chick and leaves (21:27:58); the chick continues to sniff the air in the direction of the female periodically for another 2 minutes then walks off screen still sniffing as he goes (21:30:05).
4. **Male Ridley, eight days of age (22:22:20 – 22:26:26, Video 4):** the chick leaves the nest at 22:22:20, probing a short distance from entrance; he sniffs in the direction of the male when he emerges a short time later (22:22:37). The male touches the ground near the chick and the chick visibly recoils away from the adult while making a short high pitched

noise similar to a squeak, they then sniff one another (22:22:45), the chick rears up and the father leaves the area, the chick continues to sniff the surrounding area then leaves at 22:26:26.

5. **Male Ridley, nine days of age (21:48:02 – 3:26:27, Video 5):** the chick comes out of the nest (21:48:02) and the incubating male shortly follows (21:49:06). Within 20 seconds an adult female with a transmitter approaches and all three sniff one another in front of the burrow (21:49:26). The male approaches the female and then walks off and she follows. The chick leaves the area at 22:00:53. The male returns to the nest at 23:33:40 and goes inside. He emerges from the nest again at 0:29:34, the female approaches and attacks him then he runs off (Video 6). At 02:46:03 the father had returned to the nest again and the chick is foraging nearby. A female with a transmitter comes into view at 3:24:53 and begins pushing the chick with her bill, they sniff one another and the chick grunts. The female pulls the chicks' feathers with the tip of her bill; the chick faces the female standing up and then returns to the nest (3:26:27, Video 7).
6. **Male Ridley, 10 days of age (21:27:44 – 21:33:25, Video 8):** the chick is foraging close to nest, an adult female with a transmitter walks into view, towards the chick (21:30:12) and starts pushing him with her bill. The chick faces her but tries to back away and she attempts to grab/pinch his feathers with her bill, grunting is heard from the chick. The female pulls the chick back towards her with her bill and the chick grunts again. The chick moves away from the female but does not run away from her (21:33:25). Both move out of view and 'grunting' and 'squealing' can be heard (21:33:30).
7. **Male Ridley, 22 days of age (5:11:34 – 5:11:50):** the chick (assumed as similar to noises previously heard by chicks) is heard making a repeated high pitched noise similar to a squeal in the nest with the incubating male.

Adult interactions

Two incidents were seen where an unknown adult male NIBK entered the nest when both the father and chick were present. In both incidents the unknown male exited the nest quickly and was followed by the nesting male. In one case, the nesting male proceeded to kick, growl and chase the other male (Video 9). In the second case, the nesting male chased the intruder away from the nest and was heard growling and hissing. A third incident occurred (as mentioned above: Ridley seven days) <5m from the natal nest when a chick

was foraging, although video footage was poor, an unknown female was seen approaching the chick, the chick was heard making a repeated high pitched noise, the nesting male then appeared to chase the female off and growling was heard in the distance (Video 3).

Discussion

The behaviour of NIBK chicks around their nest varied greatly with age. Chicks first emerged at an average age of 4.3 days, which is similar to the five days of age that was previously reported (Holzapfel et al. 2008). At 3 - 7 days of age chicks were observed between one and 11 times at the nest entrance per night moving in and out of the nest multiple times each night. As the chicks aged they were seen at the entrance of the nest only once when they emerged for the night and then when they returned again at the end of the night. Between five and seven days the chicks spent the longest amount of time outside of, but in close proximity to their nest. This time seemed to be spent performing exploratory and learning behaviours. At five days of age when first emerging from the nest, chicks frequently fell down slopes and tumbled over when stretching, they became more sure footed with age. This may be demonstrating a) a poor knowledge of the area, and b) how unsteady the chicks are moving around when they first emerge. It also emphasises how vulnerable NIBK chicks are to mortality from falling down steep slopes and predation. Although no chicks in this study died from falling down, one chick was depredated by a feral cat on his second night emerging from the nest, within 1m of the nest (Chapter 5). The vulnerability of young NIBK chicks is supported in other NIBK studies (McLennan et al. 1996, McLennan et al. 2004) where high levels of mortality were due to predation and accidents such as falling down cliffs. Although age was not a significant variable affecting most of the behaviours observed in this study, I found definite trends with age. Increasing the sample size may result in a decreased effect of individuals on dependent factors and a stronger trend relating variables to age emerging.

NIBK eyesight is poor so they have a greater reliance on olfactory and tactile information, particularly at night (Martin et al. 2007). I hypothesised that sniffing the surrounding area when emerging from the nest is a vigilance behaviour and that older chicks would sniff more than younger chicks. However, there was no difference between sniffing behaviours at

different ages. This may indicate that sniffing is an innate behaviour that occurs at a young age in NIBK. This may be particularly important for NIBK due to their high level of precociality and the minimal amount of parental care that is given after hatching. High vigilance from a young age may reduce the probability of succumbing to predation, or it may be related to assessing the presence of other NIBK in the vicinity. After leaving the nest chicks moved around their nest walking back and forth over some areas, tapping the ground often with their bills. They did not seem to be foraging as no probing into the ground or swallowing behaviours were seen until approximately day seven. By exploring and continually touching the area around them they may be determining their location, paths and how their natal area smells. I believe that these NIBK chicks are showing learning behaviours as with increasing age they moved further from the nest, tumbled less, and spent longer away from the nest each night. This learning of the natal area and the use of scent may be similar to that of the Procellariiform seabirds (e.g., albatrosses, shearwaters, petrels). For example, nestling European storm-petrels (*Hydrobates pelagicus*) use olfaction for nest recognition in a colony (Minguez 1997). Common diving petrel chicks (*Pelecanoides urinatrix*), in an experiment, were found to walk the shortest distance to soil taken from their nest, relative to other stimuli. This suggests that chicks use olfactory stimuli for nest recognition even before fledging (Cunningham et al. 2012). A similar result was seen in Leach's storm petrels (*Oceanodroma leucorhoa*) (O'Dwyer et al. 2008); many species use scent to find their colony location, particularly nocturnal species (Bonadonna 2002).

I hypothesised that staying in close proximity to the nest allows the chicks to explore and learn with the protection of the nest and father (possibly both parents) nearby. Although parental care has not previously been reported in NIBK, the three incidents where unknown adults entered the nest or approached the chick and were chased away by the male at the nest, could potentially represent parental care. Although, I cannot say for certain if the males were showing parental care or simply protecting their territory from other adult NIBK, because there were no visible attacks to the chick by these unknown adults. However, there appears to be a protection benefit for chicks that stay close to the natal nest when they are young.

Interestingly, chicks left the nest each evening before their father 80% of the time. Possible explanations for this behaviour are that a) the fathers were sitting on a second egg and

during incubation they greatly reduce the amount of time they spend out of the nest, this is supported by unpublished data (Jamieson et al., unpub. data), or b) chicks may require more time for foraging each night to fulfil their energy requirements. The latter explanation may also be supported because when chicks were observed foraging between three and seven days of age their success rates were very low (Wilson unpub. data). However, the second explanation could not be quantified because the total length of time that both the chick and male were outside the nest foraging each night could not always be determined (i.e., the camera battery did not allow recording the entire night). Therefore, I could not conclude if chicks spent longer outside the nest each night. If parental care in the way of protection is given by the father there are two lines of thought that should be considered with regard to the chick leaving the nest first. Firstly, if the father leaves the nest later than the chick, this may limit protection that he can give if the chick is too far away. Secondly, if the male is still in the nest he may be close enough that he can protect the chick if it is in trouble. If he leaves first he may be too far away to help.

Social interactions between birds were limited; therefore, it is difficult to make any significant conclusions. Interactions of chicks with females close to the nest did not appear to be aggressive when compared to interactions between adults, because adults tend to kick, growl, hiss and chase one another. The chick, however, did grunt and squeal, which is a noise that they occasionally make when held for fitting radio transmitters and taking measurements. Perhaps the female trying to pull the chick towards her is a way of greeting and learning who the chick is in their territory and/or preening them. It is possible that the chick then learns some behaviours from the female, both in terms of interacting with conspecifics and perhaps even foraging as in two cases the female began foraging near the chick. Because NIBK seem to use sight very little (Martin et al. 2007), other senses may be used that cannot be determined from video by the human eye or ear. Very little is known about the social behaviours of adult NIBK and even less is known about the interactions between adult and young NIBK, here I have presented results that warrant further investigation.

In conclusion, NIBK chicks are vulnerable to injury at a young age because they often fall and tumble. It is also obvious how little NIBK chicks seem to use their eyesight and how important olfactory senses are. Chicks did not tend to sniff (other than when first emerging

from the nest) unless they heard a noise, this makes them extremely vulnerable to stealth mammalian predators such as stoats and cats. Interactions and parental care may play a greater role in the behaviour of NIBK than previously thought and further research is needed to determine the context of the interactions between young NIBK and adults and how often these occur in other populations. When chicks are reared in captivity a number of these variables should be considered. Chicks should have access to an area with obstacles so they can learn to move over uneven ground, as is present in the native New Zealand bush. The importance of adult NIBK to chick learning also needs to be determined. If chicks learn skills or information from adults, new techniques may need to be implemented at BNZONE™ facilities. For example, adults may need to be released into an area prior to chicks being released if chicks are found to use adult scent to navigate in their environment. Although BNZONE™ is a good and necessary tool for the conservation of NIBK, it seems from my results that a large amount of learning takes place in the first 10 days after hatching; it is important to determine that there are no negative consequences to chicks learning necessary skills in captivity relative to the wild.

Chapter 4: Understanding movements of young North Island brown kiwi



Introduction

Dispersal of young individuals is a fundamental process that has important consequences for population dynamics, species evolution (Greenwood 1980, Johnson and Gaines 1990), local adaptation (Lenormand 2002) and survival of metapopulations (Hansson et al. 2002). There are four main hypotheses that aim to explain dispersal distances. They suggest that dispersal distances are affected by the level of resources and also competition for resources (Lidicker 1962, Grant 1978, Peacock 1997), population density (Delestrade et al. 1996, Negro et al. 1997), mating systems (Greenwood 1980), and the potential for inbreeding (Dobson

and Jones 1985, Pusey 1987, Pusey and Wolf 1996). Whilst there are hypotheses regarding the general patterns of dispersal, fewer studies have examined the variation of dispersal distances in the wild (Forero et al. 2002, Bowler and Benton 2005). Environmental, social and individual factors are increasingly being considered (Negro et al. 1997, Verhulst et al. 1997, Alonso et al. 1998, Spear et al. 1998, Forero et al. 2002, Serrano and Tella 2003, Serrano et al. 2003). This highlights the necessity for studies focusing on the dispersal patterns of individual species and populations to determine variables that influence dispersal.

North Island brown kiwi (*Apteryx mantelli*, NIBK) are completely flightless, but possess strong legs which provide a means for dispersal. NIBK are endangered, predominantly due to predation of chicks by introduced predators such as stoats (*Mustela erminea*) and cats (*Felis Catus*), resulting in a mortality rate of young NIBK of approximately 94% (McLennan et al. 1996). Conservation efforts have focused on areas where predators can be trapped and controlled (Basse and McLennan 2003, Westbrooke 2007). This type of management requires an understanding of habitat preferences and movements. Young NIBK in particular may move more than adults that have well defined territories or home ranges. Additionally, it is important to understand dispersal behaviour in terms of spatial structure of populations and genetics. By understanding how far juveniles move and the factors that affect their movement we can tailor management practices to ensure that we are meeting the needs of wild NIBK populations.

There has been some work carried out on young NIBK, with five main factors thought to influence their dispersal: age, barriers to dispersal, population density, sex and habitat choice. Young NIBK can disperse some distance after leaving the nest, from 700-2000m (McLennan 1997, Forbes 2009). However most long distance dispersal events appear to take place from nine months of age with individuals capable of dispersing 1-50km from their natal area (Chapter 1, Table 1.1; Robertson 2004, Basse and McLennan 2003, Grant 2003, Forbes 2009). Most research on NIBK dispersal has focused on the movements of sub-adult NIBK, with only two studies focusing on the dispersal movements of younger NIBK (Chan 1999, Forbes 2009). Female sub-adults were found to disperse further than male sub-adults (Grant 2003, Forbes 2009); however, studies have not looked at differences in dispersal between sexes at younger age.

Previously it has been suggested that rivers may be barriers to dispersal for NIBK (Chan 1999), however it has been noted by others that neither rivers nor fence lines were significant barriers to dispersal (Gibbs 2000, Robertson 2004). Similarly, NIBK were thought to have limited dispersal due to fragmentation of native forest habitats and that they avoided walking over large areas of exotic pasture (Diamond 1984, Forbes 2009). However, NIBK have been observed dispersing over (Chan 1999), and foraging in exotic pasture (Cunningham and Castro 2011).

Density of NIBK may affect dispersal distances however the exact effect is still unclear. Grant (2003) found that NIBK that were released into areas without resident NIBK dispersed further than those released into areas with resident NIBK. This behaviour has been seen in other species (Stamps 1991, Muller et al. 1997, Martin et al. 2008). Conspecifics may congregate because the number of conspecifics reflects habitat quality or availability and juveniles may use adults as an indicator of these resources (Stamps 1988, McPeck and Holt 1992). In contrast, Robertson (2004) hypothesised, based on population models from five kiwi Sanctuaries, that the rate of emigration (NIBK leaving an area) is density dependent, with increasing density there are fewer gaps for new individuals to establish territories therefore emigration rates and hence dispersal distances increase once a population reaches carrying capacity. However, studies to date have not measured dispersal distances in high density NIBK populations and therefore this hypothesis remains untested.

A large amount of research has taken place looking at roosting sites of NIBK during the day (Taborsky and Taborsky 1995, Chan 1999, Gibbs 2000, Forbes 2009), and what NIBK habitat use is at night (Colbourne and Kleinpaste 1983, Taborsky and Taborsky 1992, 1995, Chan 1999). NIBK have been found in a number of habitats including: all forest types, coastal sand dunes, high mountain tussock land and exotic pine forest plantations (Colbourne and Kleinpaste 1983, Taborsky and Taborsky 1992, 1995). Studies have found that roost type is highly dependent on the habitat type (Taborsky and Taborsky 1995, Miles et al. 1997, Forbes 2009) and differed significantly between sexes (McLennan et al. 1987), elevations, age classes (Forbes 2009) and seasons (Miles et al. 1997). With young NIBK showing a tendency to roost on the surface under vegetation debris and in seral habitats relative to mature forests (Forbes 2009, McLennan 1997, Chan 1999, Gibbs and Clout 2003). Young NIBK are thought to use these denser habitat types as they provide protection from native

aerial predators such as the Australian harrier (*Circus approximans*) and New Zealand falcon (*Falco novaeseelandiae*; Taborsky and Taborsky 1995, Chan 1999). However, studies to date have not determined if there is a relationship between habitat and roost type used and the dispersal distances of juvenile NIBK.

In this study I aim to fill a gap in the research of juvenile movement by studying a very precocial bird, the NIBK in a high density population. The juveniles in this study had not started to breed by the time my project finished and therefore I could not calculate natal dispersal; hence in this study I looked at juvenile dispersal movements. I explored the length of time juveniles remained in their nest, daily movements between roost location, roost type and habitat type. I also explored environmental factors that could influence these movements. From previous studies I expect that in this high density population dispersal rates will be less relative to lower density populations. I also hypothesise that dispersal distances will vary between sexes and habitat types; with females dispersing greater distances than males as in previous studies. Because young NIBK show a preference for roosting in seral or scrub habitat types, I expect that when NIBK are in these habitats they are likely to disperse shorter distances because they are in a preferable habitat, relative to when they are found roosting in other habitats. Dispersal movements in this population are restricted because it is located on an island (1770ha), therefore this study is likely to be a good model for the management of other populations that have restricted dispersal movements and are increasing in population density.

Methods

Study Species

General information regarding the study site, the species and monitoring is given in the Introduction, section: Aims, Contribution and Study Site. The NIBK laying season extended from early June to early February with chicks hatching between September and February (Jamieson et al. unpub. data, Ziesemann et al. 2011). Nests were primarily located in holes dug in the ground or in the root system of trees. Females laid on average 1.6 (SD = 0.7) and 1.3 (SD = 0.1) eggs in the 2010 - 2011 and 2005 - 2007 seasons, respectively, and up to two clutches per season (Jamieson et al. unpub. data, Ziesemann et al. 2011). On Ponui Island, most commonly a single male incubates, however two or three males in a group have also

been found incubating together in a single nest (Jamieson et al. unpub. data, Ziesemann et al. 2011). NIBK are highly precocial and chicks hatch fully feathered. They start to leave the nest for periods of time at night by themselves from 5 days of age (Holzapfel et al. 2008; Chapter 3). They fledge, and do not return to the nest to roost on average at 24 days of age (SE = 2.8, Chapter 3). NIBK feed on soil and litter dwelling invertebrates and some plant matter (Gurr 1952, Bull 1959, Reid 1982, Miles 1995, Shapiro 2005). I define a NIBK chick as a young NIBK that still resides in the nest and a juvenile as a NIBK that has been roosting away from the nest at least two days in a row.

Chicks in this study were tagged as per Chapter 1 methods with radio transmitters to allow the location of individuals. I attempted to locate and view young NIBK at least three times per week, weather permitting, over two breeding seasons: 2010-2011 (November to February; herein referred to as 2010) and 2011-2012 (September to March; herein referred to as 2011). A chick was deemed to have fledged when they were found roosting away from their nest during the day for at least two days in a row. When the exact day could not be determined (e.g., the young was not located for multiple days in a row), the average age from when they were last found in the nest to when they were no longer found in the nest was used. Once fledged, each time a juvenile was located I took note of the co-ordinates using a Garmin GPS (eTrex® H); habitat type, roost type and how visible they were in their roost. I used a visibility score where; 1 = not visible, 2 = visible from 1 - 2 sides, 3 = completely visible, 4 = foraging and moving during the day. Habitat was classified as forest (tall, mature trees with little understory), scrub (dense under-growth, most trees < 20cm in diameter), exotic pasture, exotic pasture underneath tall sparse trees (mainly *Kunzea ericoides*), or swamp. Roost type, was classified by the type of vegetation or substrate the juvenile was resting in as: a) nest, b) sedge grasses (*Carex spp.*), c) burrow in a tree, d) dug burrow in ground, e) pasture grass, f) pasture grass and fallen branches, g) gorse (*Ulex europaeus*), h) tea tree scrubs (*Leptospermum scoparium* and *Kunzea ericoides*), i) scrub (dense undergrowth mostly *Coprosma spp.*, *Leptecophylla juniperina*, *Kunzea ericoides*, and *Pseudopanax crassifolius*), j) dense short ground ferns (*Blechnaceae*), k) hawthorn (*Crataegus spp.*), l) pine needles (*Pinus radiata*), m) in the open, n) amongst large rocks and o) under fallen perching Lilies (*Collospermum hastatum*). In some instances juveniles were unable to be located precisely, due to high density bush, or they were awake and foraging

during the day. In these infrequent instances the juveniles were not pursued because I did not want to influence their behaviour. I did not follow juveniles at night, therefore day time locations, habitat types and distances moved between roost sites were used as a proxy for dispersal and habitat preference and I presumed that they forage in the same areas where they roost.

Dispersal from the natal home-range

I examined whether young NIBK leave their parental home-range after fledging and at what age they do so. To decide whether the young left I calculated the home-range of the parents using the average home-range size for female NIBK on Ponui Island of 13.00 ± 5.09 ha (Ziesemann 2011). I used the female home-range because females have a greater home-range than males and their home-range includes that of their mate. I determined that if the nest was in the middle of a perfectly circular home range, a juvenile would have to travel 206m to the edge of the home range. If the nest was at the edge of the home range a chick would need to travel a maximum of 412m to reach the opposite boundary. Hence, if a juvenile has dispersed >412 m from their nest, it is likely that they have dispersed out of their natal area; I use this distance to determine if a juvenile NIBK had moved from their parents' home-range (Figure 4.1).

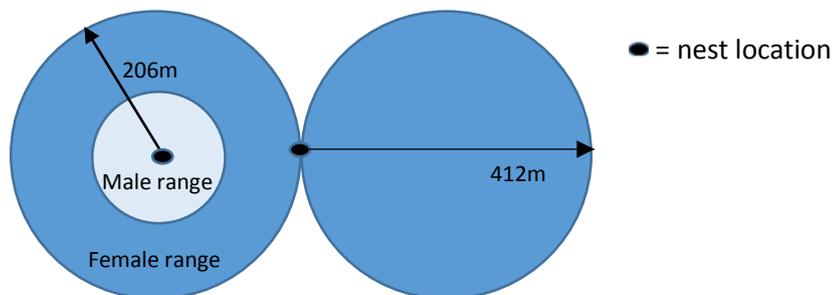


Figure 4.1. Estimate of the distance young North Island brown kiwi need to move from their natal nest to disperse outside their parent's home range. Estimated from the average home-range size of females on Ponui Island (Ziesemann 2011) and assuming that nests were located in the centre of territories.

Growth rate

Daily changes in body mass (g day^{-1}) were calculated by plotting known weights and ages in CurveExpert Professional (Version 1.6.5) and producing growth curves that best fit each individual bird (Chapter 2). From these curves I calculated the approximate increase or decrease in g day^{-1} for each individual on each day they were found.

Daily movement between roosts

Each location acquired from the GPS for individual juvenile was plotted in ESRI ArcMap (version 10.1). This program was then used to calculate the straight line distance from successive locations of individual young and the distance between their nest and each of their location points.

Seasonal measures

Methods used for the collection of invertebrates as a proxy for food abundance, and weather measurements can be found in Chapter 2, pg. 36.

Statistical Analysis

The meters per day juvenile NIBK moved between roost locations were not normally distributed (Kolmogorov–Smirnov test: $P < 0.05$). Therefore, I used generalized models to determine if there was any significant relationships between the daily distance juvenile NIBK move between roost sites, and a) their sex, age and body condition, b) the Julian date, habitat type (Macrohabitat) and the visibility of the young NIBK at each roost location c) rain, temperature, season (Spring: September–November, Summer: December–February and Autumn: March–May), and food abundance. The individual identity of each NIBK was included to account for individual variation. All statistical analyses were performed in R (R Core Development Team 2009), with the exception of significance testing which was done in SPSS (IBM SPSS Statistics for Windows, Version 20.0).

Results

In this study 17 juvenile NIBK were located 368 times in their daytime roosts from November 2010 to April 2012 after they fledged at an average age of 24 days (SE = 2.8; Chapter 3). Juveniles were found in a different roost location from previous day 96.5% of the time and moved a median of 32.3m (range: 0 – 402.5m) per day between roosts. There was a significant difference between the dispersal distances per day of individuals (Wald Chi-square = 28.94, df = 16, $P < 0.05$) and therefore identity was included as a variable to account for individual variation in all further analyses.

Dispersal from natal area (parents' home-range)

Of 17 juvenile NIBK studied, eight dispersed more than 411.5m from the natal nest at an average age of 50 days (SE = 11 days, range: 12 – 98 days), therefore most likely leaving the parental home-range (Figure 4.2). However, five of those moved back into the parental home-range at least once during the study, with the percentage of times they were found roosting in the home-range after leaving for the first time being: 3.5, 13, 24, 50 and 90%, respectively. One NIBK was not able to be located after three days most likely due to transmitter failure; this bird was not included in the analysis. Of the eight juveniles that remained in their home range, seven died at an average age of 52 days (SE = 24). One juvenile was still in the natal home-range at the end of the study at 512 days of age and was one of only three juveniles that were alive at the end of this study. At 512, 512, 768 days of age they had dispersed a maximum straight line distance from their natal nest of 246.1, 2050 and 1320m, respectively.

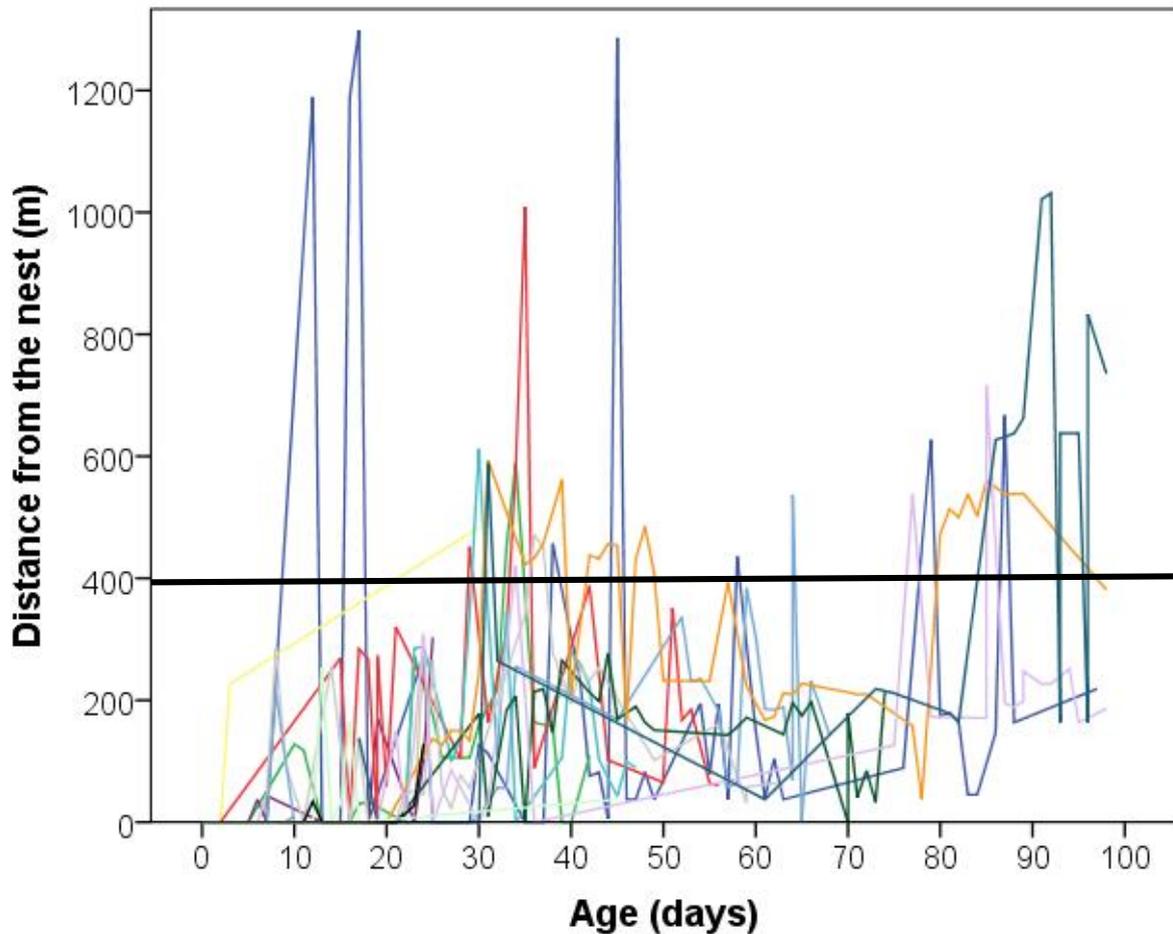


Figure 4.2. Distance from the nest that 17 juvenile North Island brown kiwi were found roosting at different ages on Ponui Island, New Zealand during the 2010 and 2011 seasons. The straight horizontal line indicates when juvenile NIBK were estimated to be roosting outside the natal area (parental home-range, see text for explanation). Each colour represents an individual brown kiwi.

Factors affecting daily movements between roosts

Age, sex and body condition did not have a significant effect on the distance juveniles travelled nightly between roosting sites (Wald Chi-square = 0.26, 0.42 and 1.72; $P > 0.1$ respectively). Juveniles were found roosting in scrub 56.3% of the times they were located, in forest 23.4%, in exotic pasture grass under large trees 16.8%, in swamp 2.4% and in exotic pasture 1.1%. This is despite 92% of nests having been situated in forest habitat, with the remaining 8% in scrub habitat. Young NIBK were initially found most often in forest habitat however this decreased with age and at five weeks of age, young NIBK were using scrub habitat more than forest (Figure 4.3). Only the three main habitat types were used in this

graph to demonstrate changes in habitat use with age because juveniles were only found a small number of times in swamp and pasture habitat.

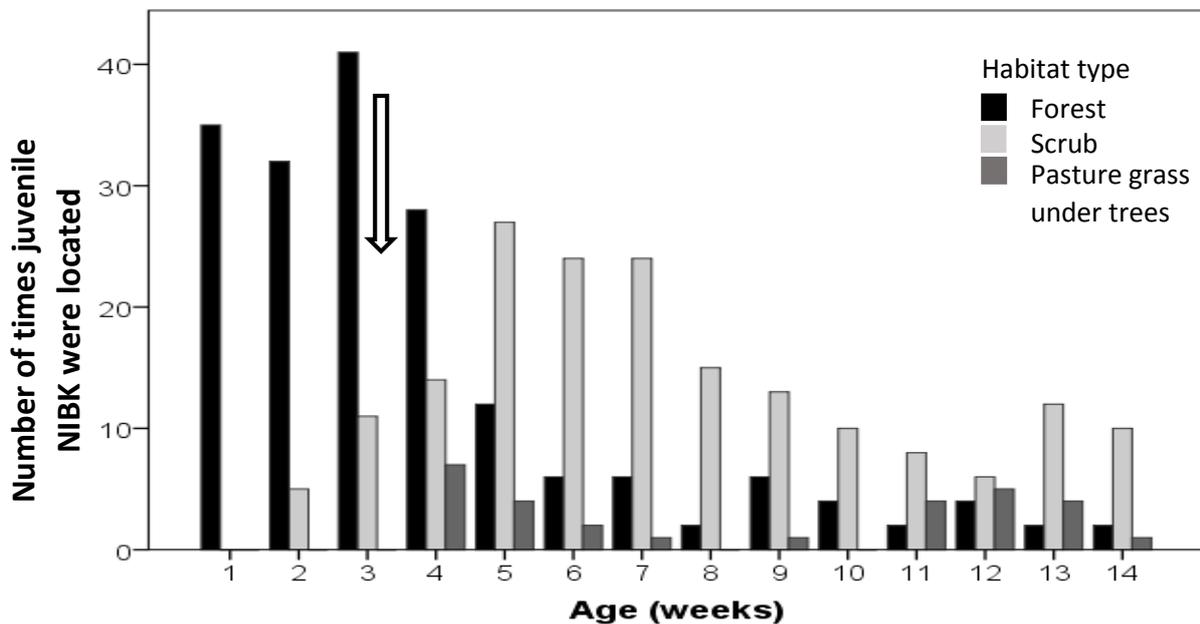


Figure 4.3. Main habitat types young North Island brown kiwi were located in from 1 - 14 weeks of age on Ponui Island, New Zealand in the 2010 and 2011 seasons. Habitat type when found in nest are included and the white arrow indicates the average fledging age of 24 days of age (SE \pm 2 days).

In these habitats juveniles were mostly found in *Carex* spp. grasses and underneath dead branches or fern fronds, although they were also found in a number of other roost types (Figure 4.4). Juveniles were not visible in their roosts 58.9% of the time, they were partly visible 32.9%, completely visible 4.9% and were found foraging and moving during the day 1.6% of the times they were found. However, habitat type, Julian date, roost type or visibility, were not found to have a significant effect on the daily movements between roosts (Wald Chi-square = 5.14, 1.14, 0.68 and 21.34; $P > 0.1$). The only significant effect on daily distance moved in both models was individual identity (Wald Chi-square 40.31 df = 16, $P < 0.001$). I also examined the effect of rain, temperature, season and food abundance on daily movement between denning locations and found that temperature had a significantly positive effect on daily movement ($P = 0.001$, df = 1, Wald Chi square = 14.145).

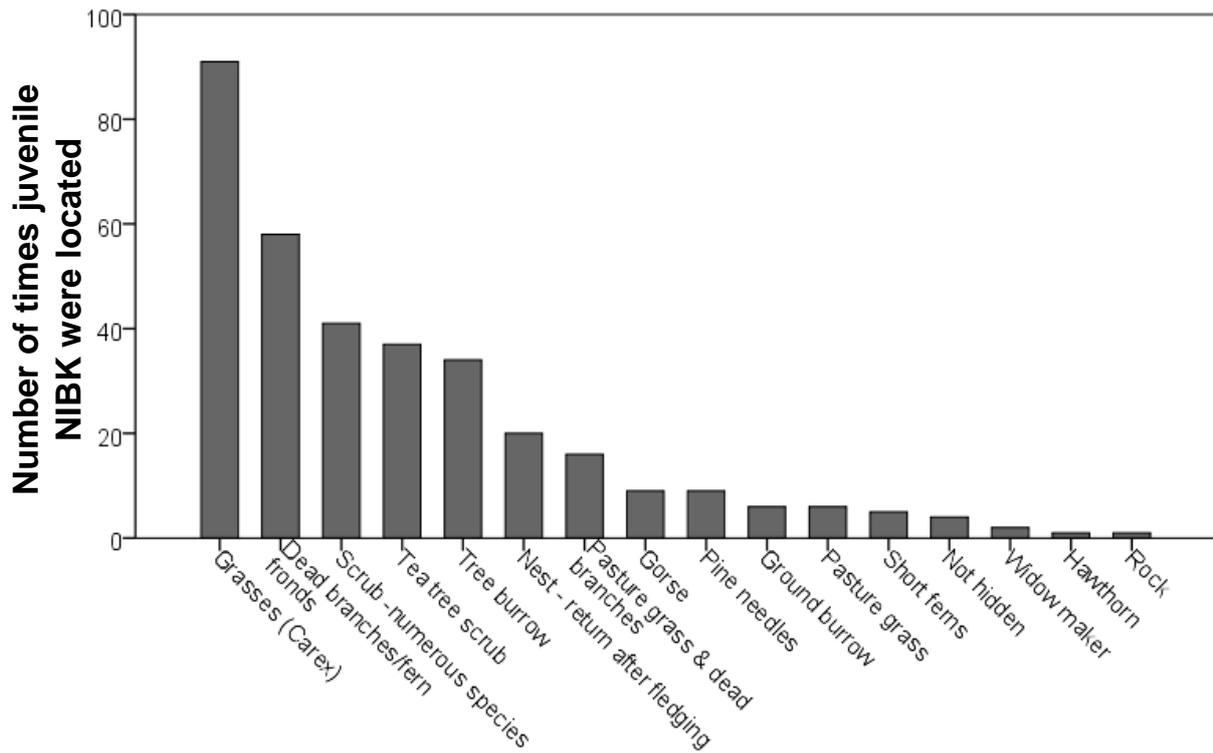


Figure 4.4. Roost types that 17 juvenile North Island brown kiwi were found hiding in or under on Ponui Island, New Zealand during the 2010 and 2011 seasons.

Discussion

The daily dispersal distances of young NIBK between roost locations differed significantly between individuals, seasons, and with varying temperature. Although food abundance was not found to significantly affect daily dispersal distances, it was measured on a monthly scale. By only measuring on a monthly scale, any variation that may have occurred within each month was not detected. Because there was a relationship between temperature and dispersal distance and my previous work shows that at temperatures, above 22°C, food availability is reduced (Chapter 2), food abundance may play a more important role in dispersal than I was able to deduce. Young NIBK dispersed further with increasing temperature, these dispersal distances may increase because young NIBK are actively searching for food resources, however further research is needed to explore this relationship. Increased dispersal distance at lower food abundance has been seen in Eurasian kestrels (*Falco tinnunculus*); as predicted by the food depletion hypothesis (Vasko

et al. 2011). Similarly, breeding tengmalm owls (*Aegolius funereus*) dispersed less when voles, their primary prey, were more abundant (Korpimäki 1993). Growing NIBK are likely to have higher relative energy requirements and subsequently higher demands for food resources resulting in the need to disperse further during the warm months/temperatures when food availability is lower. Different energetic requirements at different ages may have caused the variance in dispersal distances between individuals.

Juvenile NIBK were most often located in forest habitat from one to three weeks of age, this is likely because to the fact that they remained close to their nests which were mostly in forest habitat. After four weeks of age, scrub or seral habitat was used more often. This can be explained by chicks fledging and choosing scrub over forest habitats. These results are consistent with those found in other studies. Taborsky and Taborsky (1995) found that after young NIBK fledged they used almost entirely seral vegetation and McLennan (1997) found that they selectively inhabited dense regenerating forest. Moreover, Chan (1999) reported that young NIBK in Trounson Kauri Park, Northland showed a preference for seral vegetation over mixed podocarp/broadleaf and kauri forest. There are at least three possible reasons why young NIBK may preferentially be found in scrub/seral habitat at a young age these are, predator avoidance, adult NIBK avoidance and foraging success. Pre-human colonisation, land based predators such as the tuatara (*Sphenodon* spp.) and the now extinct adzebill (*Aptornis* spp.), and aerial predators such as the extant New Zealand falcon (*Falco novaeseelandiae*) and Australasian harrier (*Circus approximans*), and the extinct laughing owl (*S. albifacies rufifacies*) were probably the main predators of NIBK (Castro and Morris 2011). The cryptic colourations of NIBK plumage and their nocturnal nature would have allowed them to blend in with their habitat; this in combination with the use of dense vegetation may have made it hard if not impossible for these predators to catch them (Worthy and Holdaway 2002). This may explain why young NIBK show a preference for roosting under dead fern fronds and dead fallen branches because these are similar colours to NIBK plumage (Forbes 2009). Additionally, young NIBK on Ponui Island often roosted in *Carex* grass spp.; these grasses bend near the base providing a NIBK-sized 'hole'. Young NIBK that roost in scrub habitat are likely able to hide and avoid predators until they are large enough to defend themselves.

Young NIBK may also be found in scrub habitat more often than in other habitats due to foraging success. Shapiro (2005) found that over the winter, spring and summer months there was significantly more weta and spiders in scrub habitat relative to forest habitat, however, total invertebrate biomass did not differ significantly between forest and scrub habitat. Similarly in this study, although invertebrate abundance was greater in scrub habitat during summer and spring months, relative to forest habitat, this difference was not significant. However, the sample size of pitfall traps may be too small, $n = 20$, to see any significant differences between habitats, and food abundance may still account for some preference of scrub over forest habitat.

Of the three NIBK that survived to the end of this study one did not show any large dispersal movements and stayed in their natal area. The second had a large dispersal event (2170m) between 242 and 305 days of age. The last chick had two large dispersal events, one at 503 days of age (1100m) and the other at 621 days (769m). Additionally, one young NIBK between 12 and 16 days moved 1143m. However, these dispersal distances do not appear large relative to other populations, with individuals capable of dispersing up to 50km in some populations (Basse and McLennan 2003, Grant 2003, Forbes 2009). Because only a small number of individuals survived I cannot say if these dispersal distances are specifically small due to density and conspecific attraction as suggested by Grant (2003). These three NIBK may have dispersed shorter distances by chance like two NIBK in Grant's study (2003) which dispersed 1 and 1.5km from their release site after three years; or shorter dispersal distances may be due to size constraints of Ponui Island which is just over seven km long. Forbes (2009) found that large dispersal events occur after 270 days of age. Furthermore, it may be possible that I did not observe many large dispersal events because my study finished prior to them occurring. I found that NIBK on Ponui Island grew much more slowly than other mainland populations taking 225 days to reach 1000g compared to the 150 days it takes in other populations (Chapter 2; McLennan et al. 2004). These long distance dispersal events, if they take place on Ponui Island, may also occur in older individuals relative to other populations. Additionally, there was no difference in the dispersal distances between young males and females, however other studies have found that sub-adult females disperse significantly further than sub-adult males (Grant 2003, Forbes 2009). All

but three NIBK in this study died before reaching this age which may be why I did not see any dispersal differences between sexes.

On the other hand young NIBK may be restricted from dispersal by energy input. As mentioned above, NIBK on Ponui Island grow more slowly than juvenile NIBK on the mainland (Chapter 2; McLennan et al. 2004) and the cause of mortality of 24% of individuals was starvation (Chapter 5), implying that there are limited energetic resources on Ponui Island. Dispersal distance may vary between individuals and be lower than in other populations due to the lower availability and abundance of food both at higher temperatures and due to greater competition for food resources that are thought to occur on Ponui Island (Chapter 2). Young NIBK on Ponui Island may not have enough energy stores to disperse large distances, and maintain normal physiological functions and growth.

Although most young NIBK died soon after hatching and before 90 days of age (Chapter 5), of those that dispersed from their natal area, most returned or stayed in close vicinity to their natal area. One NIBK that was still alive at the end of this study at 465 days of age remained in her natal area. This may support tolerance of young NIBK by adults and reduce dispersal distances. Taborsky and Taborsky (1992) found that the territories of individual NIBK within a pair in Waitangi State Forest overlapped; however, the overlap of territories between neighbouring pairs was narrow. They suggested that territoriality in NIBK was not to protect resources such as food or shelter but to defend mates. If this is the case, then there would be little benefit to adults expending energy to defend the area around their mate from juveniles. In a different population in Northland with a higher density to that of Waitangi, Potter (1989) found that the home ranges of all birds overlapped substantially. He suggested that territoriality in NIBK may be a function of density. NIBK on Ponui Island live in very high densities of 100 birds per km² and are unable to leave the island. In this population, there is moderate overlap of neighbouring individuals' home ranges in both the non-breeding and breeding seasons (Ziesemann 2011). At higher densities of NIBK, decreased territoriality may also result in an increased tolerance of young birds and subsequently lower rates of natal dispersal.

Interestingly, juvenile NIBK changed their roost site location on consecutive days. In some instances they were found back in the same roost location some days later. Similar

observations were made by McLennan et al. (1987) of adult NIBK in the Hawkes Bay. With young NIBK this may be a mechanism for predator avoidance, by changing roost location they reduce the risk of being found if a predator has discovered their roost or scent in the area while they are away foraging. However, young NIBK may simply be roosting in a location close to where they were foraging during the night.

This study examined factors that affect dispersal movements in young NIBK. I have found that movements are highly variable between individuals. Temperature and season significantly affects movement and together with findings in Chapter 2 I suggest that differences in dispersal may be influenced by food resources. Dispersal movements may be shorter on Ponui Island as a result of later maturation, due to lower food availability and higher competition for food during the summer months (Chapter 2, Shapiro 2005). Habitat use and roost type of young NIBK on Ponui Island was found to be very similar to that found in other populations. This may be due to both the protection it gives by making it difficult for predators to manoeuvre and catch young NIBK, and the greater levels of food abundance found in scrub habitat during the warmer months when competition for food is greatest. This use of habitat needs to be taken into consideration when young NIBK are translocated to new areas and further work is needed to ascertain if dispersal distance is significantly affected by population density and conspecific attraction. To strengthen the validity of these results further research is required; more precisely determining if there is in fact a relationship between dispersal and food resources; data needs to be compared between different populations, taking into account population density. It is also important the NIBK are located regularly or systematically amongst NIBK populations so that comparisons can be made.

Chapter 5: Mortality of juvenile

North Island brown kiwi

in a population with low predator diversity



Introduction

For most avian species, the juvenile life stage is the period in which individuals are most vulnerable to mortality. Altricial species are vulnerable in their nest, they hatch with no feathers to provide warmth, any ability to move and find food, and hence are completely reliant on their parents to provide these resources. These chicks are at high risk of mortality if their parents are not able and vigilant carers. Young of precocial species hatch more developed, however face another suite of challenges. They must warm, feed and protect themselves from predation, with little help from their parents (Starck and Ricklefs 1998b). Chicks may succumb to starvation if they cannot find sufficient food, or to predation if they cannot hide and/or protect themselves (Kentie et al. 2013). Moreover, due to their small size and low surface area to volume ratio, young chicks tends to gain and lose heat faster than larger chicks or adults (Merritt 2010). For this reason they have a higher chance of

hypothermia in wet and cold conditions, or over-heating and dehydration in hot conditions (Montevecchi and Vaughan 1989).

North Island brown kiwi (*Apteryx mantelli*, NIBK) are an interesting case in which to examine juvenile mortality, because they are one of the most extreme precocial species (Chapter 2). NIBK chicks hatch with adult plumage and at five days of age NIBK begin to leave their natal nest at night to forage and explore their environment (Holzapfel et al. 2008; Chapter 3); thus far there is no knowledge of parental care outside the natal nest. The chicks fledge, leaving their nest permanently at an average of 24 days (SE = 2.8, n = 18, Chapter 3)

In 2008, it was estimated that there were 25,000 NIBK remaining, however populations continue to decline primarily due to lack of recruitment (Holzapfel et al. 2008). On the New Zealand mainland, the mortality rate of young NIBK is 94%, with at least 60% as a result of predation by introduced mammals, namely stoats (*Mustela erminea*), and at least 20% from natural causes such as entanglement and falling down cliffs (McLennan et al. 1996). Although mortality is a natural process such levels are not sustainable. Enhancing our knowledge of the levels and causes of mortality in young birds becomes extremely important when a species, such as NIBK, is threatened or endangered and this knowledge can then be applied to reduce the rate of mortality.

Due to the high levels of juvenile predation by introduced mammals, NIBK conservation efforts have mainly focused on predator removal and Operation Nest Egg (BNZONE™; Colbourne et al. 2005). BNZONE™ is a programme that collects eggs from wild nests, incubates them in captivity; the resulting chicks are reared until they reach approximately 1000g in weight and are then release back into the wild. At this weight young NIBK are considered to be safe from predation by stoats (Colbourne et al. 2005). In 2000, five kiwi Sanctuaries were established as part of the New Zealand Biodiversity strategy. Three were for NIBK; the Whangārei Kiwi Sanctuary in Northland, Moehau Kiwi Sanctuary in the Coromandel and the Tongariro Forest Kiwi Sanctuary in the central North Island. Within these sanctuaries extensive predator trapping occurred and NIBK eggs were removed for BNZONE™. The objectives for these sanctuaries included understanding the effect of pests and native species on the management of kiwi (Robertson 2004). The Bank Of New Zealand

Kiwi Recovery team experimentally showed that using these processes can allow kiwi populations to stabilise or recover (Robertson 2004).

However, despite our best efforts, most NIBK populations continue to decline, highlighting the need for better knowledge on juvenile mortality and the relationship between predators and NIBK. This study examines the mortality rate and causes of mortality of young NIBK in a population with low predator diversity. The only resident introduced predator is the feral cats (*Felix catus*) and the only native predator is the Australasian harrier. At 100 NIBK per km² this population has a density similar to accounts of NIBK density pre-human colonisation of 40-100 birds per km² (Buller 1877, 1888 cited in McLennan et al. 1996), which is higher relative to most other populations (Cunningham and Castro 2011). This study is the first to report juvenile mortality rates in an established NIBK population, with a limited predator community. It provides information on the level of young NIBK mortality that a population is able to sustain in the presence of an introduced predator. Finally, these results will provide key information for managers as NIBK population densities increase as a result of predator control at kiwi sanctuaries.

Methods

Monitoring

General information regarding the study site, the species and monitoring is given in the Introduction, section: Aims, Contribution and Study Site. I attempted to locate and view each chick at least three times per week. Each time the location was recorded using a Garmin GPS (eTrex® H). The age at which the chick left the nest and did not return for roosting was considered the fledging age. When the chick was not located in the nest for multiple days in a row, I considered the fledging age as the midpoint between the age when the chick was last found in the nest and when it was first discovered not to be using the nest. After fledging the young NIBK were considered to be juveniles rather than chicks, and juveniles become adults at sexual maturity (McLennan et al. 1996). In this chapter when young NIBK are referred to, this includes both chicks and juvenile NIBK. If a young NIBK is discovered dead and the exact age of mortality could not be determined, I considered age of death as the midpoint between the age when last found alive and when found dead. In

three instances I did not estimate the age of mortality because the chicks were found dead ≥ 20 days after they were last seen alive.

Necropsy

When a young NIBK was found dead, photos were taken of the carcass *in situ*; at camp the carcass was cut ventrally to open the abdominal cavity, then stored in 10% formalin. Photos were also taken of the internal organs and along with the carcasses were sent to Wildbase Hospital, Massey University, Palmerston North, New Zealand. Pathology reports were produced by Dr. Maurice Alley and Ms. Ellen Schoener.

Body mass gain and Mortality

I used body mass (g) and average mass gain (g/d) to indicate growth at different ages. Body mass was used to produce a growth curve for each young NIBK for the three groups: those that died from predation, those that died from natural causes (i.e., they were not depredated by introduced predators), and those that were still alive at the end of this study (survived at least 448 days) to determine average weekly mass gain (g/d). Growth curves were produced using CurveExpert Professional (Version 1.6.5). Gompertz growth curves were used to determine weekly mass gain (g/d) for each individual. The first ten days were excluded as NIBK chicks are known to lose a large amount of weight during this time while they are absorbing their yolk sac and not foraging outside of the nest (McLennan et al. 2004).

Statistical analysis

Comparisons of mass gain between the three groups (alive, natural causes, and predation) were conducted using linear mixed effects models. Two models were initially produced, one including NIBK identification (ID) to account for individual variation, the second without ID. There was a significant difference between the two models, indicating that ID should be included ($P < 0.001$). Age was also included in the model. I used One-ANOVA to determine if there was a significant difference between the ages that chicks died from different causes of mortality and if the age of mortality differed significantly between sexes, Tukeys post-hoc analysis was also done to determine which causes of mortality differed significantly from one another. Tests were carried out in SPSS (IBM SPSS Statistics for Windows, Version 20.0)

and R (R Core Development Team 2009) and graphs were produced in both SPSS 20.0 and Excel (Office Professional Plus 2013). Unless otherwise noted means are presented with standard errors.

Results

The mortality rate of 24 young NIBK studied on Ponui Island was 87.5%. In 2010, one of seven young NIBK survived and in 2011 two of 17 survived (12.5%). Eleven young died from natural causes (45.8%) and seven from cat predation (29.1%), the cause of mortality for the three remaining young NIBK could not be determined because they were too decomposed upon discovery (12.5%; Table 5.1). Some NIBK did not have a single cause of death but rather, the pathologist listed all health issues in order in which they may have contributed to the death (Table 5.1). It must also be noted that a high level of mortality may be influenced by the frequency of handling i.e. due to a stress related response. However, brown kiwi that were handled more often show fewer stress behaviours than those that were handled less frequently (pers. obs.). A study by Adams (2000) also showed that captive birds that were handled often had a reduced corticosterone response than those that were not.

Table 5.1. Mortality statistics for 21 young North Island brown kiwi on Ponui Island during 2010 - 2012. In some cases multiple potential natural causes of death were found, they are ranked in order according to how they may have contributed to mortality, with number one being the most likely direct cause of death.

Incubation code ¹	Season	Age at death (days)	Cause of death	Body Condition Score ²	Fledged Yes/No	Sex
Jenno-1-a	2010	20	1. Retained yolk sac 2. Localised peritonitis - severe bacterial 3. Bronchopneumonia 4. Hepatic lipidosis	3	Y	M
Scott-1-a	2010	Unknown	Unknown, only leg found	-	Y	U
Dario-1-a	2010	20	Predation - cat	-	U	M
Ivan-1-b	2010	65	Trauma to head and neck, cat predation	5	Y	F
George-1-a	2010	28-58	Unknown too decomposed	-	Y	F
Murphy-1-a	2010	93-106	Trauma to neck and head, too decomposed to confirm but possibly due to cat predation	-	Y	M
George-2-a	2011	58	1. Starvation/hypothermia 2. Parasitic ventriculitis - mild	3	Y	M

Dario-1-a	2011	55	1. Starvation/dehydration and anaemia 2. Tick induced dermatitis 3. Gastric nematodiasis	2	Y	M
Dale-1-a	2011	66	1. Starvation 2. Parasitic ventriculitis (gizzard) 3. Granulomatous pericarditis and pneumonia - mild, localised 4. Hepatic coccidiosis - mild	3	Y	M
Scott-2-U	2011	60-80	1. Starvation 2. Poorly reabsorbed yolk sac	-	Y	F
Bel-1-a	2011	37	1. Starvation 2. Parasitic ventriculitis	2	Y	M
George-2-b	2011	79	1. Parasitic ventriculitis due to nematodiasis 2. Right-sided panophthalmitis possibly due to avipox infection 3. Hepatic coccidiosis 4. Nephrosis with calcium cast formation	3	Y	M
Max-1-a	2011	103	Parasitic ventriculitis	5	Y	M
Bel-1-b	2011	10	Yolk sacculitis, bacterial	4	N	U
Murphy-1-a	2011	In egg	Did not uptake yolk sac	-	N	U
Max-1-a	2011	78	1. Spenitis, hepatitis and interstitial pneumonia 2. Gastrointestinal nematodes	4	Y	F
Jenno-1-b	2011	28	Predation -cat	-	Y	F
Max-1-b	2011	29	Predation -cat	-	U	F
Murphy-1-b	2011	7	Predation -cat	-	N	U
Ivan-1-a	2011	44	Predation -cat	-	Y	M
James-1-U	2011	28	Predation -cat	-	N	F

¹The code includes the name of the chick's social father followed by the clutch number the chick hatched from (1 = first clutch; 2 = second clutch) - the egg the young hatched from (first laid egg = a; second laid egg = b).

² This index was developed at Massey University Pathology where 1 = complete emaciation and 9 = overweight, assigned *post mortem* by the pathologist. Dashes = score not obtained, usually because too little of the carcass was available to assess.

Mass Gain

NIBK that succumbed to predation had the highest rates of mass gain at 5.2 and 6.9 g/d at 17 and 38 days respectively, compared to those that died from natural causes, 4.7 and 2.6 g/d and those that were still alive, 3.7 and 3.7 g/d. Young that died from predation died before 44 days of age. Young that were still alive at the end of this study grew faster at 2.8 and 2.0 g/d at 100 and 150 days of age respectively compared to young that died from natural causes that grew 0.3 and 0.0 g/d at these ages. However, there was no significant

difference in the mass dynamics of young NIBK of the three fate categories (live, predation, natural causes) once age and ID were accounted for ($F_{2,10} = 0.9743$, $P = 0.4106$), although there was a significant effect of age on mass gain ($F_{1,108} = 14.3252$, $P = 0.0003$).

Age of Mortality

Young NIBK that succumbed to predation, died at a younger average age (31.7 ± 7.0 days; $n = 7$) compared to those that died from natural causes (57.6 ± 8.9 days; $n = 10$) although the difference was not statistically significant ($F_{1,15} = 3.477$, $P = 0.083$). There was a trend for young NIBK to suffer from yolk retention/infection and predation than older NIBK, whilst older NIBK were more likely to die from parasitic ventriculitis or starvation (Figure 5.1), this trend was significant ($F_{3,4} = 7.113$, $P = 0.009$). The ages that NIBK died from yolk retention/infection, predation, starvation and parasitic ventriculitis were all significantly different from one another (parasite-predation, $P = 0.001$; parasite-yolk, $P = 0.001$; starvation-predation, $P = 0.035$; starvation-yolk, $P = 0.016$) except those that died from predation and yolk retention/infection ($P = 0.422$) and from parasitic ventriculitis and starvation ($P = 0.051$). Additionally, there was no significant difference between the age at death between young male ($n = 10$) and female ($n = 6$) NIBK ($F_{1,14} = 3.1222$, $P = 0.093$).



Figure 5.1. Average age at death for each of the primary causes of young North Island brown kiwi mortality on Ponui Island (2010 - 2012). Shown are: median, 25% and 75% interquartile ranges (box length), non-outlier minimum and maximum values (whiskers), and outliers (circles).

Discussion

Despite the low predator diversity, I discovered a surprisingly high mortality rate of 87.5% for young NIBK, similar to the estimated mortality rate of 94% for *Apteryx* spp. in mainland areas with higher predator densities (McLennan et al. 1996). However, high levels of mortality were mainly due to many young NIBK dying from natural causes. I found the main causes of death in young NIBK to be starvation, yolk retention/infection, parasitic ventriculitis, and predation. A number of secondary causes were also present and probably also contributed to the high mortality rate. These included: panophthalmitis (potentially caused by pox infection), hepatic coccidiosis, nephrosis, tick-induced dermatitis, gastric nematodiasis, early bronchopneumonia, hepatic lipidosis, granulomatous pericarditis, and pneumonia. In three instances parasitic ventriculitis was secondary to starvation as a cause of mortality. Very few of these have been reported previously in NIBK, likely because studies on wild NIBK tend to focus on predation events and carcasses are often not collected or

suitable for necropsy (*cf.* McLennan et al. 1996). However, yolk sac retention/infection, coccidiosis, tuberculosis and cryptococcosis have all caused death in captive reared young NIBK (Thompson and Wright 1978, Davis et al. 1984, Boardman 1995, Clemance 1995, Colbourne et al. 2005, Morgan et al. 2012).

Hatching can be a dangerous period for chicks. At hatching the remaining yolk sac in the egg is pulled into the abdominal cavity. This yolk is absorbed shortly after hatching and provides nourishment before the chicks are fed or can feed themselves (Khan et al. 2004). Yolk related mortality can be difficult to observe in wild populations, therefore most studies of this type of mortality focus on the poultry industry. Problems such as the yolk sac not being completely internalised into the body before hatching and infections cause 13% of mortalities in domesticated ducks (*Anas platyrhynchos domesticus*; Sharma and Kaushik 1986b), 20% in domesticated turkeys (*Meleagris gallopavo*; Sharma and Kaushik 1986b, Thyagarajan et al. 1987), 7.3% in domesticated geese (*Anser anser domesticus*; Boado and Rojas 1990) and 30% in domesticated ostriches (*Struthio camelus*; Aslan et al. 2008). Almost 20% of young NIBK in this study died from yolk related factors, indicating that yolk disease is also an important cause of mortality in wild bird populations. Yolk sacs provide ideal conditions for bacterial growth leading to yolk infections (Khan 2004). Bacteria generally enter the yolk sac via the umbilicus, therefore, omphalitis or infection of the umbilicus can also cause mortality.

Precocial chicks tend to have large yolk sacs, 12-34% of their body weight (Calder et al. 1978, Schmidt et al. 1985, Welty and Baptista 1988). NIBK eggs have one of the largest proportions of yolk to egg contents of all birds at 61.1% (Reid, 1971), when the chick hatches they have 48% of the yolk remaining which contributes 34% of the total body mass of the chick (Calder et al. 1978). The yolk can sustain the chick for up to 17 days (Calder et al. 1978). Due to the large size of the yolk sac and the length of time it sustains NIBK chicks, they are more likely to suffer from yolk infections and retention than most other birds (Khan et al. 2004). In this study, chicks that died from yolk infections died at a younger average age than any other cause of mortality, this is expected given that hatchlings may already be suffering from the condition. For example, one of the chicks died before hatching completely out of its shell. The yolk sac was only half internalised and according to the pathology, this was likely to be the cause of death. Two other chicks had retained yolk sacs

that were not completely absorbed, one died at 20 days of age and the other at an estimated 70 days of age. Finally one chick died from yolk sacculitis (yolk sac infection) and was found one metre below the nest at 10 days of age.

I found that 25% of young NIBK starved to death at an average age of 55 days. Starvation occurs when the energy input of an animal does not meet the demand for energy requirements (McCue 2012). Young animals tend to have greater relative energy requirements than adults because in addition to the maintenance of regular body processes, they need energy to grow (Ricklefs et al. 1998). All NIBK that starved died in December, 2011. It was likely the dry conditions in the previous month led to this (only one day exceeding 8mm of rain and 6 days of 3mm of rain). In Chapter 2 I found that both rainfall and temperature significantly affected food availability and food abundance. At higher temperatures food abundance increased, however at lower levels of rainfall the ground became too hard for young NIBK to probe resulting in decreased food availability and also increased levels of intra and inter-specific competition for surface litter invertebrates. These dry conditions likely resulted in particularly low levels of food availability for the young NIBK, reducing the rate of growth and likely resulting in starvation (Chapter 2). Specific attention should be paid to body condition during dry periods especially when young NIBK are kept at high densities or in areas, such as those surrounded by predator proof fences, where they cannot disperse further to find additional food.

Many of the NIBK that died from starvation also had secondary illnesses. Parasitic ventriculitis was prevalent in three of the four NIBK that died from starvation. Ventriculitis is inflammation of the gizzard or proventriculus; in parasitic ventriculitis the inflammation is caused by the presence of parasites, mainly nematodes, but is often also associated with bacterial infection (Senties-Cue et al. 2011). Parasitic infections often occur when the host's immune system is depressed, so it is not surprising that young that died of starvation in this study were also suffering from parasitic infection. Parasitic ventriculitis occurred at varying levels; nematodes were found in the mucosal and sub mucosal walls of the gizzard and viable nematode larvae were found in many dilated glands. There was severe necrotising and inflammatory necrosis in some areas of the gizzard's koilin, superficial mucosa and mucosa. There were also many dilated glands that contained bacteria and mucus, and bacteria extended into the submucosa in some areas. Other regions showed disrupted

mucosal glands with both glandular atrophy and hyperplasia with fibrosis of the lamina propria. In at least one instance the nematode found was an endemic kiwi nematode (Maurice Alley pers. comm.). The gizzard plays an important role in the mechanical digestion of food therefore, it is likely that the breakdown of the above mentioned structures resulted in a reduced ability to process food and may have heightened mortality caused by starvation. A negative effect of nematodes on survival has also been demonstrated in Red Grouse (*Lagopus lagopus*; Hudson and Dobson 1991). Brood survival was also greater when parasite loads were experimentally lowered (Hudson and Dobson 1991). Further research is required to determine which nematodes were present in the young in this study, where they came from and if they can be avoided in the future particularly when new populations are established from translocated individuals.

Of 24 chicks, seven were depredated by cats (29%). On the mainland, 27% of deaths have been attributed to predators although this is likely to be at least as high as 60% as many young kiwi (*Apteryx* spp.) were not located (McLennan et al. 1996). Of those killed by known predators most were taken by stoats and only 5% were killed by cats (McLennan et al. 1996). A greater proportion of young NIBK were killed by cats on Ponui Island than are on the mainland. This highlights the impact cats can have and may indicate that if cats are not targeted in addition to mustelids in trapping regimes young NIBK may be at a higher risk of predation from cats once mustelids are removed.

Whilst there is no argument that predator control is important for NIBK conservation, more focus is needed on other causes of mortality. Predator-prey relationships are complicated and dynamic and several factors must be considered before making large-scale management decisions. For example, starvation is related to food availability which is influenced by climate and intra- and inter-specific competition. However, by focusing on only one part of the system, such as removing inter-specific competitors such as rats, we may cause cats to increase their predation rate on young NIBK because they can no longer depredate rats (alternative prey hypothesis; Angelstam et al. 1985). Furthermore, releasing captive-reared chicks may have a detrimental effect for populations in the distant future. By allowing all young to survive when many would not have in the wild, we may produce genetically (and behaviourally) weak populations that are not able to cope with stressors. This has been found in one study where NIBK chicks that were reared in captivity and

released into the wild had a greater mortality than those that hatched in the wild (Forbes 2009). My study demonstrates the importance of understanding the causes of mortality in NIBK and proposes that mortality rates in NIBK are naturally high in this high density, stable population due to life history traits, even when predator diversity is limited.

Chapter 6: Main discussion

North Island brown kiwi are unique ratites in many ways, importantly to my thesis they are highly developed at hatching and receive little parental care, making them very independent and highly vulnerable. The aims of this thesis were to: determine the growth rates of young NIBK and environmental factors that influence growth rate; describe the behaviour of young NIBK around their nest and any social interactions that take place between adults and/or chicks; investigate the dispersal movements of juveniles, determining the effect of habitat and climate variables on movement; and accurately report the causes of mortality of young NIBK.

Growth is the proliferation of cells to form tissues and organs, and energy used for growth comes from a balance of energy input (food) and the energetic requirements of other physiological functions. Birds that are more precocial, larger, breed in the absence of predators tend and have high levels of competition for food tend to grow slower than other birds. I found that NIBK are highly precocial and grow incredibly slowly with a growth rate constant of $K_g = 0.0052$. These traits are likely related to their evolution largely in the absence of mammalian predators but yet in an environment where they faced high levels of competition for food resources. Their growth rate is much slower than at least 296 bird species that have been measured. With the closest counterpart the malleefowl (*Leipoa ocellata*) a highly precocial species in the Megapodiidae family, of similar size to NIBK, having a growth constant of $K_g = 0.007$ (Ricklefs 1979). Because NIBK are so unique in this field it is important that we understand exactly how and why they grow so slowly.

I found that females grew faster than males in their body mass, bill length and tarsus length. This may be because NIBK are sexually dimorphic and females are the larger sex, although McLennan et al. (2004) found that at Lake Waikaremoana both sexes grew at the same rate until at least 20 weeks of age. Interestingly growth rates were highly variable both within the 2011 season and differed significantly between the 2004, 2010 and 2011 seasons. This appears to be linked to seasonal variables such as temperature, rainfall, food abundance (soil invertebrates) and food availability (soil penetrability). On a monthly scale with

increasing temperature, soil invertebrate numbers increased, although soil penetrability decreased at higher temperatures and was likely to have affected the ability of NIBK to probe and forage in the soil. These factors did not influence growth rates on a weekly scale, however, this may be due to a lag effect of environmental variables on growth rate or highlights the necessity of measuring variables on a finer time scale. Temperature did influence growth rates on a weekly scale, with growth rates greatest between 19 - 22°C, although a large amount of variation in growth rates could not be explained by temperature or the other variables measured.

The high variability of the growth rates of young NIBK within seasons, between seasons and between populations in NIBK, may give some insight into why NIBK grow so slowly. Growth rates appear to be linked to environmental variables; this link may be stronger in high density populations due to the greater competition for food from both intra- and inter specific species. If NIBK were to grow at a faster rate, I think death from starvation would likely occur more often. However, in populations that persist at lower densities slow growth may be less important because there is less competition for food from other NIBK. Although, inter-specific competitors may also influence food availability and need to be taken into account. The evolution of slow growth rates in NIBK is likely to have arisen when there were high densities of NIBK across the North Island of New Zealand and greater abundances of other native ground-feeding insectivores which all competed for the same food. This in combination with the high precociality and medium size of NIBK is likely to contribute to their incredibly slow growth rates. Slow growth rates should be an important focus of future research both to contribute to wider research and also for the conservation of NIBK. For example, do all populations grow at a slow rate similar to those at Lake Waikaremoana (McLennan et al. 2004) and in this population; can we determine exactly why slow growth occurs and why do NIBK grow so incredibly slowly relative to a large number of other bird species measured. Secondly, do individual NIBK that are reared in captivity and have access to *ad libitum* food, negatively affected by fast growth rates with regard to development? Lastly, how do fast or slow growth rates affect the mortality rates and how might this effect the conservation status of NIBK?

With an aim to stabilise then increase the NIBK population it is important for conservationists to understand the dynamics of their ecological system, particularly with

respect to introduced mammalian predators. For example, if NIBK grow slower in higher density populations they are at greater risk of predation from stoats for a longer period of time, because they take longer to reach the 1000g safe weight. Additionally, the effect of temperature and rainfall on food abundance and availability should be considered when translocating individuals particularly if they are restricted to an area such as a mainland island. For instance, if there is little rainfall and temperatures are high, NIBK cannot probe into the soil and may not be able to find enough food; these challenges may be amplified if the birds cannot disperse elsewhere to find food.

Prior to this study the behaviour of NIBK around the nest had not been studied. Due to the nocturnal nature of this species behavioural observations are difficult. By using remote infra-red cameras set-up outside nests I was able to obtain behavioural observations with little interference. Chicks on average began leaving the nest at night at 4.3 days of age, this is the same as described in a number of other NIBK studies. The number of times chicks were seen in the nest entrance, leaving the nest and the amount of time in the vicinity of the nest (2 - 5m), each night, was greatest at 5 days of age but decreased with age although this decrease was not significant. Chicks appeared to spend a large amount of time when initially emerging from the nest exploring their nest and the surrounding area moving in and out of the nest. I hypothesised that this is how the chicks learn to move about their environment by sniffing and touching the surrounding areas. These behavioural observations also show how vulnerable these young chicks are, frequently seeming unsteady on their feet, losing balance or tumbling over and indeed one individual was depredated by a cat on the second night out of the nest just one metre from the nest.

NIBK are not known to provide parental care to their young after hatching, with the exception of the father providing warmth to the chick whilst in the nest. Although infrequent, seven interactions between chicks and adults were observed, most of which included the nesting male, the chick and likely the female mated to the incubating male. These interactions were interesting although their context is still unknown. Chicks also have a range of vocal noises that warrant further research. In some observations the females seemed very interested in the chicks sniffing in their direction, pulling the chicks feathers and pushing the chicks with their bill. I am uncertain if this is a recognition behaviour, preening or protective behaviour, however the chicks did not run away from the female,

potentially indicating that this is not a negative interaction. A large amount of research is required to determine the context of these behaviours in a species that was previously thought to have no interactions with their parents outside the nest. NIBK that are reared in captivity and then released at an older age may be disadvantaged if chicks in the wild learn any behaviours by being in contact with adults at this a young age when chicks are close to the nest. A great deal more research is needed in this area, and it may be necessary to provide ONE chicks with obstacles, adult NIBK scents and signs if it is found that they acquire important skills from these. With increasing technological advances remote surveillance video cameras are smaller, more discrete and more can be obtained leading to potential for increased behavioural observations of NIBK in the wild. If more observations of these behaviours can be made in the wild, their context and necessity may become clearer.

It is difficult to measure dispersal distances of individuals when finding them at irregular intervals. For this reason juvenile NIBK were found on a regular basis, daily if possible and daily movements between roost sites were calculated rather than straight line dispersal distances from the nest location. I found that individual identity, season and temperature were all significant factors affecting the daily dispersal distance between roosts sites and there was no significant effect of age, sex, body condition, habitat type or roost type. There was also no significant effect of food abundance on dispersal distance, however, because food abundance and dispersal distances were measured on different scales this may have limited the power of my analysis. Particularly because temperature and season were found to influence dispersal, and from my other findings temperature was an important factor on both food abundance and availability. Therefore, I hypothesised that dispersal distances may be influenced by food availability and that individuals move further in warmer temperatures in search of food resources. On the other hand, individuals that are in very poor condition may be less able to disperse due to energetic constrains. Although there was no significant effect of body condition on dispersal distances there may be a lag effect whereby condition declines to a particular threshold or does not increase, then some time later dispersal distance is influenced. Regardless, temperature and season have a significant effect on the daily dispersal distances of juvenile NIBK between their roost sites. These factors should be considered when translocating individuals or considering the size of an area that NIBK inhabit. If these variables affect all populations of NIBK in the same way,

further research may find that NIBK in the northern, warmer part of the country may disperse further and may subsequently need large areas to inhabit.

The mortality rate on Ponui Island was high at 87.5% and similar to the estimated mortality rates (94%) of mainland populations that are not protected from introduced mammalian predators. The most important finding in this study was that the mortality rate was high even though only cats were found to depredate NIBK chicks on Ponui Island, and at least 52% of mortality was attributed to natural causes whereas on the mainland at least 60% of mortality is attributed to predators (stoats) and the remaining mortalities are due to accidents such as falling down cliffs. In the absence of stoats on Ponui Island, cat predation occurred at a higher rate of 30% relative to the 5 – 9 % rate of cat predation seen on the mainland. This may have management implications if solely stoats are targeted in trapping regimes, because predation by cats may increase when stoat numbers are lowered. Therefore both stoats and cats may need to be targeted simultaneously.

The second important finding highlights the importance of accurate assessment of the cause of death. In most NIBK studies when natural causes are reported as a reason for mortality, they are due to factors such as falling down cliffs and entanglement in vines. However, in this study the main, natural causes of mortality were due to yolk infection or retention, starvation, and parasitic ventriculitis, with a number of other diseases contributing to mortality. Young NIBK on Ponui Island may be more at risk to disease due to the higher density population resulting in lower food availability, slower growth rates and a higher chance of immune compromise due to a negative energy balance. However, because accurate autopsies are difficult if NIBK are not found soon after death, these diseases may be more prevalent than we think in lower density populations. Great care must be taken not to misdiagnose the cause of mortality when carcasses are not found shortly after dying.

Whilst this thesis has shown some important trends regarding the behavioural ecology of young NIBK it has also started a long list of questions for future research on NIBK. I think that further research should focus on: the growth of chicks in other populations of NIBK and how fast they grow relative to chicks in the two populations that have now been measured (Ponui Island and Lake Waikaremoana). Knowledge of growth rates is important because it has knock-on effects to other areas, if NIBK grow more slowly, for instance at higher

densities, they are more at risk of predation from stoats for longer periods of time which may have long term implications for population size. Secondly, NIBK are not known to exhibit parental care or interact with their chicks outside the nest, however this study shows that interactions do occur. Further research is required to determine if these interactions only occur at the nest, what their context is and how important they are to the survival of individual chicks. If these interactions are important for learning, and young reared in captivity miss out on this interaction, this will have long term implications for populations and the species. Thirdly, season and temperature were found to affect dispersal distances, however there was a large amount of variation in dispersal distances that could not be explained. It is important to design a uniform way that dispersal of NIBK can be measured so that distances and also habitat preference can be compared between populations. By having a uniform way to measure dispersal distances, we can determine how important temperature and season are to dispersal in other populations. What other variables may influence dispersal, and ultimately from a management point of view how large and what type of habitats need to be in a reserve that will support a NIBK population of a certain size, and how this may change with changes in density. Lastly, this thesis showed that mortality by predation may not be the only issue facing the survival of NIBK. Further research should determine if these diseases are present in other populations, or more so in this one because of the higher density; and also how important predation by cats on young NIBK is in the absence of stoats.

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