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BREEDING ECOLOGY OF A TRANSLOCATED POPULATION OF RED-CROWNED KAKARIKI (*CYANORAMPHUS NOVAEZELANDIAE*) ON TIRITIRI MATANGI ISLAND, NEW ZEALAND

A thesis submitted in partial fulfillment of the requirements for the degree of

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New Zealand

Luis Ortiz Catedral

(2006)

For my two families in México, again





Red-crowned kakariki (Cyanoramphus novaezelandiae)



Photo: Tiritiri Matangi Archives

Tiritiri Matangi Island

ABSTRACT

The reproductive ecology of a translocated population of red-crowned kakariki (Cyanoramphus novaezelandiae) was monitored during 2004-2006, covering two breeding seasons on Tiritiri Matangi Island. Red-crowned kakariki nested in tree cavities, ground burrows and in vegetation clusters located in forest remnants, grasslands and replanted vegetation as well as in nestboxes. There was a marked difference in reproductive success between the two breeding seasons. In 2004-2005 1.4 fledglings per breeding pair were produced. In contrast, 3.4 fledglings per breeding pair were produced in 2005-2006. This increase was the result of changes in loss rate during the nesting cycle. Nest failure occurred in 57% of nests in 2004-2005 whereas only 8% of nests were affected in 2005-2006. In both breeding seasons, incubation was the main stage of losses. Clutches hatched with various degrees of asynchrony. Brood sizes ranged from one to nine nestlings. Within broods, nestlings of different hatching ranks reached similar mass at fledgling. Likewise, nestlings of different hatching ranks gained similar weight over the linear portion of the growth curve and grew wings at a similar rate. However, last hatched nestlings fledged with shorter wings. Furthermore, mortality was higher for last hatched nestlings. Sex ratios at the clutch level and at fledgling did not deviate from parity. However, at the clutch level there was a higher proportion of males in clutches laid early and middle in the breeding season. Various lines of evidence suggest that food availability has a direct effect on reproductive success of red-crowned kakariki and can exacerbate the costs of asynchronous hatching. Therefore it is a priority to investigate natural changes in food resources of the red-crowned kakariki and to assess the potential of direct management to improve the conservation of the species.

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In New Zealand I discovered that it was difficult to communicate the significance of a word in another language if there was not an experience attached to it. I could say the words, but there was always something missing; a feeling of incompleteness followed my sentences. I had to experience words to fully express their meaning. So, this resolves the question as I believe now I can say at least one word in different languages and express my appreciation to everybody without necessarily naming them individually. I have the satisfaction to thank this exceptional people in their own languages:

THANK YOU

GRACIAS

OBRIGADO

TERIMA KASIH

DANC JE

DANKE

KÖSZÖNÖM

DANKIE

TAKK

KA PAI

TLAZOHCAMATI

DZIĘKUJĘ

设出户(M) 谢谢你

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CHAPTER 1: GENERAL INTRODUCTION

1.1 Diversity of parrots in New Zealand

The Order Psittaciformes (parrots and cockatoos) includes 350 species (Juniper and Parr, 1998). Most of these occur naturally in the Southern Hemisphere, mainly in South America and the Australasian Region (Forshaw, 1989); however several species have been introduced to the Northern Hemisphere (Long, 1981). There are 154 species in the Australasian Region (Forshaw, 1989). In New Zealand, nine endemic species are present (Table 1.1), representing 5.8 % of the Australasian species and 2.6 % of the world's parrot fauna. In addition, five species have been introduced into New Zealand in recent times, mostly from Australia. Currently they occur discontinuously in the North and South Island (Table 1.1). Although New Zealand is modest in terms of diversity, it is one of the few countries with 100% endemicity in its extant parrot fauna (Table 1.2).

The uniqueness of life history traits found in New Zealand parrots has long attracted ornithologists. For instance, the Kaka (*Nestor meridionalis*), Kea (*N. notabilis*), the Antipodes parakeet (*Cyanoramphus unicolor*) and the Red-crowned kakariki (*C. novaezelandiae*) are the only parrots known to feed on vertebrate flesh (live animals or carcasses) in the wild (Higgins, 1999), and the Kakapo (*Strigops habroptilus*) is the only nocturnal and lek breeding parrot (Merton *et al.*, 1984). New Zealand parrots occupy a wide variety of habitats, including high-level forests, subalpine shrubland, temperate rainforests and subantarctic grasslands (Heather and Robertson, 1996; Juniper and Parr, 1998). Before the arrival of humans into New Zealand, parrots occupied most of the

North, South, Stewart and outlying islands (Beggs and Wilson, 1991; Clout and Craig, 1994; Forshaw, 1989; Taylor, 1979; Wilson *et al.*, 1998).

Table 1.1 Parrot species found in New Zealand. E=Endemic, I=Introduced. Data from (Boon *et al.*, 2001; Forshaw, 1989; Higgins, 1999; Juniper and Parr, 1998).

Genus	Species	Common name	E	I	Natural Distribution
Cyanoramphus	auriceps	Yellow-crowned parakeet	*		North, South and Stewart Islands; offshore island groups
	erythrotis	Reischek's parakeet	*		Antipodes Islands
	forbesi	Forbes'parakeet	*		Chatham Islands
	malherbi	Orange-fronted parakeet	*		Canterbury area, South Island
	novaezelandiae	Red-crowned parakeet	*		North, South and Stewart Island; offshore island groups
	unicolor	Antipodes Island parakeet	*		Antipodes Islands
Nestor	meridionalis	Kaka	*		North, South and Stewart Islands; offshore island groups
	notabilis	Kea	*		South Island
Strigops	habroptilus	Kakapo	*		North, South and Stewart Islands; Extinct in the wild
Cacatua	galerita	Sulphur-crested cockatoo		*	Indonesia, Papua New Guinea, Australia
Eolophus	roseicapillus	Galah		*	Australia
Platycercus	elegans	Crimson rosella		*	Eastern Australia
	eximius	Eastern rosella		*	South-East Australia and Tasmania
Trichoglossus	haematodus	Rainbow lorikeet		*	Indonesia, Papua New Guinea, Solomon Islands, New Caledonia, Northern and eastern Australia and Tasmania

At present, some species still persist in their former ranges (i.e. Antipodes parakeet), but the majority of the species have experienced drastic reductions in distribution due to the combined result of habitat modification, shooting, competition for resources and predation by introduced mammals (Heather and Robertson, 1996; Higgins, 1999).

The most diverse genus in New Zealand is *Cyanoramphus*, comprising eight extant species, six of them endemic to the country and two others found in Norfolk Island and New Caledonia, respectively (Boon *et al.*, 2000). This genus has also experienced significant extinctions in the Pacific Region in recent times (Figure 1.1). Members of this genus are collectively known as parakeets or "kakariki" in Maōri language. These are medium sized parrots (20-30 cm) with long gradated tails. The general colouration is green, except for contrasting colour markings on the crown, forehead and periophtalmic region in most species, excluding the Antipodes parakeet. All species show blue markings on the outer margin of primary and secondary feathers ("wing-flash") (Forshaw, 1989; Juniper and Parr, 1998).

1.2 Conservation of parrots in New Zealand

As a group, parrots have long been recognised as one of the most threatened groups of birds (Bennett and Owens, 1997; Collar, 2000; Collar and Juniper, 1991).

Currently, 90 species are considered at risk of global extinction and another 40 have been identified as near threatened (Collar *et al.*, 1994).

Table 1.2. Countries with 100% endemicity in their parrot faunas. Data compiled from Forshaw (1989); Juniper and Parr (1998); Boon *et al.* (2001) and Avibase (2006) (www.bsc-eoc.org/avibase).

Country	Number of Species	Species name
Dominica	2	Amazona arausiaca, A. imperialis
Mauritius	1	Psittacula echo
Micronesia	1	Trichoglossus rubiginosus
New Zealand	9	Refer to Table 1.1
Saint Lucia	1	Amazona versicolor
Saint Vincent and the Grenadines	1	Amazona guildingii

The majority of these species occur in South America. Nearly all of the New Zealand parrots are under threat (Table 1.3). The reasons for parrot decline in the world vary from region to region. In South America habitat modification and poaching for the bird trade are identified as the main causes threatening populations (Beissinger and Snyder, 1992; Evans, 1988; Wright *et al.*, 2001), while in New Zealand case studies have shown predation by exotic mammals as the main cause behind species declines (Beggs and Wilson, 1991; Clout and Merton, 1998; Elliot *et al.*, 1996a; Moorhouse, 1991; Taylor, 1979; Wilson *et al.*, 1998)

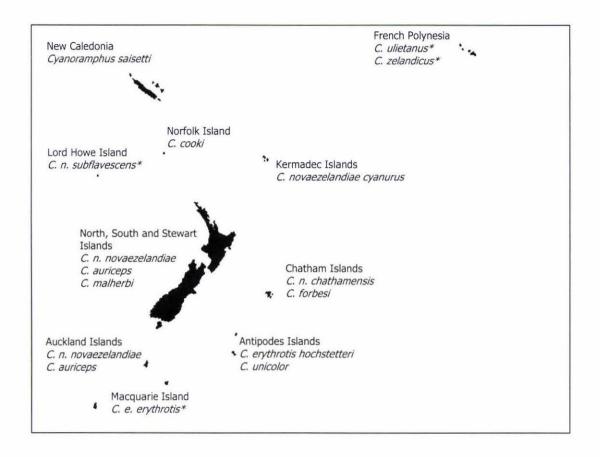


Figure 1.1. Schematic representation of the historical distribution of *Cyanoramphus* parakeets in the South Pacific. *Extinct species. Map based on Juniper and Parr (1998); Boon *et al.*, (2001) and Higgins (1990).

However additional factors such as habitat modification and reduction have also played a role (Elliot *et al.*, 1996b; Elliot and Kemp, 1999; Nixon, 1982; Taylor, 1985). Clearly, the causes of decline are diverse and our understanding of them is limited given the small number of long term studies of parrots, both in New Zealand and overseas.

Efforts have been made towards the conservation of New Zealand parrots and these can be classified as translocation of individuals to establish new populations (Berry, 1998; Lloyd and Powlesland, 1994; McHalick, 1999); eradication of predators (Greene *et*

al., 2004b; O'Connor and Eason, 2000); intensive predator control through trapping and regular poisoning (Greene *et al.*, 2004a; Moorhouse *et al.*, 2003) and captive management (Berry, 1998; Greene *et al.*, 2004a; West *et al.*, 1995). In general these approaches have been successful in the conservation of New Zealand parrots.

1.3 Conservation of Cyanoramphus

The diversity and phylogenetic relationships of the genus Cyanoramphus has long been a subject of debate. The great morphological similarity of its members has made taxonomic analysis difficult. Recent molecular studies have resolved the number of taxa in this genus and proposed a detailed biogeographic framework to understand the diversification of Cyanoramphus in New Zealand (Boon et al., 2001). Moreover the importance of correct taxonomic identification when establishing conservation priorities has been stressed (Boon et al., 2000; Kearvell et al., 2003). Nevertheless, the advance in our understanding of the systematics of New Zealand parakeets has not been mirrored by an improved knowledge of their basic biology and ecology. Most of the New Zealand Cyanoramphus species are considered under some category of threat (Table 1.3); yet only a few studies have addressed aspects of their biology (Dawe, 1979; Elliot et al., 1996a; Greene, 1998; Kearvell et al., 2002). The rarest taxa are the Forbes' parakeet (C. forbesi) restricted to the Chatham Islands (Greene, 2001) and the Orange-fronted parakeet (C. malherbi) from the Canterbury region in the South Island (Boon et al., 2000). Both species have been the subject of intense management involving predator control, revegetation of habitat as well as nest box provisioning in the case of Forbes' parakeet

Table 1.3. New Zealand parrot taxa and their categories of threat. Data from BirdLife International (www.birdlife.net) and Hitchmough (2002). *Classification according to the International Union for the Conservation of Nature (www.redlist.org); VU=vulnerable; NT=near threatened; EN=endangered; CR=critically endangered; NC=Not classified.

			Conservation Rating		
Genus	Species	Common name	IUCN*	Department of Conservation New Zealand	
Cyanoramphus	auriceps	Yellow-crowned parakeet	NT	Gradual decline	
	erythrotis hochstetteri	Reischek's parakeet	NC	Range restricted	
	forbesi	Forbes' parakeet	EN	Nationally endangered	
	malherbi	Orange-fronted parakeet	CR	Nationally critical	
	novaezelandiae	Red-crowned parakeet	VU	Not threatened	
	unicolor	Antipodes Island parakeet	VU	Range restricted	
Nestor	meridionalis	Kaka	VU	Nationally endangered	
	notabilis	Kea	VU	Nationally endangered	
Strigops	habroptilus	Kakapo	CR	Nationally critical	

(Greene, 2001) and captive breeding in the case of the Orange-fronted parakeet (van Hal and Small, 2005). Another important approach to conservation in New Zealand has been the translocation of parakeets to offshore islands and mainland sites (Taylor, 1975; Dawe, 1979; McMillan, 1990). Several translocations have failed, many have not been

documented and others lack consistent post-release monitoring (Higgins, 1999). As a result, assessment of relative success for a given parakeet translocation is often speculative. The species for which the most translocations have occurred is the red-crowned kakariki (*C. novaezelandiae*) (McHalick, 1999); the focus of this research.

1.4 State of knowledge of the red-crowned kakariki (Cyanoramphus novaezelandiae)

The most variable and widespread species of *Cyanoramphus* is the red-crowned kakariki (*C. novaezelandiae*). Four subspecies are recognised and their range includes the Kermadec Islands, North, South and Stewart Islands and the Auckland Islands group (Figure 1.1). However, sightings of the species on the North and South Island are scarce (Elliot *et al.*, 1996a). Stewart Island and various offshore islands have become the last stronghold for most populations (Higgins, 1999). Until recently the species was considered common and classified as a "least concern" species by the IUCN. However in June 2005 the species was reclassified as "vulnerable" in recognition of its continuous decline throughout its range (BirdLife International 2005, www.birdlife.net). There have been several studies of red-crowned kakariki; however, many aspects of its biology are still not understood.

There are no accurate estimates of the world population. Juniper and Parr (1998) propose that the world population exceeds 15 000 individuals, although only two recent estimates from two sites are available. Greene *et al.* (2002) estimated that there were between 8 000-10 000 individuals of the subspecies *C. n. cyanurus* on Macauley Island (282 ha). Brunton and Stamp (pers. comm. 2004) estimate the population size to be 700 individuals on Tiritiri Matangi Island (220 ha) for the nominal subspecies *C. n.*

novaezelandiae. Additional systematic estimations covering the present range of the species are necessary, since population size is one of the criteria used for listing species under the IUCN classification system (www.iucn.org).

The general habitat preferences and feeding ecology of red-crowned kakariki are relatively well known. The species occupies a mixture of habitat types including coastal scrub and forest, temperate rainforest, scrubland, open areas and forest edges as well as subantarctic tussock grasslands (Higgins, 1999). It feeds on a variety of fruits, seeds, flowers, leaves, invertebrates, molluscs and animal carrion (Higgins, 1999). In contrast to other congeneric species, red-crowned parakeets are commonly seen foraging on the ground (Greene, 1998), a trait shared with the Antipodes Islands parakeet (Higgins, 1999).

Various researchers have addressed aspects of the breeding biology of redcrowned kakariki; mostly in areas where exotic predators occurred at the time (Bellingham, 1987; Dawe, 1979; Greene, 2003; Sagar, 1988). Some information on the nesting habits, clutch size and incubation period exist. However, only two studies have taken a systematic approach; Dawe's study on captive birds as well as breeding pairs on Tiritiri Matangi Island and Little Barrier Island (1979), and Greene's study on Little Barrier Island (2003). These studies provide a valuable framework to approach theoretical questions and to explore issues related to species management and conservation.

1.5 The relevance of breeding studies from a theoretical and management perspective

Understanding the breeding biology of a species can fundamentally influence management decisions. It can also help identify intrinsic factors related to extinction risk (Bennett and Owens, 1997) and open opportunities to explore theoretical issues of ecological and evolutionary relevance. For example a study on the kakapo found that breeding occurs infrequently and it is promoted by mast seeding of temperate forest trees (Powlesland et al., 1992). In order to promote breeding and increase population size, a program of supplementary feeding was established (Powlesland and Lloyd, 1994). Although supplementary feeding promoted breeding, it also appeared to have the effect of skewing offspring sex ratios towards males (Clout et al., 2002). This phenomenon has been explained by Trivers and Willard's (1973) hypothesis of differential investment in offspring sex ratio according to the nutritional condition of breeding females. According to this hypothesis, females in good condition will obtain greater fitness benefits by rearing more males than females (males are commonly the larger and more costly sex to raise). There is increasing evidence in favour of this hypothesis across avian orders (Nager et al., 1999; Whittingham and Dunn, 2000). Clearly, a change in the supplementary feeding programme for the kakapo has to be attempted in order to increase production of females, as these represent a minor proportion of the world population for this species (Robertson et al., 2000).

Threatened species offer only limited possibilities to address ecological and evolutionary questions. This is mainly due to the low number of individuals and the analytical and logistical problems associated with small sample size. An alternative is to

perform a comparative analysis of closely related species to identify possible solutions that can reduce extinction risk of the taxa in question (i.e. the surrogate species approach see Armstrong, 2002). However, a major constraint of this approach is the number of studies available. As a group, parrots are insufficiently studied in the wild. The breeding ecology of only 10% of the species has been studied in a natural situation (Masello and Quilfeldt, 2002). Most of these studies have been conducted in Australia, the Caribbean Islands and North and South America and have focused on relatively large psittacines such as amazons, cockatoos and macaws (Garnett *et al.*, 1999; Gnam, 1991; Gnam and Rockwell, 1991; Iñigo-Elias, 1996; Munn, 1992; Murphy *et al.*, 2003; Pepper, 1996; Renton and Salinas-Melgoza, 2004; Rowley, 1990). In contrast, only a few studies have been conducted in the Pacific Region, where smaller species occur (Boon *et al.*, 2001; Rinke, 1989; Robinet and Salas, 1999) and where taxa phylogenetically related to *Cyanoramphus* are present (Boon *et al.*, 2001; Christidis et al., 1991).

1.6 The current study: Breeding ecology of a translocated population of redcrowned kakariki (*Cyanoramphus novaezelandiae*) on Tiritiri Matangi Island, New Zealand

The research presented here was conducted on Tiritiri Matangi Island, in the Hauraki Gulf of New Zealand during September 2004 to February 2006 and examines two breeding seasons of the red-crowned kakariki. For several reasons, this locality is an attractive one for the study of this species. First, red-crowned kakariki occurs at high densities and breeding pairs readily use artificial nesting boxes which allow straightforward monitoring of breeding pairs. Second, the resident population was

translocated to the island between 1974 and 1976 (Dawe, 1979). This situation makes it possible to obtain baseline data on reproductive output of an established translocated population which can be incorporated in the design of future translocations. More importantly, the present status (in terms of productivity) of a translocated population is quantifiable for this species for the first time. Similarly, the monitoring scheme of other translocated populations would benefit from information gained during this study. Third, Tiritiri Matangi Island does not have exotic mammalian predators, as Polynesian rats (kiore *Rattus exulans*) were eradicated in 1993 (Rimmer, 2004). This work represents the first detailed study of the breeding biology of red-crowned kakariki in an environment free from exotic predators. Sagar (1988) studied the species on the Poor Knights Islands, another predator free site; however aspects of breeding were only a minor part in that study.

This study is a first approach to understand the breeding ecology of red-crowned kakariki on Tiritiri Matangi island, and the seasonal variability in reproductive success, quantitative descriptors of reproductive investment (i.e. clutch size, egg volume) and factors affecting nestling survival of a translocated population. The analyses presented in the following chapters are based on a data set with limited sample sizes including some natural nests but mostly nesting boxes. Every effort was made to obtain as much information as possible from every nest. Methods and statistical procedures were chosen accordingly by an examination of sample sizes available, normality of data and power of the different tests.

Some active nests were found early in the breeding season and it was possible to monitor them closely. Others were found later in the breeding season and less complete information was obtained. Moreover, the monitoring regime changed for the 2005-2006 breeding season due to time and budget constraints. Consequently nests were incorporated into each analyses based on the information obtained and in some cases, the same nest formed part of more than one analysis (Table 1.4).

1.7 Outline of the present study

This study was designed to document several aspects of the breeding ecology of a translocated population of red-crowned kakariki, and to analyse changes in parameters of breeding success over two breeding seasons. It was planned to explore the consequences of hatching asynchrony and survival of nestlings across broods of different sizes. The information obtained and the analyses performed over a two year period are presented and discussed in five chapters (including the current chapter).

A brief description of the study site and study species is presented in Chapter 2. In the same chapter, the relationship between laying date, clutch size and nesting success is discussed. In addition, the diversity of nesting sites used by red-crowned kakariki and its relationship with breeding success is presented along with a comparison of estimates of nesting success between the 2004-2005 and 2005-2006 breeding seasons on Tiritiri Matangi Island.

Three main subjects are addressed in Chapter 3: changes in productivity during this study, variation in physical parameters of reproductive investment and reproductive success, and changes in expected reproductive success. Chapter 3 also examines the relationship between clutch size and hatchability and brood size and fledging success.

Finally, Chapter 3 includes a description of stage specific losses during the nesting cycle and an overview of causes of loss identified in the field.

The focus of Chapter 4 is the relationship of hatching asynchrony on nestling growth and survival and the relationship between laying date, brood size and primary sex ratios. Chapter 4 also includes a between-sexes and between-breeding season analysis of parameters of nestling growth.

Finally, a comprehensive discussion of this project in the context of other parrot studies around the world is presented in Chapter 5. In the same chapter, the relevance of this study from a management perspective is examined and lines of future research are identified and briefly discussed.

Permission to conduct this research was granted by the New Zealand Department of Conservation (Appendix 1). Additionally, permission to mist-net and band red-crowned kakariki was given by the Department of Conservation, New Zealand Banding Scheme (Appendix 2). Handling of nestlings and collection of samples were done with approval of the Animal Ethics Committees of Massey University and The University of Auckland (Appendix 3).

Table 1.4. Summary of analyses performed in this study, sample sizes and selection criteria. Refer to specific chapters for more detail regarding variables chosen and description of models.

Comparison (Chapter)	Sample size	Variables	Analysis	Selection criteria
Natural nesting sites	esting 20 nests -Nest cavity and -Analysis of nest-bearing coefficient of	-Evident use by breeding pairs		
(2)		plant characteristics	variation	-Cavity characteristics measured
				-Accessibility
Nest success between	50 nests	-Daily survival probabilities	-Stanley's method (Stanley, 2000)	-Nesting stage clearly determined
breeding seasons		during incubation nestling and overall nesting cycle per season	-Two sample <i>t</i> -test	(i.e. incubation, hatching, nestling)
(2)				-Regular monitoring (i.e. upon discovery
				of nest at least a weekly check was made)
Effect of laying date on clutch size and nest success	te on clutch laying correlation e and nest -Clutch size		-Date of egg laying was accurately determined	
Nest re-use between seasons (2)	43 nests	-Re-use of nesting site	-Fisher's exact test	-Use of nest was observed directly over the two years of study
Differences in nesting habitat (2)	60 nests	-Nesting success classified by habitat type	-Chi-square test	-Active nests found in any of the habitat type considered

Table 1.4. Continued

Comparison (Chapter)	Sample size	Variables	Analysis	Selection criteria
Effect of nest monitoring on nest success (2)	26 nests	-Nesting success classified by monitoring intensity	-Fisher's exact test	-Nests could be assigned to one of two categories: low or high monitoring intensity
Differences in productivity between seasons (3)	30 nests	- Vectors of means of variables for clutch size, egg volume, fertility, hatchability, hatchlings and fledglings)	Hotelling's T ² test (Two group MANOVA)	-All variables were determined accurately
Differences in egg volume and fertility between seasons (3)	30 clutches	-Egg volume (cm³) and fertility (%) per clutch	Two sample <i>t</i> -test	-Egg volume of all eggs in a given clutch was accurately determined -Fertility was unambiguously determined
Differences in Expected Reproductive Success (3)	43 nests	-Number of hatchlings and fledglings per nest, per season	-Gnam and Rockwell's model (Gnam and Rockwell, 1991) -Wilcoxon-Mann- Whitney two sample test	-Nesting stage clearly determined (i.e. incubation, hatchling, nestling) -At least one egg hatched in a clutch
Differences in hatchability between seasons (3)	46 clutches	-Mean hatchability	- Wilcoxon-Mann- Whitney two sample test	-Clutch size was accurately determined -Fertility and hatchability of eggs was precisely determined
Between season differences in clutch size (3)	46 clutches	-Total number of eggs in a clutch	-Wilcoxon-Mann- Whitney two sample test	-Clutch laying and final size was accurately determined

Table 1.4. Continued

Comparison	Sample	Variables	Analysis	Selection criteria
(Chapter)	size			
Between season differences in number of hatchlings	46 clutches	-Total number of hatchlings in a brood	-Wilcoxon-Mann- Whitney two sample test	-Fate of all eggs in a clutch was undoubtedly determined (i.e. hatched or not)
(3)				natched of not)
Between season differences in number of fledglings	50 broods	-Number of fledged nestlings per nest	- Wilcoxon-Mann- Whitney two sample test	-Exact number of fledglings was recorded
(3)				
Between clutch	50 clutches	-Mean	-Kruskal-Wallis test	-Clutch size is known
differences in number of hatchlings	number of hatchlings		-Number of hatchlings is known	
(3)				
Between clutch	50 clutches	-Mean hatchability	-Kruskal-Wallis test	-Clutch size is known
differences in hatchability				-Hatchability was determined accurately
(3)				
Between brood differences in levels	50 broods	-Mean values of brood	-Kruskal-Wallis test	-Clutch size is known
of brood reduction		reduction (number of		-Hatchability was determined accurately
(3)		dead nestlings/total		-At least one nestling hatch per clutch
		number of nestlings hatched)		-Death of chicks was accurately recorded
Between brood	50 broods	-Mean	-Kruskal-Wallis test	-Brood size is known
differences in number of fledglings	in number of nestlings fledged per		-Hatchability was determined accurately	
(3)		brood		-At least one nestling hatch per clutch
				-Death of chicks was accurately recorded

Table 1.4. Continued

Comparison (Chapter)	Sample size	Variables	Analysis	Selection criteria
Primary sex ratio (prop. of males in clutches) (4)	61 samples (11 broods)	-Proportion of males in a clutch (Number of males/total number of nestlings)	-Binomial test	-Samples were sexed
Sex ratio at fledgling (4)	59 fledglings (11 broods)	-Proportion of males/total number of fledglings	-Binomial test	-Nestling survived to fledgling
Fit of growth data to a logistic model (4)	13 fledglings	-Data on mass increase for the nesting period -Data on wing growth for the nesting period	-Fit to logistic model in CurveExpert 1.3 [©]	-More than 10 measurements of mass and skeletal growth were taken during the nesting cycle
Differences in mortality between sexes (4)	30 nestlings (8 broods)	-Proportion of dead nestlings per sex	-Chi-square test	-Dead nestlings were sexed
Differences in mortality between hatching ranks (4)	96 nestlings (16 broods)	-Proportion of dead nestlings per hatching rank	-Chi-square test	-More than 10 measurements of mass and skeletal growth were taken during the nesting cycle
Differences in number of fledglings and number of dead nestlings per broods (4)	30 nestlings (8 broods)	-Proportion of dead nestlings per sex	-Chi-square test	-Dead nestlings were sexed

Table 1.4. Continued

Comparison (Chapter)	Sample size	Variables	Analysis	Selection criteria
Relationship between laying order and laying date on primary sex ratio	61 nestlings (11 broods)	-Proportion of males per clutch in early, middle and late laid clutches	-Logistic regression, logit link option, binary response variable (sex)	-embryos or nestlings sexed unambiguously. No more than one sample in a clutch failed to be sexed
(4)		-Proportion of males per clutch in early, middle and late laid eggs		
Differences in growth parameters between nestlings of different hatching ranks (group A nestlings) (4)	13 nestlings	-Asymptotic mass	-Kruskal-Wallis tests -One-way ANOVA	-At least 10 measurements taken during nestling growth -Nestlings survived to fledging - At least one nestling per hatching rank category
	(4 broods)	-Final mass		
		-Mass increase		
		-Asymptotic wing length		
		-Growth rate for wing growth		
		-Mass loss after asymptote		
		-Time interval from 10 to 90% of asymptotic values of mass and wing length.		
Differences in growth parameters between nestlings of different hatching ranks	59 nestlings	-Asymptotic mass	-Kruskal-Wallis tests	-At least four measurements were taken during nestling growth
	-A	-Final mass		
		-Asymptotic		
		culmen length		 Nestlings survived to fledging
(group B nestlings) (4)		 -Asymptotic tarsus length 		-At least one nestling
		-Asymptotic wing length		per hatching rank category

Table 1.4. Continued

Comparison (Chapter)	Sample size	Variables	Analysis	Selection criteria
Differences in growth parameters between nestlings from broods with different levels of hatching asynchrony (group B nestlings) (4)	59 nestlings (16 broods)	-Asymptotic mass -Final mass -Asymptotic culmen length -Asymptotic tarsus length -Asymptotic wing length	-Kruskal-Wallis tests	-At least four measurements were taken during nestling growth -Nestlings survived to fledging -Nestlings came from broods with at least one nestling per hatching rank category
Differences in growth parameters between nestlings from broods laid middle or late in the breeding season (4)	59 nestlings (16 broods)	-Asymptotic mass -Final mass -Asymptotic culmen length -Asymptotic tarsus length -Asymptotic wing length	-Wilcoxon-Mann- Whitney tests	-At least four measurements were taken during nestling growth -Nestlings survived to fledging -At least one nestling per hatching rank category -Clutches could be classified as middle or late laid in the breeding season
Differences in growth parameters between nestlings from broods of different size (group B nestlings) (4)	59 nestlings (16 broods)	-Asymptotic mass -Final mass -Asymptotic culmen length -Asymptotic tarsus length -Asymptotic wing length	-Kruskal-Wallis tests	-At least four measurements were taken during nestling growth -Nestlings survived to fledging -Nestlings came from broods with at least one nestling per hatching rank category -Broods could be classified as small, medium or large

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CHAPTER 2: NATURAL NESTING SITES, REPRODUCTIVE PARAMETERS AND NESTING SUCCESS OF A TRANSLOCATED POPULATION

2.1 ABSTRACT

Translocations are central in New Zealand conservation; yet several translocated populations remain unmonitored. I studied red-crowned kakariki breeding on Tiritiri Matangi Island. This is the first breeding study of this species at a mammalian predatorfree site and the first detailed study on a translocated population of this species. A total of 60 nests were found in natural sites and nesting boxes. These nests occurred in remnant forest, grassland and replanted habitat. Natural nests occurred in trees, clusters of thick vegetation, logs and ground burrows. Nests showed considerable variability in cavity characteristics reflecting the diversity of nesting sites used by kakariki. Clutch size was similar to figures reported for natural populations (4-9 eggs). Hatchability was lower in 2004-2005. However, it reached other reported values when pooled between seasons. Nesting success was lower for the 2004-2005 season than in 2005-2006 (40%-79%) respectively). Two second clutches were found in 2005-2006, associated with a longer egg laying period than in 2004-2005. In the first year, the egg laying period was 51 days, whereas in the following year it reached 99 days. There was no relationship of laying date on either clutch size or nest success. Similarly, nest type did not affect nest success. Kakariki exhibited flexibility in nesting site and habitat use, thus increasing their potential for translocation to fragmented areas. Seasonal variability greatly impact nest success; perhaps through changes in food availability. It is thus essential to identify and monitor key food resources that could enhance nesting success via direct management.

2.2 INTRODUCTION

Studies on the nesting ecology of psittaciformes are concentrated in three geographical regions: North and South America (Fernandes Seixas and de Miranda Mouráo, 2002; Martuscelli, 1995; Masello and Quilfeldt, 2002; Monterrubio-Rico and Enkerlin-Hoeflich, 2004; Navarro *et al.*, 1992; Renton and Salinas-Melgoza, 1999) and Australia (Garnett *et al.*, 1999; Heinsohn and Legge, 2003; Mawson and Long, 1994; Pepper, 1996; Rowley, 1990). These studies have focused on species which in general exhibit narrow nest site preferences and lay few eggs. Consequently patterns of nest site use and nesting success are difficult to extend to species with broader nest site preferences or more variable clutch sizes even within the same geographic area.

Studies on the nesting ecology and variability in nesting success of psittaciformes in the South Pacific have been few (Moorhouse, 1991; Rinke, 1989; Robinet and Salas, 1999; Saafi, 2002); therefore the diversity of causes limiting productivity of many parrot populations in this geographical region are only partially documented and insufficiently understood. Patterns of nest success and variability between breeding seasons have been difficult to study due to low densities of parrot populations, low numbers of active nests (Robinet *et al.*, 1996) or small numbers of breeding pairs in consecutive seasons (Beggs and Wilson, 1991; Igag, 2002). This situation is of concern given that geographical and temporal variation in nesting success is pivotal in understanding the ecology of a species and to determine the effectiveness of conservation measures.

There is evidence indicating a strong association between diversity and complexity in nesting sites and social structure in birds (Winkler and Sheldon, 1993).

Moreover, nest type is of phylogenetic relevance and can be incorporated into

evolutionary frameworks to understand the taxonomic and ecological diversification of a particular group (Brightsmith, 2005b; Eberhard, 1997). Clearly, our understanding of the ecological and evolutionary significance of psittaciformes will benefit from a more integrated analysis considering species from other geographical regions and exhibiting different reproductive characteristics and nesting habits.

Nest site characteristics are often associated with nesting success (Dawson *et al.*, 2005; Szentirmai *et al.*, 2005). Thus, detailed knowledge about the nesting habitat, diversity of nesting sites and variability in nesting success of a species can greatly impact conservation practices (Brightsmith, 2005c) and our understanding of avian community structures (Marsden and Pilgrim, 2003; Martin and Eadie, 1999).

Translocation of psittaciformes to historical ranges as a conservation strategy has been used worldwide (Franklin and Steadman, 1991; Wiley *et al.*, 1992) and currently they form part of recovery plans for several species (Berry, 1998; Hill, 2002; Orangebellied Parrot Recovery Team, 1998). Although the results are mixed, successful examples include the Ultramarine lories (*Vini ultramarina*) in Tahiti (Kuehler *et al.*, 1997), Thick-billed parrots (*Rhynchopsitta pachyrhyncha*) in the United States of America (Snyder *et al.*, 1989) and Blue and Gold macaws (*Ara ararauna*) in Trinidad (Oehler *et al.*, 2001). In contrast, some efforts have failed but the causes are not completely understood (MacMillan, 1990). Moreover, unsuccessful translocations are often not well documented (see Wiley *et al.*, 1992).

Interestingly, several parrot species have established successfully outside their historical distributions (Long, 1981). It has been demonstrated that likelihood of successful establishment is not a random process (Cassey, 2002; Sol and Lefebvre, 2000).

Rather, several attributes might play a role at different stages of the "invasion pathway" (sensu Cassey et al., 2004). For instance, in parrots, the available information indicates that sedentary species with broader diets are more likely to establish successfully outside their natural areas of distribution (Cassey et al., 2004). This highlights the importance of basic knowledge of life-history traits to interpret patterns of establishment at a global scale. Similarly, at a local scale and within the native distribution of some taxa, case studies have shown that detailed knowledge of the basic biology of a species greatly influences the success of translocations (Collazo et al., 2003; Sanz and Grajal, 1998; Snyder et al., 1987).

In New Zealand *Cyanoramphus* parakeets have been subjected to several translocations within and outside their historical distribution areas in the last 95 years (McHalick, 1999; van Hal and Small, 2005; Waite, 1909). In general these are considered successful (Higgins, 1999; Juniper and Parr, 1998). However, at present no detailed study has been conducted on the nesting sites and nesting success of any translocated population. Therefore, the relative importance of translocations as a conservation option for New Zealand kakariki has not been fully evaluated. Most studies of breeding kakariki have focused on remnant populations on mainland New Zealand and a few offshore islands (Elliot *et al.*, 1996b; Greene, 2003). These studies have occurred in the presence of introduced mammalian predators, which are known to adversely affect nesting pairs and are likely to obscure natural patterns of nest site selection, clutch formation, incubation and overall nesting success, since the New Zealand avifauna evolved in an environment free of terrestrial mammalian predators (Wilson, 2004).

This chapter describes natural nesting sites of a translocated population of redcrowned kakariki (*Cyanoramphus novaezelandiae*) and compares nesting success, over
two consecutive breeding seasons. It also describes nest site re-use and general
parameters of reproduction (i.e. clutch size, fertility, hatchability etc.). This is the first
detailed study on nesting success for the species in an introduced predator-free
environment. This study adds to the body of research on New Zealand psittaciformes and
provides new information for a more inclusive understanding of the factors limiting
productivity of parrot populations in the South Pacific and presents elements that can be
incorporated into management plans. This chapter also includes opportunistic
observations of conflicts around nests between kakariki and tieke (*Philesturnus carunculatus*).

2.3 OBJECTIVES

The general objective of this chapter is to present a detailed overview of the nesting biology of a translocated population of red-crowned kakariki. The specific objectives developed in this chapter are:

- Describe natural nesting sites of red-crowned kakariki on Tiritiri Matangi
 Island with emphasis on cavity parameters and habitat type.
- 2. Describe egg laying period, clutch size, fertility, hatchability and production of fledglings over two seasons.
- 3. Determine the relationship of laying date on clutch size and nest success
- 4. Determine the relationship of nest type on nest re-use and nest success
- 5. Determine nest success using Stanley's model of daily survival probabilities

2.4 METHODS

2.4.1 Study site and study species

I studied red-crowned kakariki breeding on Tiritiri Matangi Island (36° 36' S, 174° 53' E) from October 2004 to March 2005 and from October 2005 to February 2006. This time interval corresponded to the main stages of the breeding cycle: nest-site selection, egg laying, incubation, nestling and fledging (Higgins, 1999). Tiritiri Matangi is an open sanctuary for conservation in the Hauraki Gulf, Auckland region. It is a 220 ha island 28 km North East of Auckland City and 3 km East of Whangaparaoa peninsula (Figure 2.1). The vegetation on the island consists of remnants of broadleaf forest, areas of grassland and native trees planted under a revegetation programme (Mitchel, 1985). Red-crowned kakariki were the first species to be translocated to Tiritiri Matangi Island between 1974 and 1976 (Dawe, 1979). Red-crowned kakariki (Figure 2.2) are medium sized parrots measuring 23-28 cm and weighing 70-100g. They have a monomorphic plumage but males are slightly larger than females. Sexes can accurately be determined by the morphology of the beak and its dimensions (Sagar, 1988). Potential breeding pairs were identified by opportunistic observations of pre-nesting behaviours such as cavity inspection, pair roosting, courtship feeding, and aggressive displays towards conspecifics in or around potential nesting sites.

2.4.2 Nesting sites, nesting habitat and nest monitoring

Data were collected from natural nesting sites and nesting boxes already present on the island and others provided in the course of the study. Given the relatively homogeneous age of most replanted vegetation and the scarcity of large, mature trees, artificial wooden boxes were placed around the island prior to this project. These provide nesting sites for red-crowned kakariki and other cavity nesters (i.e. hihi *Notiomystis cincta* (Thorogood, 2004) and tieke (Stamp *et al.*, 2002)). In addition to these, 30 'kakariki' nesting boxes with removable lids were mounted on trees 1-1.5 m above the ground in areas of low nesting box density. The boxes are made of un-treated plywood and measure 30 x 30 x 45 cm (length, width, height). The design follows Beggs et al (1984) and Krebs (1998).

Natural nests were located by inspection of tree cavities, rock crevices, vegetation clusters, trunks and burrows for signs of kakariki activity (i.e. droppings, feathers, egg shells). For every natural nest found, location, plant species and the following parameters were measured: distance to nearest vegetation gap (m), distance to nearest fresh-water body (m), height of entrance above the ground (m), internal height of entrance (cm) (i.e. base to roof of nest tunnel), length and width of entrance rim (cm), and distance from entrance rim to nest chamber (cm). For nest trees, trunks and other nest-bearing plants (i.e. Flax, harakeke *Phormium tenax*) circumference at nest entrance was measured (m). Finally, for nest trees major and minor canopy axes were recorded (m) (i.e. the two perpendicular axes of a tree crown). None of these descriptors were recorded for nesting boxes. Habitat type was recorded for both natural nests and nesting boxes. Habitat was categorised as remnant forest, grassland or replanted bush. These are broad categories but are considered appropriate for the purpose of this study. "Remnant forest" refers to patches of coastal broadleaf forest found on the North side of the island. "Grassland" encompasses areas of grass and a mixture of grass and harakeke. "Replanted bush" includes re-vegetated areas (see Mitchel, 1985 and Rimmer, 2004).

Nesting site re-use and nest usurpation between years was also recorded. Nesting site re-use refers only to nests successively active in 2004-2005 and 2005-2006 (some cavities showed evidence of use prior to 2004 but it was not clear if they were active the previous year). The nest monitoring regime changed during the study. For the breeding season of 2004-2005, nests were checked weekly before egg laying. After laying of the first egg, nests were visited on a daily basis to accurately determine egg laying sequence. Upon completion of the clutch, nests were visited once a week to monitor incubation activity. Close to hatching, daily visits were restarted to determine the sequence of hatching. After hatching, nests were visited every second day to collect data on nestling growth (see Chapter 4). For the breeding season of 2005-2006 nests were monitored less intensively, with only weekly visits for the duration of the nesting cycle. Nest contents were inspected only after females flew out of the cavity to be fed by males in order to avoid female disturbance while incubating or brooding (see Greene, 2003). In both seasons, number of eggs or nestlings were recorded each visit to calculate reproductive success per breeding pair. Nests were checked with an extendable mirror.

Pairs breeding in natural nests or nesting boxes were found sequentially, not simultaneously. In some cases, nests were found with nestlings or in extreme cases, fledglings. Therefore, different groups of nests were included in different analyses depending on the information that they could provide. Consequently, sample sizes differ between analyses (Chapter 1, Table 1.4).

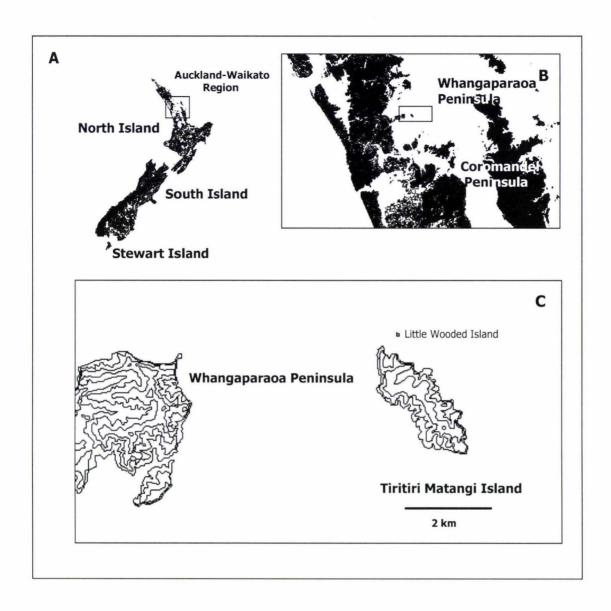


Figure 2.1. Geographical position of the study site. (A) Map of New Zealand showing the Auckland-Waikato Region . (B) Auckland-Waikato Region, showing Location of Whangaparaoa Peninsula. (C) Tiritiri Matangi Island. Contour lines 20m. Maps based on New Zealand Vector Data, Massey University (http://atlas.massey.ac.nz/vector/index.asp).

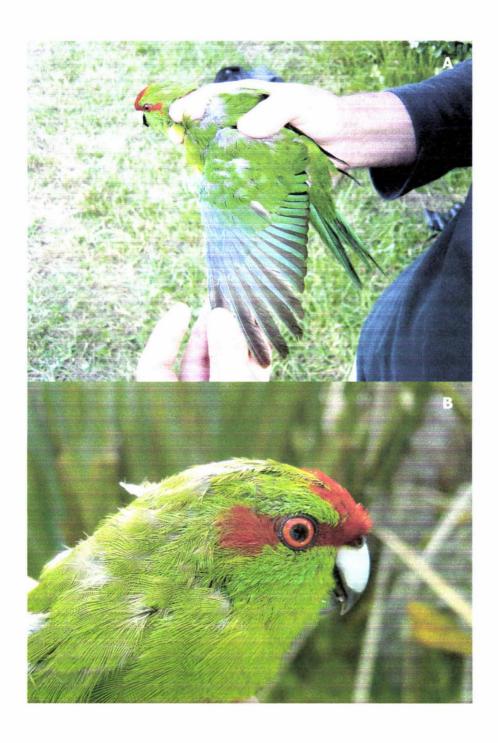


Figure 2.2. Red-crowned kakariki (*Cyanoramphus novaezelandiae*). (A) Detail of the wing-flash (Male); (B) Detail of the head (Female). Photos by M. G. Anderson (A) and L. Ortiz-Catedral (B).

2.4.3 Nesting success

Nesting success was determined using Stanley's method for stage-specific daily survival probabilities (Stanley, 2000). Stanley's method allows the incorporation into the data set of nests checked at irregular intervals and nests encountered at different stages of the nesting cycle. As mentioned previously, the nest monitoring regime was different between breeding seasons and several nests were found at advanced stages, especially in the second year of study (i.e. hatching or nestling stages). Therefore, this method was deemed as appropriate. Stanley's program is available in the SAS[©] programming language from Ecological Archives (http://www.esapubs.org/archive/ecol/E081/021). Armstrong et al., (2002) suggest changing the starting p values during the iterative phase of the program from p = 0.90 to p = 0.99. This procedure is recommended to avoid convergence into incorrect estimates of p values (i.e. a p value greater than 1 for any given nest stage). Similarly, Stanley (2000) and Armstrong et al., (2002) recommend calculation of confidence intervals following the Delta method (Seber, 1982) as PROC NLIN in SAS retrieves confidence intervals with the incorrect degrees of freedom. Both these recommendations were followed. I used the statistical software SAS Version 8[©] to run Stanley's program. Survival during the laying stage was not included in the analysis given that most nests in 2005-2006 were found during incubation or early nestling stages. This did not affect the overall estimation of nest success as only one nest failed during laying over the two years of study. Accordingly, Stanley's program was modified to suit the database. Equations to calculate survivals during egg laying were deleted from Stanley's program (see Armstrong et al., 2002).

Nest success rate was calculated as:

where p^1 and p^2 are estimated survival probabilities for the incubation and nesting stage respectively, and t_1 and t_2 represent mean duration of incubation (1) and nesting (2) (Stanley, 2000; but see Armstrong *et al.*, 2002).

2.4.5 General statistical analyses

I performed Fisher's exact tests to determine the relationship between nest type, (i.e. natural vs nesting box) success, and re-use between seasons. To determine differences in the occurrence of nests in different habitat types, I carried out a Chi-square test of heterogeneity. The relationship between laying date and clutch size and nest success was analysed using Spearman-Rank correlations. For Spearman-Rank correlations I included clutches from both seasons. Laying dates were accurately determined in 2004-2005. For nests of the 2005-2006 breeding season I estimated approximate date of laying by back-dating chicks of known ages. Age of chicks was assigned retrospectively using a regression of wing length and weight on chicks of known age, together with an examination of feather development (see Chapter 4). I assumed a 21 day incubation period and a 1.5 day interval between successive eggs (data based from focal nests in 2004-2005). There is an obvious difference between direct estimates of egg laying (i.e. data from 2004-2005) and a retrospective assignation of egg laying dates (i.e. the onset of incubation can vary individually and seasonally (Grenier and Beissinger,

1999)); however the purpose of this analysis is only to outline patterns of egg laying. I classified clutches as small (4-5 eggs), medium (6-7 eggs) or large (8-9 eggs). Finally, given the potential influence of nest monitoring regime on nest failure I classified nests as 'high' or 'low' monitoring intensity to determine if researcher visits and nest checks could explain failure or success of nests. I considered high monitoring those nests that were followed from egg laying to fledgling and low monitoring those that were found at advanced stages of the nesting cycle and therefore were visited less often (i.e. nests found with nestlings or fledglings). I analysed monitoring regime applying a Fisher's exact test on intensity vs nest outcome. Only nests from the 2004-2005 breeding season were included given that the following year all nests were monitored equally. All analyses were performed in SAS Version 8[©] using PROC FREQ for Fisher's exact test and PROC CORR for Spearman-Rank correlations.

2.5 RESULTS

2.5.1 Natural nesting sites, nesting habitat and nest site re-use

A total of 60 nests were found in the course of this study. Of these 40 (66%) were located in artificial nesting boxes. Six out of the 30 'kakariki' nesting boxes (20%) were used over two breeding seasons. Overall 20 nests (33%) were in natural nesting sites in tree cavities, tunnels in vegetation clusters and ground burrows. Two plant species (Pohutukawa *Metrosideros excelsa* and Harakeke *Phormium tenax*) accounted for 72% out of 18 natural nesting sites found in plants (Figure 2.3). Nesting site re-use was low with only 12 (20%) of the nest sites being active in both seasons. Nest re-use was not related to nest type (Fisher's exact test P > 0.99, N = 43 nests). Nests occurred equally

between habitat types ($\chi^2_2 = 1.69$, P = 0.42, N = 60 nests). Active nesting boxes were more common in replanted bush, a reflection of the nest provisioning scheme.

Cavity dimensions and nest plant characteristics showed considerable variation, reflecting the wide range of nesting places used by kakariki. All natural cavities had a horizontal entrance. Internal height of the cavity $(17.06 \pm 6.68 \text{ cm})$, and the entrance width $(21.32 \pm 11.06 \text{ cm})$ were the descriptors with the less amount of variation between nests. The most variable descriptors were height of nest cavity from the ground $(46.55 \pm 60.45 \text{ cm})$ and distance to nearest vegetation clearing, or forest edge $(12.22 \pm 16.90 \text{ m})$ (Table 2.1).

2.5.2 Egg laying period, reproductive parameters and conflict behaviours

There was a marked difference in the egg laying period between both seasons. In 2004-2005 the first egg was laid on 4th December and the last egg was laid on January 23rd 2005, representing a total of 51 days (30 clutches). In 2005-2006 egg laying started 32 days earlier, extending from October 31st to February 6th. This gives a total of 99 days (30 clutches). It is likely that the egg laying period during the second season was even longer than 99 days given that on the last day of fieldwork (February 8th) females were still observed to be prospecting cavities. It was not possible to determine if they laid eggs or not, but it seemed likely considering their behaviour. During the first season, no second clutches were found and only in one instance a replacement clutch was noticed. It failed shortly after laying. In the second season, two second clutches were recorded but no replacement clutches were found.

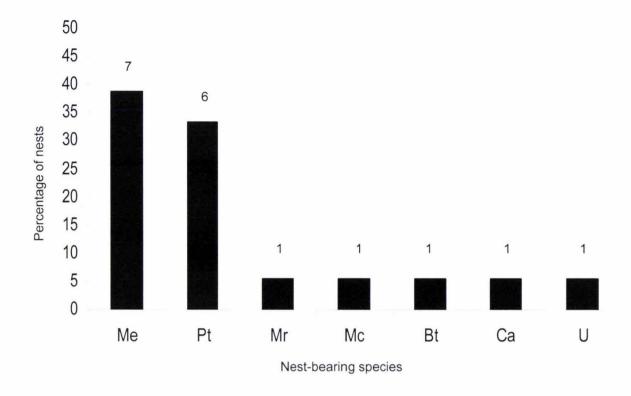


Figure 2.3 Percentage of nests of the red-crowned kakariki in different plant species 2004-2006, on Tiritiri Matangi Island. Numbers above bars represent number of nests found. Me =Metrosideros excelsa (Pohutukawa); Pt=Phormium tenax (Harakeke); Mr=Melicytus ramiflorus (Mahoe); Mc=Muehlenbeckia comlexa (Pohuehue); Bt=Beilschmiedia tarairi (Taraire); Ca=Cordyline australis (Ti kouka); U=unknown species, fallen log.

Second clutches represent simultaneous use of two nests by the respective pairs.

Second clutches were laid when the first nest still contained nestlings. When the females started incubating the second clutches, the males were solely responsible for food provisioning for the incubating females and the nestlings. The birds were identified as

members of the same pair because females visited both nests in succession before laying of the second clutch. After laying of the second clutch, males flew sequentially between nests containing nestlings and the incubating female. The two pairs of nests had a mean inter-nest distance of less than 25 m and were easily observed concurrently.

Interspecific conflicts for cavities were noticed in only two cases were tieke and kakariki displayed aggressive behaviours around the cavity entrance. These behaviours included chases, alarm calls and wing flapping. In both cases female kakariki reacted more actively than males towards tieke. However in both cases, conflicts were short in duration (less than 5 mins) and the disputed cavities were left unused for both breeding seasons. Intraspecific conflicts between kakariki were noticed commonly but were short in duration (less than 5 mins) and appear to be of low intensity. The intruders moved approximately 25 meters of the cavity and residents stop reacting aggressively.

Reproductive parameters were variable within seasons. Clutch size ranged from four to nine eggs; fertility from 57.14% to 100% and hatchability from 0% to 100% (Table 2.2). Between breeding-season variability is presented in chapter 3. There was no effect of laying date on either clutch size (Spearman-Rank correlation $r_s = 0.02$, P = 0.91, N=23) or nest success ($r_s = -0.2$, P = 0.30, N=23) for clutches laid in 2004-2005 or 2005-2006 ($r_s = 0.13$, P = 0.55, N=21 for clutch; $r_s = -0.15$, P = 0.15, N=21 for success). Similarly, no effect of intensity of monitoring on nest success was found (Fisher's exact test, P > 0.99, N = 26).

Table 2.1. Nest characteristics of red-crowned kakariki nests 2004-2006, on Tiritiri Matangi Island.

Measurement	Mean	SD	Range		N	Coefficient of variation
Nesting tree						
Circumference at nest entrance (m)	4.06	2.59	0.99	8.73	8	63.97
Major canopy axis (m)	14.46	7.95	3.8	23.1	8	55
Minor canopy axis (m)	10.30	5.42	3.3	18.5	8	52.65
Nesting plant or vegetation cluster						
Circumference at nest entrance (m)	5.15	2.09	1.6	7.3	7	40.67
Cavity						
Above ground entrance height (m)	46.55	60.45	0	183	20	129.86
Internal height (cm)	17.06	6.68	7	36	20	39.15
Length of entrance rim (cm)	23.56	14.59	7	54	20	61.94
Width of entrance rim (cm)	21.32	11.06	6	45	20	51.91
Length to nest chamber (cm)	60.05	33.86	1.1	160	20	56.38
Distance to nearest vegetation gap (m)	12.22	16.90	0.45	65	20	138.33
Distance to nearest fresh-water body (m)	35.08	28.57	0.85	105	20	81.46

2.5.3 Nesting success

Of 50 nests considered in the nesting success analysis, 33 fledged at least one young. This figure gives an apparent nest success of 66%. Stanley's daily survival probability model provides a more conservative estimate of 60.5%. This estimate is based on a mean incubation period of 21 days and a mean nestling period of 40 days (average for 64 hatched eggs and 83 fledglings; see Chapter 4).

In both seasons, the incubation stage presented a lower daily survival probability than the nestling stage. Estimated survival probability during incubation for 2004-2005 was lower than the corresponding 2005-2006 value (Table 2.3).

Table 2.2. Breeding parameters of red-crowned kakariki on Tiritiri Matangi Island. Values are means \pm SE and range (minimum-maximum).

	N	Clutch size	Fertility %	Hatchability %
2004-2005	25	6.36 ± 0.34	90.8 ± 3.22	45.07 ± 7.9
		(4-9)	(66.66 - 100)	(0 - 100)
2005-2006	26	7.19 ± 0.27	94.82 ± 3.15	63.82 ± 7.1
		(4-9)	(57.14 – 100)	(0 - 100)
Overall	51	6.82 ± 1.6	92.82 ± 2.24	76 ± 5.52
		(4-9)	(57.14 – 100)	(0 – 100)

Table 2.3. Estimates of daily survival probability for the incubation and nestling stages and success rates for the nesting period (incubation + nestling).

Breeding season	Nests	Incubation Stage	Nestling Stage	Estimated survival % (incubation)	Estimated survival % (nestling)	Estimated survival % (incubation-nestling)
2004- 2005	25	0.9773	0.9915	61.74 (61.73- 61.75)	71.07 (71.07-71.07)	43.88 (43.87-43.88)
2005- 2006	25	0.9913	0.9989	83.235 (83.23-83.24)	95.69 (95.69-95.69)	79.65 (38.81-96.02)
Overall	50	0.9833	0.996	70.81 (70.20-70.81)	85.52 (85.18-85.52)	60.56 (26.83-86.54)

2.6 DISCUSSION

2.6.1 Natural nesting sites

Most studies to date on nest site selection and breeding biology of Psittaciformes have shown tree cavities as the main nesting site used (Brightsmith, 2005c; Igag, 2002; Marsden and Pilgrim, 2003; Mawson and Long, 1994). Although, alternative nesting sites such as sand banks, limestone burrows and elaborated stick nests are also well documented for several species (Eberhard, 1998a; Eitniear *et al.*, 1997; Snyder *et al.*, 1982). Usually, parrot species exhibit a consistent nest type throughout their geographical range, for instance Palm Cockatoos (*Probosciger atterrimus*) nest in skyward-facing hollows in Papua New Guinea and Cape York, Australia (Igag, 2002; Murphy *et al.*, 2003). Alternatively, some species present local nest type preferences, presumably

related to availability of tree hollows or other cavities. For example, Bahama Parrots (*Amazona leucocephala*) nest in tree cavities on Inagua island, while on Great Abaco Island they exclusively nest in underground limestone cavities (Snyder *et al.*, 1982).

In contrast to these cases, different nest type use within a small geographical area has been documented only for New Zealand parrots (Higgins, 1999). For the red-crowned kakariki, Greene (2003) reported nests mainly in large trees but also one case of a nest at ground level. Other authors have also mentioned a number of nesting sites used by this species but in general do not include measurements of cavity characteristics or nest bearing plants (Bellingham, 1987; Sagar, 1988). In this study I found natural nests in tree cavities, vegetation clusters, fallen logs and ground burrows excavated by Grey Faced Petrels (Pterodroma macroptera). Of particular relevance is the range of cavity heights above ground (0 to 183 cm). Indeed there are higher cavities on Tiritiri Matangi Island, especially in large Pohutukawas around cliffs and it is possible that red-crowned kakariki also makes use of them; however I could not obtain any information regarding these. Only a few parrot species have been observed to make use of different nesting sites in the same area. In the Amazon basin, some species nest in tree hollows as well as termitaria (Brightsmith, 2005a) but in both cases the nest cavity is found above the ground. Among Cyanoramphus the red-crowned kakariki and Antipodes Island parakeet (C. unicolor) are the only species known to nest at ground level (Forshaw, 1989; Greene, 1999). Another three New Zealand parrot species have been recorded nesting at ground level: kaka (Moorhouse, 1991), kea (Heather and Robertson, 1996) and kakapo (Powlesland et al., 1992).

It appears that nesting kakariki on Tiritiri Matangi Island are not restricted to the densest vegetation areas as distance to nearest vegetation clearing varied considerably, however, only a small number of nests were monitored.

Nest re-use was low for both natural nesting sites and nesting boxes and was documented in only 12 cases (20%). When considering natural nests alone, re-use was very low with only two confirmed cases (10%). Not all nests studied were found in the first year of study and therefore, interannual nest use is biased towards nests found first in the breeding season 2004-2005. For nests found only in 2005-2006, previous use was unknown given the habit of nesting kakariki of loosening the nest floor substrate, which covers egg-shell remains or any other evidence of previous use.

This low re-use does not correspond to nest usurpation by other species as most nesting sites remained vacant for the breeding cycle of kakariki, despite presence of other cavity nesters on Tiritiri Matangi (i.e. hihi and tieke). Nest usurpation was noticed only twice. Once involving a little spotted kiwi (Pukupuku *Apteryx owenii*) roosting in a cavity at ground level at the base of a Pohutukawa tree. The previous year, kakariki nested in the same cavity. The second case was a tieke constructing a nest in a nesting box formerly used by kakariki. For these cases interactions between kakariki and the intruder species were not documented. Low re-use of nesting cavities was also documented by Greene (2003).

Many authors have stressed the importance of competition as a driving force behind nest site selection by parrots (Heinsohn *et al.*, 2003; Pell and Tidemann, 1997). More importantly, there is ecological and evolutionary evidence for predation as a crucial factor determining nest selection and nest niche diversification for parrots (Brightsmith,

2005b; Eberhard, 1998b). Even though the evidence is limited, it seems that competition for cavities on Tiritiri Matangi is low. Observations in support of this are variability in cavity characteristics, low cavity re-use, and low-intensity interactions around the cavity. Other studies have described a pattern of increased high intensity interactions attributed to nest defence and territoriality, corresponding to development of the breeding season (Beissinger *et al.*, 1998; Renton, 2004) but these were not seen for kakariki despite regular visits to nests. It has been proposed that low cavity re-use by parrots is a mechanism to avoid predators (Renton and Salinas-Melgoza, 1999). However, no events of predation were recorded over two years despite the presence of potential native predators such as pukeko (*Porphyrio porphyrio*) and morepork (*Ninox novaezelandiae*). It is possible that nest-site selection by kakariki is driven by causes other than competition or predation, for instance nest microclimate characteristics. These were not measured in this study and need to be addressed by further studies.

Natural nests occurred with the same frequency across different habitat types.

Active nesting boxes were more common in replanted bush, an obvious reflection of the original distribution scheme for nesting boxes. These have been provided for cavity nesters (i.e. hihi, tieke) due to the low density of large cavity-bearing trees, especially within revegetated areas (Rimmer, 2004; Stamp and Brunton, 2002). Nesting boxes have also been installed in remnant forest but occupancy there was lower than in replanted bush. Natural cavities in remnant forest occurred almost as commonly as nesting boxes in the same habitat. Clearly some active nests were not monitored and this study is only a first approximation to the nesting habitat preferences of kakariki. It is biased towards accessible nests, namely all nesting boxes are easy to find, occur at about the same height

and are quite visible within replanted areas. The relevance of these results however is related to the management of the species and highlights the potential of kakariki for translocations to fragmented areas or recently revegetated sites (Chapter 5).

2.6.2 Laying date, clutch size and nest success

The data available do not show a relationship of laying date on clutch size. Small, medium and large clutches were laid throughout the breeding season rather than being limited to the beginning or end of the breeding season. Similarly, nest success was not related to laying date. There is abundant evidence explaining the relationship between laying date and clutch size (Beissinger and Waltman, 1991; Navarro et al., 1995). Generally, clutches laid early in the season are larger and out-perform later clutches in terms of success. This is due to a combination of temporal changes in food supply or weather conditions associated with the progression of the season and parental experience of the breeding pair (see Rowley, 1990 for a detailed discussion). However, laying date can also have an effect after fledgling. For instance, the breeding opportunities and survival might differ between fledgling hierarchies and brood position within the season (Daan et al., 1990; Krebs et al., 2002). The results of this study are thus not conclusive regarding the effect of laying date and clutch size and success. Failure to find significant differences might be an effect of sampling method on a small sample size. It is possible that many early and later laid clutches went unnoticed. When nest searches begun in the first breeding season, some fledglings were noticed but the nest of origin could not be located and it was unknown if they came from a small or large clutch or the precise date of laying. Moreover, total brood reduction occurred commonly in 2004-2005; in contrast only one case was documented in 2005-2006 (Chapter 3). Thus the effect of laying date might be confounded with high rates of brood reduction in the first breeding season and high rates of success across all nests in the second breeding season. Most fledged chicks from focal nests have been banded (Chapter 4, Appendix 5) and thus provide a starting point for upcoming studies to explore the interaction between laying date, clutch size and recruitment into the population.

2.6.3 Nesting success

Temporal and spatial variability in nesting success is a well documented phenomenon in avian ecology. Several studies have determined territorial quality (Przybylo *et al.*, 2001), parental condition (Masello and Quilfeldt, 2003) or parental experience (Rowley, 1990; Stone *et al.*, 1999; Wilson *et al.*, 1997) as explanatory causes of nest success. More commonly, variability is expected to be the result of a combination of these and other factors (Nooker *et al.*, 2005).

In this study, the combined probability of survival for the entire nesting cycle (incubation to nestling) was 60.5 %, however annual differences in nesting success were found. During 2004-2005 the combined probability of survival was 43.8 % whereas in 2005-2006 increased to 79.6 % as estimated by Stanley's method of daily survival probabilities. A given nest was more likely to fail in 2004-2005 especially during incubation, mainly due to low hatchability of eggs $(45.07 \pm 7.91\%; n=112 \text{ eggs})$. Hatchability increased in 2005-2006 $(63.82 \pm 7.16\%; n=115 \text{ eggs})$ and was reflected in higher nesting success. The difference in hatchability is significant (Chapter 3). Overall hatchability between 2004 and 2006 reached 76% (n=227 eggs), close to the value

reported for a natural population of red-crowned kakariki (hatchability = 83.6 % n= 140 eggs, Greene, 2003) and other bird species (Koenig, 1982).

Temporal differences in hatching success have been documented for various parrot species. Crimson rosellas (*Platycercus eximius*) hatch more eggs during years of high rather than low rainfall (Krebs, 1998). Similarly, Blue-fronted amazons (*Amazona aestiva*) exhibit variability in hatching values between years (Fernandes Seixas and de Miranda Mouráo, 2002); however the associated causes are not known.

Causes of loss during the nesting cycle of parrots have been documented widely and in general, most losses occur during the nestling stage. Predation is the main cause of nestling losses in a wide range of species (Eberhard, 1998a; Garnett *et al.*, 1999; Koenig, 2001). Other causes include heavy rains (Murphy *et al.*, 2003); human disturbance or poaching (Fernandes Seixas and de Miranda Mouráo, 2002; Martuscelli, 1995) and intra and interspecific interference (Beissinger *et al.*, 1998; Heinsohn *et al.*, 2003). In contrast, losses during the incubation stage have been reported infrequently and are usually the result of infertility (Eberhard, 1998a; Saunders, 1986), seasonal low hatchability (Krebs, 1998) or predation of incubating parents (Moorhouse *et al.*, 2003).

The 2004-2005 breeding season, was characterised by low hatchability, high nestling mortality and low production of fledglings. Even though nests in this season were visited often, there was no relationship between nest outcome (failure or success) and intensity of monitoring. Higher hatchability, lower nestling mortality and greater production of fledglings typify the 2005-2006 breeding season. This pattern is similar to that reported for burrowing parrots (*Cyanoliseus patagonus*) were differences in several parameters of reproductive success were associated with differences in parental condition

affected by environmental factors (Masello and Quilfeldt, 2003). Similarly, food supply has been shown to affect the annual nesting success of numerous species (Shochat *et al.*, 2005; Zanette *et al.*, 2003).

There is also experimental support for the role of food on incubation performance. In the reed warbler (Acrocephalus australis) (Eikenaar et al., 2003), food-supplemented females increased incubation attendance and hatched more eggs than control females. Incubation performance was not directly assessed in the present study, nor was food availability measured. However, the occurrence of second clutches in the 2005-2006 breeding season further suggests that this was a year of higher food availability. For the closely related Orange-fronted parakeet Cyanoramphus malherbi, second clutches have been recorded when the birds are feed ad libitum (D. Small and J. van Hal, pers. comm. 2005). An exceptional example is yellow-crowned parakeet (C. auriceps) which can raise five broods during years of heavy beech (*Nothofagus* sp) seed production ('mast years') in Fiordland (Elliot et al., 1996a). The connection between food availability and reproductive performance across avian orders has been extensively documented (Martin, 1987). Clearly food supply not only affects incubating parents but also nestling survival. For the breeding season 2004-2005, nestling survival was low and total brood reduction common. In most cases, dying nestlings lost weight prior to death, and crops of dead nestlings were found empty, indicating starvation as a cause of death. In contrast, during 2005-2006, nestling survival was high and total brood failure was rare, with only one recorded case (Chapters 3 and 4).

However, food availability is not in some cases the sole determinant of nesting success. It has been shown that older, more experienced galahs (*Eolophus roseicapillus*)

are able to raise young even under conditions of low food supply (Rowley, 1990). In cockatiels (*Nymphicus hollandicus*), inexperienced pairs have lower nesting success even when food supply is not limited (Stone *et al.*, 1999). If food availability is a critical factor determining yearly nesting success of kakariki it is necessary to identify and monitor key resources that could potentially be managed to enhance nesting success. This will be particularly relevant in the case of forthcoming translocations (Chapter 5).

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CHAPTER 3: CHANGES IN PRODUCTIVITY AND EXPECTED REPRODUCTIVE SUCCESS BETWEEN BREEDING SEASONS

3.1 ABSTRACT

Differences in productivity for red-crowned kakariki were determined on Tiritiri Matangi Island. Physical parameters of reproductive investment and success between breeding seasons were contrasted and stages of loss identified. Furthermore, I analysed changes in expected reproductive success (ERS) per breeding season. Multivariate analysis revealed significant differences in productivity during this study. However, no differences were found in clutch size, fertility and egg volume. In contrast, hatchability and number of nestlings varied significantly. Only 1.4 fledglings per clutch were produced in the 2004-2005 breeding season, whereas 3.4 fledglings were produced in 2005-2006. Likewise, ERS was markedly different between breeding seasons, being lower in 2004-2005 than in 2005-2006 (0.71 vs 3.12 fledglings respectively). Considering both breeding seasons, 7 eggs were laid per breeding pair but only 2.55 nestlings fledged. This corresponds to a 63.8% loss of their initial investment. Incubation was the principal period of failure with total hatching and brood failure accounting for most losses in the 2004-2005 breeding season. In contrast, these were rare in the second year and most losses were the result of hatching failure and brood reduction. The contrast between breeding seasons in hatchability and number of fledglings produced, highlights the need to determine underlying agents driving changes in reproductive success. These must be identified to anticipate the likely outcome of future breeding seasons in monitored populations and also in forthcoming translocations of the species.

3.2 INTRODUCTION

Variation in clutch size, egg size and reproductive success in birds are central questions in avian ecology and conservation. Several studies have documented variation in measures of reproductive success in relation to diet, age of breeders, health and, environmental factors. For instance, in Florida scrub jays (*Aphelocoma coerulescens*) food availability advances laying date and increases clutch size (Reynolds *et al.*, 2003). In Prothonotary warblers (*Protonotaria citrea*) clutch size is smaller and fertility is lower in first clutches of one-year-old breeders than older pairs (Blem *et al.*, 1999). In Great tits (*Parus major*) females parasitised with *Trypanosoma* lay smaller eggs, hatch less young and raise nestlings in poorer condition than non-parasitised females (Dufva, 1996). In the same species, females lay lighter eggs if pre-laying ambient temperatures are variable (Pendlebury and Bryant, 2005). Therefore, an understanding of the temporal and spatial variability of parameters of investment and measures of reproductive success are essential to describe the evolution of life history traits.

Documenting annual variability in reproductive success as well as components of reproductive investment is especially relevant for the management of threatened species, since increasing population size to reduce chance extinction is a top priority in restoration plans (Jamieson and Ryan, 1999; Swinnerton *et al.*, 2004). Identifying factors limiting investment and success can thus lead to improvements in management protocols and direction of conservation efforts (Powlesland and Lloyd, 1994).

Reproductive success is affected by sequential losses through the nesting cycle. In most studies on parrots, the nestling stage is the main period of loss with predation and poaching as the main causes; although losses during incubation have also been recorded

(Heinsohn and Legge, 2003; Koenig, 2001; Smith and Saunders, 1986; Wright *et al.*, 2001). Recognising critical periods of loss during the nesting stage allows estimation of loss rate and expected reproductive output which directly impacts on the design of management interventions (Wilson *et al.*, 1997), increasing the efficiency of conservation measures (Wilson *et al.*, 1997) and allocation of funds (White and Vilella, 2004).

Changes in measures of reproductive success between breeding seasons have been documented for various long-lived species (Laaksonen *et al.*, 2002; Nooker *et al.*, 2005) but only rarely in parrots. More commonly, variation in nesting success has been reported (Fernandes Seixas and de Miranda Mouráo, 2002; Monterrubio *et al.*, 2002; Renton and Salinas-Melgoza, 2004). Even though most studies provide a detailed summary of parameters of investment (i.e. clutch size, fertility, egg volume) these have rarely been analysed simultaneously with measures of reproductive success. Multivariate analysis of measures of investment and success can reveal patterns not perceptible by independent univariate analyses applied to the same data set, therefore increasing our ability to detect changes in productivity between breeding seasons.

Commonly, studies on breeding birds focus on changes in clutch size, hatchability, number of hatchlings and fledglings given that egg volume and fertility show little variation between years (Christians, 2002). However, there is evidence indicating associations between egg volume and female condition (Dufva, 1996; Fidler *et al.*, 2000). Moreover, a complex association between inbreeding, translocation and infertility has been documented for a New Zealand bird, the takahe (*Porphyrio mantelli*) (Jamieson and Christine, 2000). It is thus relevant to document variability in fertility and egg volume as well.

This chapter presents a multivariate analysis of differences in productivity of redcrowned kakariki. It also includes a comparison of individual parameters of physical
investment and measures of reproductive success between breeding seasons.

Furthermore, this chapter presents a stage-specific analysis of loss for the nesting period
to determine main stages of failure and differences in expected reproductive output
during this study. Finally, a description of causes of nest loss is presented. This represents
a first approach to understand the variability in measures of productivity and reproductive
success of red-crowned kakariki between breeding seasons.

3.3 OBJECTIVES

The general objective of this chapter is to analyse overall differences in productivity and measures of physical investment and reproductive success between breeding seasons for red-crowned kakariki on Tiritiri Matangi Island. Hereafter, "physical investment" refers to clutch size, egg volume and fertility; "reproductive success" refers to hatchability, number of hatchlings and number of fledglings. The specific objectives developed in this chapter are:

- Determine differences in productivity of red-crowned kakariki between two successive breeding seasons.
- Determine differences in physical investment and reproductive success between breeding seasons.
- 3. Analyse the relationship between clutch size, hatchability, and number of hatchlings.
- 4. Analyse the relationship between brood size and reproductive success.

- 5. Identify principal stages of nest loss and failure.
- Determine and compare expected reproductive success between breeding seasons.
- 7. Document causes of partial and total nest failure

3.4 METHODS

The study site and study species are described in section 2.4, chapter 2.

3.4.1 Definition of terms

The use of terms 'reproductive success', 'breeding success', 'productivity' and 'reproductive output' are commonly used as synonyms in the ornithological literature causing some confusion regarding the phenomenon to be analysed. To avoid misunderstanding, the following terms are used in this document:

Productivity: Describes six variables: clutch size, egg volume, fertility, hatchability, number of hatchlings and number of fledglings per breeding pair. These individual terms where entered as variables into a multivariate analysis to analyse combined effects.
Productivity can also be defined in a statistical way as the vector of means of these six variables.

Reproductive success: Comprise hatchability, number of hatchlings and number of fledglings. Hatchability is expressed as the percentage of fertile eggs successfully hatched from the total number of fertile eggs laid. Number of hatchlings is the number of nestlings hatching in a given brood. Fledglings are the number of nestlings successfully leaving the nest.

3.4.2 Variation in productivity between breeding seasons

An analysis of productivity between breeding seasons was performed using a multivariate approach (Table 1.4, chapter 1). As the power of the multivariate test chosen (Hotelling's test, see below) is sensitive to the number of variables considered in the model (Kaplan and George, 1995) it was preferred to test a more complex model (i.e. more variables) on a sub-set of 30 nests for which all variables were measured. An alternative option would have been to reduce the number of variables in multivariate comparisons to allow the inclusion of more nests; however this would lead to unequal sample sizes and an unbalanced design due to missing measures for some variables.

Six variables were included in the multivariate analysis: three describing parental investment and three describing reproductive success. Variables describing parental investment are: clutch size, egg volume, and fertility. These have been shown to vary between individuals and between breeding seasons in other studies (Nooker *et al.*, 2005) and thus were considered appropriate to explore variability in the red-crowned kakariki. In addition, three variables describing reproductive success were included: hatchability, number of hatchlings, and number of fledglings produced.

3.4.2.1 Egg volume

Every egg found was measured to the nearest 0.1 mm with a stainless steel vernier calliper. In most cases, eggs were measured on the day of laying or up to 7 days after laying. The dimensions taken were length and width. The volume of eggs was determined following the formula of Tatum (1975):

$$V = \pi LB^2/6$$

where L is length and B is maximum breadth. This formula was used instead of the widely used Hoyt's formula (Hoyt, 1979) since Tatum's formula does not require a general egg volume coefficient (K_{ν}) making estimations more accurate using length and breadth only.

3.4.2.2 Fertility and hatchability

Fertility of eggs was determined in the field by candling with a small hand torch. The egg shell of red-crowned kakariki eggs is almost translucent and embryos could be seen clearly. Fertility was calculated as number of fertile eggs divided by total eggs laid in a clutch. Hatchability was determined as the proportion hatched eggs divided by total number of fertile eggs in the clutch. Infertile eggs were not included in the analysis of hatchability.

3.4.3 Multivariate analysis

Two data matrices including all variables described above were analysed using Hotelling's T^2 test (Two group MANOVA) (Gotelli and Ellison, 2004), to test for changes in productivity between breeding seasons. This method was chosen because it provides statistical power (1- β) with limited sample sizes (Bai and Saranadasa, 1996). In addition, this approach reduces type I error when compared with multiple univariate tests applied to the same data set (Gotelli and Ellison, 2004). Multivariate analysis also allows a joint examination of variables that might show differences between groups not perceptible by conventional univariate analyses (Lu *et al.*, 2005). Data were square-root

transformed to meet the assumption of normality required for parametric analysis. Similarly, data were standardised before performing analysis to allow comparisons between parameters measured in different scales (i.e. millimetres, percentages etc.). Data analysis and calculation of exact P-values were performed in SAS Version 8° using PROC IML for matrix operations. Finally a power analysis for Hotelling's T^2 test was performed (Efird and Alimineti, 2004).

3.4.4 Variation in measures of reproductive investment and reproductive success

A series of analyses was carried out to contrast differences between breeding seasons in the following variables: clutch size, egg volume, fertility, hatchability, and number of hatchlings, levels of brood reduction, number of dead nestlings and number of fledglings. Given the small founder population of red-crowned kakariki on Tiritiri Matangi the population is likely to have some degree of inbreeding and thus, documenting egg volume and fertility levels is of central interest. Therefore egg volume and fertility were also assessed between seasons as alternative explanatory variables for reproductive success. The analyses were carried out at three levels: breeding season, clutch and brood. Normality of data sets was tested with Shapiro-Wilks test in SAS PROC UNIVARIATE Version 8[©]. When the data did not fulfil assumptions of parametric tests, non-parametric tests were applied. All statistical tests were performed in SAS Version 8[©].

Differences in egg volume and fertility between breeding seasons were contrasted by two sample *t*-tests on a total of 30 clutches (Chapter 1, Table 1.4). To estimate differences in clutch size, hatchability, number of hatchlings and nestlings, 43 nests were

considered and the differences compared using independent non-parametric tests (Wilcoxon-Mann-Whitney two sample tests) (Chapter 1, Table 1.4).

A later analysis was performed to test for differences associated with clutch and brood size. The variables considered were: hatchability, number of hatchlings, degree of brood reduction, number of dead nestlings and number of fledglings. Mean values for these variables were compared using Kruskall-Wallis tests (Conover, 1980). For comparisons, clutches were classified as small, medium or large (Chapter 2). Similarly, broods were categorised as small (1-3 nestlings), medium (4-6 nestlings) or large (7-9 nestlings). Data on clutch and brood size were pooled for analysis.

3.4.5 Expected reproductive success and stage-specific losses

Reproductive success is the result of cumulative failure or success through stages of the nesting cycle (i.e. egg laying to fledgling). To determine stage specific losses, and *per capita* reproductive success between years, I applied Gnam and Rockwell's (1991) model to 43 nests (Chapter 1, Table 1.4). This model allows calculation of expected reproductive success considering loss rate between consecutive stages of nesting (i.e. from egg laying to fledgling). A given nest can contribute to the model in two ways: calculation of nest failure probability and stage specific losses. Nest failure probability was calculated as the number of failed nests divided by total number of nests. Nest failure probability was divided in three categories: total nesting failure (TNF: nest desertion before completion of incubation); total hatching failure (THF: nests that failed to hatch any egg when incubation was completed) and total brood failure (TBF: all nestlings died before fledgling). Stage specific losses only included nests for which at least one young

hatched and incorporates nesting failure probabilities from the previous dataset. Partial hatching failure and brood reduction were also recorded. Gnam and Rockwell's Expected Reproductive Success model (ERS) is defined as:

$$ERS = TCL \times (1-TNF) \times P_1 \times (1-THF) \times P_2 \times (1-TBF) \times P_3$$

where TCL = Total Clutch Laid, TNF= Total Nest Failure, THF=Total Hatching Failure TBF= Total Nest Failure, P_1 = Egg survival, P_2 = Hatching success and P_3 = Fledging success.

3.4.6 Causes of nest loss

Nest losses were recorded to provide an overview of the causes affecting reproductive success of red-crowned kakariki. Nest losses were classified as partial or total losses. "Partial loss" includes **a**) Clutches that failed to hatch at least one fertile egg (partial hatching failure) and **b**) Clutches that experienced brood reduction (i.e. at least one young died during the nestling stage). "Total loss" considers **a**) Total nest failure (i.e. clutches lost due to environmental causes or abandonment during incubation); **b**) Total hatching failure (no eggs hatched in a clutch but females remained sitting on eggs for a period equivalent or longer than normal incubation); and **c**) Total brood failure (all hatched young died before fledgling due to starvation or environmental causes).

3.5 RESULTS

3.5.1 Seasonal variation in productivity

Multivariate analysis revealed significant differences in productivity between breeding seasons (Hotelling's T^2 test $F_{6.24} = 68.36$, P < 0.001). The power of this test

was found to be high (*Power* > 0.99, N=30). The 2005-2006 breeding season presented larger clutch sizes, higher hatchability, higher number of hatchlings and higher number of fledglings (Table 3.1).

3.5.2 Variation in measures of reproductive investment and reproductive success

All measures of reproductive success varied significantly between breeding seasons. Hatchability in 2005-2006 was higher than in 2004-2005 (hatchability: 2004-2005 = 44.65 %, 2005-2006 = 65 %, Wilcoxon-Mann-Whitney two sample test $Z_2 = 2.03$, P < 0.05). Number of hatchlings doubled in 2005-2006 (number of hatchlings: 2004-2005 = 2.5, 2005-2006 = 4.9, Wilcoxon-Mann-Whitney two sample test $Z_2 = 3.19$, P < 0.01) while number of fledglings presented a three fold increase (number of fledglings: 2004-2005 = 0.96, 2005-2006 = 3.33, Wilcoxon-Mann-Whitney two sample test $Z_2 = 3.94$, P < 0.01). In contrast, there were no differences in clutch size, egg volume and fertility between seasons (Table 3.2).

Levels of hatchability varied according to clutch size (Figure 3.1). Not only did large clutches presented a higher proportion of hatched eggs than small or medium clutches (Kruskal-Wallis $\chi^2_2 = 6.06$, P < 0.05) but also large clutches resulted in larger broods than small and medium clutches (Kruskal-Wallis $\chi^2_2 = 17.97$, P < 0.01). Levels of brood reduction were similar for small, medium, and large broods (Kruskal-Wallis $\chi^2_2 = 1.10$, P > 0.57) (Table 3.4, Figure 3.2). However, the number of dead nestlings in a brood was related to brood size, with larger broods presenting more dead nestlings than other brood classes (Kruskal-Wallis $\chi^2_2 = 10.07$, P < 0.01) (Table 3.4, Figure 3.2). Despite

presenting more dead nestlings, large broods produced more fledglings than small and medium broods (Kruskal-Wallis χ^2 2= 10.47, P < 0.01) (Table 3.4, Figure 3.2).

Table 3.1. Differences in productivity between two breeding seasons of the red-crowned kakariki on Tiritiri Matangi Island.

Breeding	Measures of reproductive investment (n=30)			Measurements of reproductive success (n=30)			
	Clutch size Mean ± SE	Egg volume (cm³) Mean ± SE	Fertility (%) (Median, range)	Hatchability (%) (Median, range)	Number of Hatchlings $Mean \pm SE$	Number of Fledgings Mean ± SE	
2004- 2005	7.43 ± 0.33	5.46 ± 0.18	100 66.66-100	50 0-100	3.2 ± 0.64	1.27 ± 0.32	
2005- 2006	7.67 ± 0.27	5.23 ± 0.12	100 57.14-100	71.42 12.5-100	5 ± 0.60	3.13 ± 0.52	

3.5.3 Expected reproductive success and stage specific losses

Expected reproductive success (ERS) of breeding pairs differed between seasons. In 2004-2005, ERS was significantly lower than in 2005-2006 (2004-2005 ERS = 0.71 \pm 0.16 fledglings; 2005-2006 ERS = 3.12 \pm 0.37 fledglings; Wilcoxon-Mann-Whitney two sample tests $Z_{18,25}$ = -1.58 P < 0.01, N = 43) (Figure 3.3).

Table 3.2. Variability in parameters of parental investment and reproductive success of red-crowned kakariki on Tiritiri Matangi Island between the 2004-2005 and 2005-2006 breeding seasons. Sample size in parentheses. Z = Statistic for Wilcoxon-Mann-Whitney two sample test; t = Two sample t test

Parental Investment	2004-2005	2005-2006	Statistic	P value
Clutch size	6.23 ± 0.34 (26)	7.15 ± 0.31 (20)	$Z_2 = 1.84$	> 0.06
$Mean \pm SE$				
Egg Volume (cm3)	5.46 ± 0.18 (15)	5.23 ± 0.12 (15)		> 0.30
$Mean \pm SE$			$t_{28} = 1.04$	
Fertility (%)	100	100		> 0.38
Median, range	66.66-100 (15)	57.14-100 (15)	$t_{28} = -0.89$	

Reproductive Success	2004-2005	2005-2006	Statistic	P value
Hatchability (%)	45 0-100	71 0-100	$Z_2 = 2.03$	< 0.05
Median, range	(26)	(20)		
No. Hatchlings	2.5 ± 0.47 (26)	4.9 ± 0.52 (20)	$Z_2 = 3.19$	< 0.01
$Mean \pm SE$			$L_2 = 3.19$	
No. Fledglings	0.96 ± 0.25 (26)	3.33 ± 0.44 (24)	7 - 2 04	< 0.01
$Mean \pm SE$			$Z_2 = 3.94$	

Stage-specific losses through the nesting cycle were determined for 43 nests.

Incubation was identified as the main period of loss. Overall, 18% of nests failed during incubation. The remaining losses took place during the nestling stage and accounted for 16% of the cases (Figure 3.4).

Table 3.3. Variability in parameters of reproductive success of red-crowned kakariki between the 2004-2005 and 2005-2006 breeding seasons on Tiritiri Matangi Island. Values are means \pm SE. Sample size in parentheses. χ^2 = Kruskal-Wallis statistc

	Clutch / Brood size			Statistic	P value
	Small	Medium	Large	-	
Hatchability	36.25 ± 12.10	50.19 ± 7.05	69.49 ± 5.92	$\chi^{2}_{2} = 6.06$	P > 0.05
Number of	1.75 ± 0.60	3.13 ± 0.45	5.81 ± 0.54	$\chi^2_2 = 17.97$	<i>P</i> > 0.01
hatchlings Brood reduction	52.22 ± 11.01	39.64 ± 8.24	50.19 ± 11.43	$\chi^{2}_{2}=1.10$	<i>P</i> > 0.57
Number of	0.86 ± 0.21	2 ± 0.41	3.85 ± 0.85	$\chi^2_{2} = 10.07$	<i>P</i> > 0.01
dead nestlings Number of fledglings	1.2 ± 0.31	3.15 ± 0.46	3.85 ± 0.88	$\chi^2_2 = 10.47$	<i>P</i> > 0.01

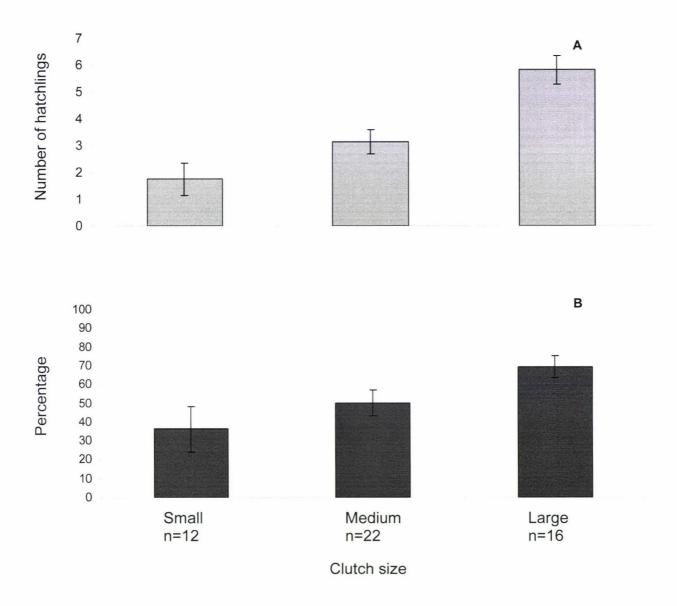


Figure 3.1. A) Relationship between clutch size and number of hatchlings. B) Relationship between clutch size and hatchability. Numbers included in bars represent sample size. Values represent means \pm SE.

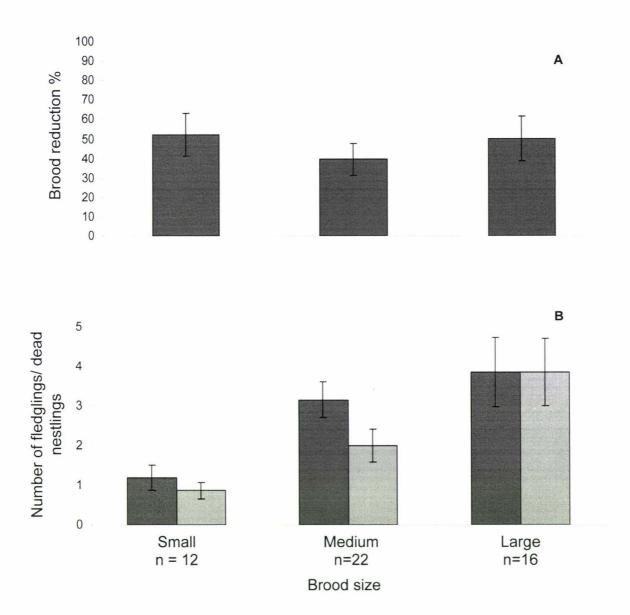


Figure 3.2. A) Relationship between brood size and brood reduction. B) Relationship between brood size-number of fledglings (dark grey) and brood size-number of dead chicks (light grey). Numbers included in bars represent sample size. Values represent means \pm SE.

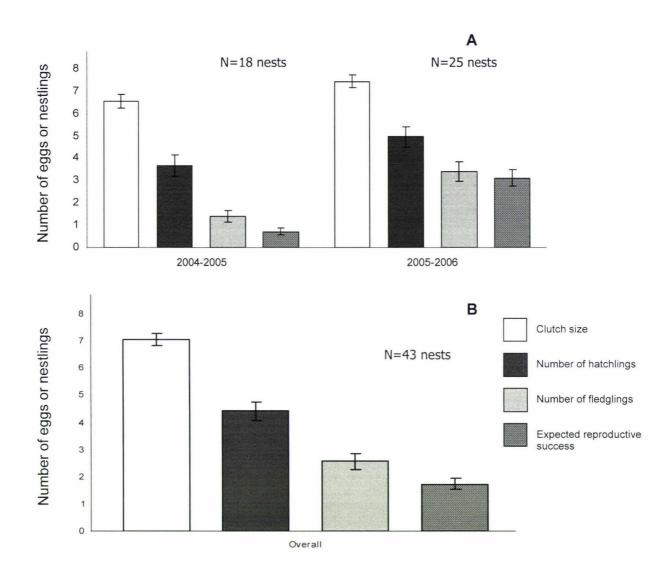


Figure 3.3. Contrast between initial clutch size, observed reproductive output and expected reproductive success of red-crowned kakariki. A) Interannual differences. B) Overall figures for this study.

3.5.4 Causes of partial and total nest losses

Twenty six nests experienced partial losses through the nesting cycle during both breeding seasons. These included partial hatching failure and brood reduction. In general, partial hatching failure was accompanied by brood reduction due to starvation of nestlings. In 2004-2005, 34% of clutches presented partial hatching failure and 34% of broods suffered partial brood reduction (Figure 3.4). In 2005-2006, partial hatching failure affected 62% of clutches and partial brood reduction was recorded in 70% of broods (Figure 3.4). Total losses varied considerably between seasons. In 2004-2005, 57% of clutches failed completely; these included clutches failing to hatch any young (23%), total brood failure (27%), and two instances of total nest failure (7%) (Figure 3.4). Total nest failure in 2004-2005 includes a clutch lost due to flooding of the nest and one case of desertion soon after completion of the clutch due to unknown causes. The clutch was left intact with no signs of predation at the nest.

In contrast, total losses in 2005-2006 only occurred in 8% of clutches and included one case of total hatching failure (4%) and one case of total brood failure (4%). No instances of total nest failure were noticed. The only case of total brood failure was due to flooding of the nest close to fledging of most nestlings. No instances of total brood failure due to starvation of nestlings were recorded. Despite partial losses being more common in 2005-2006, 91% of clutches produced at least one fledgling. In comparison, during the 2004-2005 breeding season only 42% of clutches resulted in at least one fledgling (Figure 3.4). In both years, the main stage of loss (partial and total) was the incubation stage.

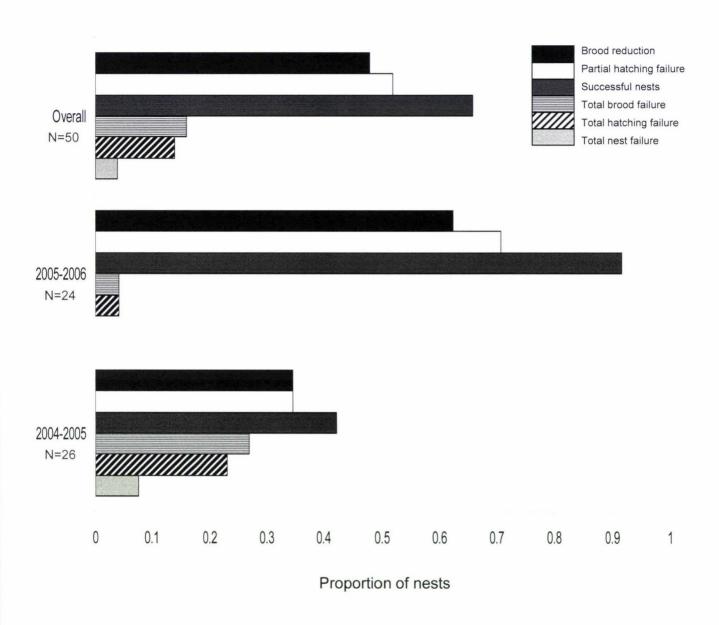


Figure 3.4. Between-season comparison of partial and total losses during the nesting cycle of red-crowned kakariki on Tiritiri Matangi Island.

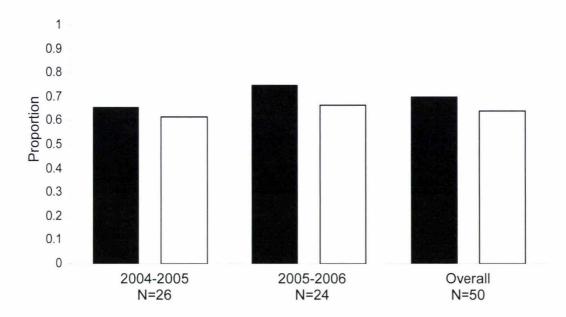


Figure 3.5. Proportion of nests losses (partial + total) during the nesting cycle of redcrowned kakariki. Incubation period in black, nesting period in white. Data represent two breeding seasons on Tiritiri Matangi Island. Percentage values represent only nests that suffered loss, either partial or total.

3.6 DISCUSSION

3.6.1 Interannual variation in productivity, parameters of parental investment and reproductive success

The contrasting differences in productivity and reproductive success between the breeding seasons covered in this study have not been previously reported for red-crowned kakariki. In particular, hatchability, number of hatchlings per clutch and number of fledglings produced increased significantly from 2004-2005 to 2005-2006. However, this

increase in reproductive success was not accompanied by a change in physical parameters of parental investment. Clutch size, egg volume, and levels of fertility remained similar between years. Although, in the second year of study two second clutches were recorded; this can be interpreted as an increase on clutch size for those two particular females (Chapter 2). On Little Barrier, Greene (2003) recorded only slight interannual differences in clutch size and hatchability. In the same study, a similar number of fledglings were produced between two consecutive breeding seasons, and similar mortality of nestlings occurred also between seasons (Greene, 2003). These results contrast with the present study, where number of fledglings increased three-fold from 2004-2005 to 2005-2006. The consistency in number of fledglings produced on Little Barrier Island possibly reflects similar environmental conditions during the study period.

Other studies of New Zealand birds have documented a dramatic reduction in reproductive success and these have been attributed to unfavourable environmental conditions in a temperate environment, affecting food supply. These studies include kaka (Nestor meridionalis) (Beggs and Wilson, 1991; Moorhouse, 1991); kea (N. notabilis) (Diamond and Bond, 1999); kakapo (Strigops habroptilus) (Powlesland and Lloyd, 1994; Powlesland et al., 1992) and keruru (New Zealand Pigeon, Hemiphaga novaezelandiae) (Clout et al., 1995). The relationship between resource availability and reproductive success have also been documented for parrot species elsewhere (Beeton, 1985; Long, 1990; Renton, 2002; Rowley, 1990).

Observations in kea and kaka indicate that in years of low food availability only a few pairs attempt to breed (Beggs and Wilson, 1991; Diamond and Bond, 1999; Moorhouse, 1991). For crimson rosellas (*Platycercus elegans*) (Krebs, 1998) and galahs

(Eolophus roseicapillus) (Rowley, 1990) a similar pattern has been reported: fewer pairs breed during unfavourable years. Although the present study concerns only two breeding seasons, such a pattern was not noticed. A similar number of nests was found in both seasons. The differences are related more to timing of egg laying and number of clutches produced (Chapter 2) than actual number of breeding pairs. Although given the absence of banded breeding pairs it is not clear if the same pairs attempted to breed in both seasons.

Other researchers have reported variability in clutch size for parrots between breeding seasons, for instance Puerto Rican Amazons *Amazona vittata* (Snyder *et al.*, 1987) and Monk Parakeets *Myopsitta monachus* (Peris and Aramburú, 1995). More commonly, a decline in clutch size towards the end of the breeding season has been noticed. Some examples are Burrowing parrots (*Cyanoliseus patagonus*) (Masello and Quilfeldt, 2004); Monk parakeets (Navarro *et al.*, 1995) and Crimson rosellas (Krebs, 1998). In the present study, neither between nor within year variation in clutch size was noticed. Furthermore, egg volume and fertility remained constant. In Psittaciformes, fertility values are reported less often than hatching success, due in part to minimum monitoring during incubation to prevent nest desertion (i.e. Heinsohn and Legge, 2003). Therefore information regarding levels of fertility in parrot species is scarce. However, the values reported here are similar to other parrot populations (Garnett et al., 1999; Renton, 1998). Similarly, the egg volumes presented here fall within the reported dimensions for other populations of red-crowned kakariki (Greene, 2003; Higgins, 1999).

Although, observed changes in reproductive success of this study population could not be explained by variation in parameters of parental investment, field

observations suggest that breeding pairs of different condition occur on Tiritiri Matangi Island. Two breeding pairs in the present study showed small clutch sizes, small eggs, low fertility values and reduced reproductive success (Chapter 5). For one of these females, this pattern was consistent over two breeding seasons therefore indicating variation in body condition and parental performance in the study population. It is therefore necessary to assess female body condition and parental behaviour and its relationship to breeding success in forthcoming studies (Chapter 5).

3.6.2 Expected reproductive success and losses

ERS showed a three-fold increase from the 2004-2005 breeding season (ERS = 0.71 ± 0.16 fledglings) to the 2005-2006 breeding season (ERS = 3.12 ± 0.37) primarily as a result of changes in the loss rates between stages of the nesting cycle. Total losses occurred in 57% of study nests in 2004-2005 whereas only 8% of nests in 2005-2006 showed total losses. Partial losses however were more common in the second year occurring in 37% of study nests. During this study, the incubation stage showed a higher loss rate than the nesting stage over both seasons, which contrasts with most studies on Psittaciformes were the nesting stage is the critical period of loss, mainly due to predation of nestlings (Gnam, 1991; Koenig, 2001; Renton and Salinas-Melgoza, 2004).

In the 2005-2006 breeding season, breeding pairs hatched more young and fledged more nestlings mainly due to the low occurrence of total loss of clutches (Table 4). Even though the occurrence of partial losses accrued in the same year, higher number of hatchlings and low occurrence of total hatching failure counterbalanced partial losses, resulting in a higher expectancy of fledglings.

In 2004-2005 causes of total nest failure included a nest which flooded following a heavy rain and a nest abandoned soon after completion of the clutch for no apparent reason. In 2005-2006 causes of total nest failure were unknown. Causes of total hatching failure especially in the first year are unclear as females remained inside the nest for a period equal or longer than normally incubating females (those that hatched young). However I collected no data on incubation behaviour and it is not clear if females were actually incubating between nest observations. However, patterns of asynchronous hatching suggest that females varied in their incubation attendance. Similar sized clutches hatched with different degrees of asynchrony indicating variation in the onset of incubation (Chapter 4).

Hatching is directly associated with incubation behaviour (Deeming, 2002; Grenier and Beissinger, 1999; Stoleson and Beissinger, 1999) and a decrease in hatching success is expected to occur due to irregular incubation (namely increase in recess times of females). The likely influences on incubation behaviour of females are related to the social environment and/or food availability. Examples related to social environment are intraspecific interference during incubation by non-breeding green-rumped parrotlets (*Forpus passerinus*) (Beissinger *et al.*, 1998; Grenier and Beissinger, 1999); crimson rosellas (Krebs, 1998) and Eclectus parrots (*Eclectus roratus*) (Heinsohn and Legge, 2003).

In the case of red-crowned kakariki, it seems unlikely that hatching failure was due to conespecific interference. First, in the referred examples above, interference is provoked by prospecting pairs due to low availability of nesting sites. In this study, red-crowned kakariki were found to use a wide range of nesting sites that do not appear to be

in short supply. Moreover, intraspecific and interspecific conflicts were rare (Chapter 2). Furthermore, it seems that red-crowned kakariki have high tolerance thresholds for intraspecific and other types of disturbance. Greene (2003) reports a pair of red-crowned kakariki entering and inspecting a cavity occupied by an incubating female. The resident female did not show signs of disturbance. During nest checks in this study, an extendable nest mirror was used in nest visits to check for the presence of the incubating female (Chapter 2). In only one nest, a female repeatedly showed signs of disturbance (short alarm calls, wing flapping) however, she did not abandon the clutch and fledged nestlings in both breeding seasons. During the current study I noticed most females perching close to the nest and emitting short alarm calls during egg measurements, but after a few seconds they would preen and stretch wings with no apparent signs of disturbance. Once the eggs were returned to the nest, all females returned to the nest. In no instances were nests abandoned due to nest inspection and moreover, nest inspections did not affect reproductive success (Chapter 2).

Two lines of evidence suggest that food availability is most likely to play a role in determining the observed differences in hatchability and reproductive success: occurrence of second clutches and a decrease in total brood failure. As mentioned in chapter 2, other *Cyanoramphus* parakeets are known to boost breeding success when food supply is abundant (Elliot *et al.*, 1996) During the present study second clutches only occurred in 2005-2006, and prospecting breeding pairs were still observed during the last day of data collection (Chapter 2). In contrast, there is no evidence of second clutches for the first year of study.

In addition, during the 2004-2005 breeding season almost 30% of nests suffered total brood failure mostly due to starvation of nestlings (Chapter 4). Only three cases of nestling deaths were not related to starvation during this study. Two cases in 2004-2005 involved broods with a single nestling which previously experienced brood reduction due to starvation. In one case, the nestling was found by the nest entrance after heavy rain. The corpse presented a full crop; however it was wet and still warm, suggesting a recent death. The other case was a nestling with deformities in the wings and neck. This nestling survived to fledgling age and was fed until the end, however eventually died. The third case of total brood failure not related to starvation occurred in 2005-2006 as a result of drowning of five nestlings. The nest chamber filled up with water during a heavy rain.

For kaka it has been suggested that shortage of high net energy food sources (honeydew) limits reproductive success (Beggs and Wilson, 1991). Furthermore, field observations indicate that kaka undertake movements, following nectar of the flowering mountain flax (*Phormium cookianum*) (J. Beggs, pers. comm. 2006); further reinforcing the view of a dependence on high-energy resources for successful reproduction.

Availability of high-energy foods allows kaka to engage in foraging of low-energy but high-protein food sources (Beggs and Wilson, 1991). Finally, for a temperate population of crimson rosellas it has been proposed that low food availability leads to reduced incubation attendance resulting in low hatching success (Krebs, 1998).

There is anecdotal information connecting food availability and reproductive success of red-crowned kakariki (Forshaw, 1989; Higgins, 1999); however no data is available for comparisons with the present study. For the red-crowned kakariki, Greene (1998) has reported a varied diet with flowers, fruits and seeds of 57 different species on

Little Barrier Island. The diet of red-crowned kakariki was not assessed in the present study, although some observations were made just prior to the 2004-2005 breeding season. During these observations, it was noticed that kakariki fed extensively on flowers and flower buds of Harakeke (*Phormium tenax*), Ti Kouka (*Cordyline australis*) and Pohutukawa (*Metrosideros excelsa*) (Appendix 4). Although, there are no data for comparisons breeding seasons. Nevertheless, 2005-2006 was considered an exceptional year of flower production by Harakeke and Ti Kouka (Velvin *et al.*, 2006) which coincided with the breeding season of kakariki. Clearly, future studies should focus on annual changes of foods of the red-crowned kakariki and in the feeding ecology of this species. If reproductive success relies on the abundance of particular high-energy resources that enhance incubation behaviour promoting a higher hatchability, those resources must be identified and their predictability and reliability included into management plans (Chapter 5).

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CHAPTER 4: HATCHING ASYNCHRONY, NESTLING GROWTH AND SEX RATIOS

4.1 ABSTRACT

Life history traits in Psittaciformes suggest that asynchronous hatching is less costly than in other avian groups. Furthermore, in some species females have the ability to bias primary sex ratios. These aspects have just started to be addressed in New Zealand parrots despite their theoretical and conservation relevance. I describe the pattern of hatching of red-crowned kakariki and present an analysis of fledgling growth in relation to natural levels of hatching asynchrony. I also present novel information on patterns of sex allocation for this species. Regardless of hatching rank, nestlings reached similar asymptotic mass, mass at fledging and tarsus length. Similarly, first, middle and last hatched nestlings showed similar rates of mass increase and wing growth. However, nestlings from highly asynchronous broods presented slower wing growth. Furthermore, third hatched nestlings had shorter wings at fledging. Last hatched nestlings showed higher mortality than other nestlings, suggesting a pattern of adaptive brood reduction. Broods were equally productive despite levels of asynchrony. Males reached higher final mass, and grew longer tarsi and wings than females. Mortality was higher for males, possibly as a result of higher metabolic demands. Primary sex ratio and sex ratio at fledging did not differ from parity; however there seemed to be a higher proportion of males in clutches laid earlier in the season. Further research is needed to determine if age of first reproduction differs between sexes in kakariki and to establish if parents obtain greater fitness returns by producing the sex that reproduces sooner, as in other species.

4.2 INTRODUCTION

Hatching asynchrony (HA) is the sequential egg-emergence of altricial or semiprecocial nestlings within a clutch. It can vary from a few hours to several days (Stoleson and Beissinger, 1997) and it is primarily controlled by the onset of incubation (Stoleson and Beissinger, 1995), although some studies have also suggested a role of sexspecific embryonic development rates in the regulation of HA (Arnold *et al.*, 2001; Blanco *et al.*, 2003). HA is present in nearly 80% of bird species, excluding precocial species (Bucher, 1983) and has been widely documented for various members of several avian orders (Beissinger and Waltman, 1991; Margalida *et al.*, 2004; Rosivall *et al.*, 2005; Wiehn *et al.*, 2000). Despite its prevalence the functional nature of HA across species is not the same. As a result, HA has received meticulous reviews (Clark and Wilson, 1981; Laaksonen, 2004; Magrath, 1988; Magrath, 1990; Slagsvold, 1990; Stenning, 1996; Stoleson and Beissinger, 1995) and around 19 hypotheses have been formulated to explain its occurrence (Laaksonen, 2004; Ricklefs, 1997; Stenning, 1996; Stoleson and Beissinger, 1995).

There is still debate on the nature and fitness benefits of HA since costs and benefits can be expressed differently in parents and offspring. For instance, broods with low HA in Eurasian kestrels (*Falco tinnunculus*) result in more and heavier fledglings than broods with high HA (Wiehn *et al.*, 2000), a clear benefit for later hatched nestlings since these attain equal asymptotic masses and fledgling success than older nest mates when hatching spans are short. However, in a closely related species, the lesser kestrels (*Falco naumanni*) survival is higher for parents rearing broods with high HA than pairs rearing more synchronous broods (Aparicio, 1997). Ricklefs (1997) emphasises that in

combination with species-specific explanations of HA, it is necessary to analyse lifehistory syndromes within monophyletic groups to disentangle the diversity of factors associated with HA. Such an analysis would identify the different levels at which the costs and fitness benefits of HA can be expressed.

HA results in chicks of different ages within the same brood. Commonly, last hatched nestlings present reduced growth and survival when compared to first-hatched nestlings. Some examples of this pattern are blackbirds (*Turdus merula*) (Magrath, 1989); marsh tits (*Parus palustris*) (Nilsson and Svensson, 1996); bearded vultures (*Gypaetus barbatus*); (Margalida *et al.*, 2004) and tree swallows (*Tachycineta bicolor*) (Johnson *et al.*, 2003). However, it has been shown that HA alone is insufficient to explain patterns of nestling growth and survival and that it is relevant to incorporate information on the sex ratio of clutches and broods as well as the sequence of sex allocation during egg laying. For instance in laughing kookaburras (*Dacelo novaeguinae*) aggression between first hatched nestlings towards second and third hatched nestlings increases if second hatched nestlings are female, aggravating the survival prospects of third hatched nestlings (Nathan *et al.*, 2001).

Psittaciformes hatch their eggs with variable degrees of asynchrony, the only exceptions being single-egg laying species such as large cockatoos (Saunders *et al.*, 1984). The degree of HA in this order ranges from a few hours to several days (Beissinger and Waltman, 1991; Greene, 2003; Krebs, 1998; Masello and Quilfeldt, 2002; Stamps *et al.*, 1985). In addition, complex patterns of sex allocation have been reported for a number of species (Clout *et al.*, 2002; Heinsohn *et al.*, 1997; Krebs *et al.*, 2002). These attributes make parrots an ideal group to explore the interaction between

HA and sex composition within broods. However, as has been pointed out through this document, several aspects of the biology of parrots are poorly studied and HA and sex ratios are no exception.

Detailed field studies of HA and sex ratios in parrots are available for two species: green-rumped parrotlets (*Forpus passerinus*), a tropical South American species, and crimson rosellas (*Platycercus elegans*), a mainly temperate Australian species. The effects of HA and its interaction with sex ratios differ between these species. In green-rumped parrotlets, later hatched nestlings grow more slowly than earlier counterparts and there is no evidence of control over the sex ratio of progeny (Budden and Beissinger, 2004; Stoleson and Beissinger, 1997). In contrast, nestling crimson rosellas have similar growth rates regardless of hatching rank. Furthermore, crimson rosellas can control the sex ratio of their progeny and tend to produce female biased broods early in the season (Krebs, 1999; Krebs *et al.*, 2002).

Even though these studies are insufficient to make generalisations regarding sex ratios it is interesting to note that for other tropical species of parrot, no control over primary sex ratios has being documented; these species are Yellow-naped amazons (*Amazona auropalliata*) (South and Wright, 2002) and Hyacinth macaws (Miyaki *et al.*, 1998). In contrast, for the kakapo, a New Zealand temperate species, there is evidence indicating control of sex ratios (Clout *et al.*, 2002). Crimson rosellas occur in tropical Australia as well (Juniper and Parr, 1998) although nothing is known in relation to sex ratios for those populations. To date only one tropical species of parrot is known to control the sex ratio of progeny: Eclectus parrots (*Eclectus roratus*) (Heinsohn *et al.*, 1997); however this information on sex ratio allocation came from captive birds and no

information regarding primary sex ratios is available from wild populations (see Heinsohn and Legge, 2003).

Krebs et al. (2002) have proposed that the costs of HA in parrots are lower than in other avian orders. Evidence in favour of this view are the patterns of food delivery observed in budgerigars (*Melopsittacus undulatus*) (Stamps *et al.*, 1987; Stamps *et al.*, 1985) and crimson rosellas (Krebs, 2001; Krebs *et al.*, 1999; Krebs and Magrath, 2000) where parents have control over food distribution and sibling competition levels are low. In both species, parents differ in their response to begging behaviour of nestlings with females allocating food on the basis of size regardless of begging intensity whereas males are more responsive to begging calls. Female allofeeding behaviour in these species has been described as a counteracting mechanism to the begging-biased feeding behaviour of males. Furthermore, parental control over rate of brood loss in parrots is a flexible mechanism; if the whole brood experience hunger, then females preferentially feed first hatched nestlings; in contrast they allocate food equally among nestlings when hunger affects only a few nestlings (Krebs and Magrath, 2000). These patterns are consistent with an adaptive strategy of brood reduction when food supplies decrease.

Field observations by Greene (2003) indicate that female red-crowned kakariki may distribute food equally among nestlings. Furthermore marked differences in fledgling production presumably related to food supply in other *Cyanoramphus* species suggest that this group exhibit a similar breeding pattern to rosellas (Chapters 2 and 3). Both genera belong to an Australo-Papuan clade (Christidis *et al.*, 1991); however their relationships at a finer scale are ambiguous. Traditionally New Zealand parakeets have been placed in the sub-familiy Platycercidae (rosellas and allies), however allozyme

studies show that the affiliation of *Cyanoramphus* to the *Platycercus* clade is unclear (Christidis *et al.*, 1991).

In this chapter, I present an analysis of asynchronous hatching in red-crowned kakariki and its relationship to nestling growth and survival during the nesting cycle. I also analysed the effects of HA on reproductive success and the consequences of clutch size, laying date and laying order on primary sex ratios for this species. This represents the second study analysing primary sex ratios for a New Zealand parrot.

4.3 OBJECTIVES

The general objective developed in this chapter is to present an overview of the variability in HA for the red-crowned kakariki and its effects on reproductive success, nestling mortality and aspects of nestling growth. It also aims to describe the relationship between clutch size, laying order and laying date on primary sex ratios for this species. The specific objectives presented here are:

- 1. Describe patterns of HA for the red-crowned kakariki
- 2. Determine the effects of hatching rank on the growth and survival of nestlings
- 3. Determine the role of sex in patterns of growth
- 4. Determine intra-clutch and fledglings sex ratios
- 5. Document the effect of variable levels of HA on reproductive success

4.4 METHODS

Study site and species are described in section 2.4, chapter 2. The present chapter contains information collected following different sampling regimes during two breeding seasons of contrasting reproductive success (Chapters 2 and 3). As a result the final data set is fragmented since it was not possible to obtain all necessary information for all broods, both seasons and all nestlings (Chapter 3). In the second year of study brood sizes were larger and it was not possible to visit the study population as often as the previous year. Therefore, to approach the different questions associated with the objectives outlined above, a series of analyses were carried out using appropriate subsets of data.

4.4.1 Clutch and brood monitoring: laying date, laying sequence and clutch size

In the 2004-2005 breeding season it was possible to document exact egg laying sequence, whereas this level of detail was not obtained in 2005-2006. For both breeding seasons, clutches were classified as being laid early, middle or late in the season.

4.4.2 Hatching sequences

During the 2004-2005 breeding season every nest was visited daily close to hatching. Once the first egg hatched, daily visits continued until hatching of the last young. Non-hatched eggs were collected (section 4.4.3). For the 2005-2006 breeding season, hatching order was determined in two ways: by opportunistic direct observation of hatching sequence as in the previous breeding season, or if more than one nestling was already hatched in a brood, hatching order was assigned by a combination of dryness of feather down, feather development, and wing length. Wing length has been shown to be a

good predictor of nestling age in a variety of species (Krebs, 1999; Saunders, 1986). Cross checks were made by looking at nestling weight of known age nestlings. The hatching ranks considered are first, middle or last hatched. Hatching ranks were assigned retrospectively by considering brood size and degree of hatching asynchrony. In the case of broods containing four or more nestlings, more than one nestling was given the hatching rank first, middle or last. For example, in a brood of six, the first two nestlings were considered first hatched, the next two middle hatched and the last two were considered last hatched. If the brood size was an odd number (i.e. 5 or 7), hatching ranks were assigned considering hatching gap (in days) from the nearest hatched nest mate. For example, if nestling "a" hatched two days after a middle nestling and one day before a last one, nestling "a" was considered a last hatched nestling.

All nestlings were given a specific mark on the head with non-toxic colour markers to allow individual identification. All nestlings were weighed to the nearest 0.01 g using a precision portable scale. During every nest check the following skeletal measurements were taken on all nestlings: wing length (right wing; from the base of humerus to tip of largest primary feather) from ages 1-25 days was measured to the nearest 0.1 mm with a dial calliper and subsequently with a plastic ruler to the nearest 1 mm and culmen length (from base of cere to tip of upper mandible) and tarsus length (right tarsus; outer joints) with a dial calliper to the nearest 0.1 mm. Nestlings were measured every other day or in some cases every three days during 2004-2005. Nestlings in 2005-2006 were measured only once a week or once every two weeks. In both years, measurements ceased when nestlings were 34-39 days old to avoid premature fledgling due to handling. Most fledglings were banded with a numbered New Zealand banding

scheme (Department of Conservation) metal D band and a unique combination of coloured plastic bands. Fledglings were banded at ages 25-39 days old (Chapter 5; Appendix 2).

4.4.3 Sex determination of nestlings and sex ratios

Egg, tissue and feather samples were collected for molecular determination of sex in 2004-2005. A total of 20 eggs failing to hatch in 2004-2005 were collected, 38 tissue samples from dead nestlings (either left or right leg) and two feathers from 17 fledglings for molecular sex determination. All samples were labelled and frozen at -20° C prior to being analysed by Allan Wilson Centre at Massey University. Nine nestlings from study nests, fledged before sampling of feathers; however these were assigned sex on the basis of culmen dimensions. Culmen length of molecularly sexed fledglings showed no overlap between males and females (mean culmen length males = 14.83 ± 0.91 SD, n= 11; mean culmen length females = 12.09 ± 0.71 SD, n=13). Morphological sexing was applied in all fledglings produced in 2005-2006.

Only broods containing no more than one un-sexed sample were included into analyses of primary sex ratios. A total of 61 sexed samples representing 11 broods were analysed. This represents 42% of all broods monitored. Sex ratios were analysed at two levels: primary sex ratios for the 2004-2005 breeding season and fledging sex ratios for both breeding seasons. Primary sex ratios were not analysed in 2005-2006 due to incomplete samples from clutches and broods. Sex ratio at fledging was determined for "group B" nestlings (see definition below).

4.4.4 Nestling growth

Analysis of growth was restricted to nestlings surviving to fledging age.

Individual growth curves for nestling mass and wing length were calculated for 13 nestlings in 2004-2005. These nestlings were the only members of broods of three or four that survived to fledging. This group of nestlings will be referred as "Group A" throughout this chapter. The logistic equation was considered adequate after trials of logistic, Gompertz and von Bertalanffy models according to Ricklefs (1967). There are other growth models available, such as the Richard's model (Richards, 1959); however those models require estimation of more parameters and are very sensitive to variability in data collection; for instance, unequal number of measurements taken for two nestlings would give different estimated values even if the nestlings are of similar age, mass and hatching rank, thus inflating the differences as a result of sampling (see Zach (1988) and Zach et al., (1984) for a discussion).

Growth curves for culmen and tarsus were initially calculated but were not included in subsequent analyses. The reason is that these structures are 36% of the final length at hatching and therefore close to the inflection point of the curve, a situation also reported for other parrot species (Renton, 1998). This proximity to asymptotic values resulted in a short plateau of the growth curves where only a few measurements could be taken and estimated values are thus unreliable (Ricklefs, 1967; Zach, 1988). Growth curves were not included for analyses of nestlings of the 2005-2006 because of the same reason. Four or less measurements per nestling were taken during that year, giving unreliable estimates of mass and wing length values. As an alternative estimates of asymptotic mass (g), mass at fledgling (g), wing and tarsus length (mm) were recorded

for fledglings in the 2005-2006 breeding season. The fit of data to the logistic model was tested using CurveExpert 1.3[©]. Due to limited sample size, nestlings of different hatching ranks and sexes were pooled (Chapter 1, Table 1.4).

4.4.5 Mortality

During every nest visit any dead nestlings were recorded. Dead nestlings were molecularly sexed only during the first breeding season and thus analysis of sex and mortality was conducted for only the 2004-2005 breeding season. The analysis was restricted to clutches were at least three eggs hatched and at least three nestlings were sexed. Finally, broods that failed due to environmental causes such as flooding were excluded (Chapter 3). A total of 30 nestlings representing eight broods were included in the analysis of pre-fledging sex specific mortality (Table 1.4, Chapter 1). Dead nestlings during the 2005-2006 could not be sexed morphologically because nestling dimorphism is noticeable at age 25 and most deaths occurred before that age.

The relationship between mortality and hatching rank was explored on a larger sample size since sex of nestlings is not required to assign hatching ranks. Only broods with at least one nestling per hatching rank category (first, middle, last) were included. Broods were excluded from analysis if mortality was the result of environmental factors (Chapter 3). A total of 96 nestlings representing 16 broods were included in the analysis of mortality per hatching rank. These 16 broods were also assigned one category of HA: low, medium or high. Number of fledglings and number of dead nestlings per HA category were compared (Table 1.4, Chapter 1).

4.4.6 Analyses

Normality of data sets was tested with Shapiro-Wilks test in SAS PROC UNIVARIATE Version 8°. When the data did not fulfil assumptions of parametric tests, alternative non-parametric tests were applied. All statistical tests were completed in SAS Version 8°. To describe natural levels of HA in the red-crowned kakariki, data on the degree of HA for 22 broods is presented; however statistical analysis only included 16 broods with at least three nestlings.

Primary sex ratios and sex ratio at fledging (proportion of males in both cases) where analysed by the binomial test (Wilson and Hardy, 2002) (Chapter 1, Table 1.4) using SAS PROC FREQ. To explore the relationship between, laying date, laying order and nestling sex, I used a logistic regression in SAS PROC LOGISTIC using the default logit matrix link function (SAS Institute; www.sas.com). Laying order and laying date were included as independent explanatory variables with a binary coded response variable (sex). A more comprehensive analysis of the factors influencing nestling sex would include more variables such as nest, breeding season, clutch size, egg volume and fertility (a hierarchical mixed model). However, trying to fit such a model converged into a non-positive Hessian matrix in SAS PROC MIXED resulting in uncertainty regarding fit of the general model and selection of the best sub-model, therefore a logistic regression was used as an alternative. Laying date and laying order where the only variables that meet the convergence criteria in SAS Version 8°C.

Analyses of HA and its effects on growth and survival of nestlings were done in two ways. First, for group A nestlings growth curves were calculated (section 4.4.4) allowing the estimation of the following variables: asymptotic mass (g), final mass (g) mass

increase (g ^{day}), asymptotic wing length (mm), growth rate for wing (mm ^{day}), mass loss after asymptote (g), time interval between 10 to 90% of asymptotic mass (t_{10-90} mass) and time interval between 10 to 90% of asymptotic wing length (t_{10-90} wing). Time intervals between 10 to 90% of asymptotic values were calculated as: $t_{10-90} = 4.4$ / k where k is the constant rate of growth from the logistic curve (Ricklefs, 1976).

Mass increase and growth rate for wing refer to the average increase in mass and wing length during the linear portion of the growth curve. These measures were chosen because they are easier to interpret and are biologically more informative than inflection points or growth constants (k) (Krebs, 1999).

Second, the variables asymptotic mass (g), mass at fledgling (g), wing and tarsus length (mm) were contrasted between 59 nestlings produced during the two years of this study. This group of nestlings contains group A nestlings and all the fledglings from broods with at least three fledglings from the 2005-2006 breeding season. These 59 nestlings will be referred as "Group B". All nestlings were assigned to broods with low, medium or high degree of HA. The levels considered take into account the time elapsed between first to last hatchlings, giving the categories low HA= 2-4 days; medium= HA 5-8 days and high HA= 9-13 days. Furthermore, nestlings were assigned to one of three brood sizes: small = 3-4 nestlings; medium = 5-6 and large = 7 nestlings. Finally, nestlings were classified according to laying date. The breeding season was divided into three parts and thus, relative laying dates were assigned accordingly. Early laid clutches contain those laid between 30th of November to 20th of December; middle laid clutches were those laid between 23rd of December to 13th of January and late laid clutches those laid from the 15th of January onwards. All broods considered for analyses were laid early

or middle in the breeding season. No nestlings from late laid clutches were available for comparisons.

The structure of the combined data set resulted in a mixed hierarchical, nested design with fixed (i.e. hatching rank, level of HA) and random (brood) effects. Initially, data collection was organized to satisfy the assumptions of this design. Initial trials were made to fit a mixed model using SAS[©] and R[©] statistical software; however several difficulties were found. First, the data set was heavily unbalanced. For instance, different number of broods per season, different number of first hatched nestlings within broods etc. Even though mixed models are more suitable for unbalanced data than ordinary glm (Wolfinger and Chang, 1995) non-convergence into a positive Hessian matrix due to collinearity of variables (Verbeke and Molenberghs, 1997) and unbalance of the data (SAS Institute Notes 2005; www.sas.com) caused problems of model fitting and selection. Therefore, an alternative approach using separate models for each variable was taken. The main disadvantage is the inability of this approach to examine interaction terms. One way ANOVAs, Kruskal-Wallis tests, Wilcoxon-Mann-Whitney two sample tests and two sample t-tests were conducted in SAS PROC GLM and SAS PROC NPAR1WAY. Decision of parametric or non-parametric models was based on normality of data.

Mortality between nestlings of different hatching rank was analysed using a Chisquare test in SAS PROC FREQ. Number of fledglings and number of dead nestlings between broods with different levels of HA were compared using Kruskal-Wallis Tests.

4.5 RESULTS

4.5.1 Patterns of hatching

Red-crowned kakariki broods presented a variable pattern of hatching. Hatching asynchrony ranged from one to 13 days between first and last hatched nestlings but females varied in the time they took to hatch the same number of nestlings (Figure 4.1).

4.5.2 Primary sex ratios, sex ratio at fledging and effects of laying date and laying order

No biases in the proportion of males were found. The primary sex ratio of 11 broods containing 61 nestlings consisted of 34 males and 27 females, a 55:44 sex ratio, a non-significant deviation from 0.50 (binomial test P = 0.44). Similarly, at fledgling the proportion of both sexes was similar; a total of 26 males fledged vs 33 females, a 44:55 sex ratio. Once again, the proportion of males did not differ significantly from 0.50 (binomial test P = 0.43).

The proportion of males appeared high for early and middle laid clutches but comparatively low for last laid clutches (Figure 4.2) (Table 4.1). Nevertheless the difference did not reach significance (Wald Chi-square 10.95, P > 0.35). The proportion of males did not change significantly between first, middle or last laid eggs (Wald Chi-square 0.53, P > 0.46) (Table 4.1).

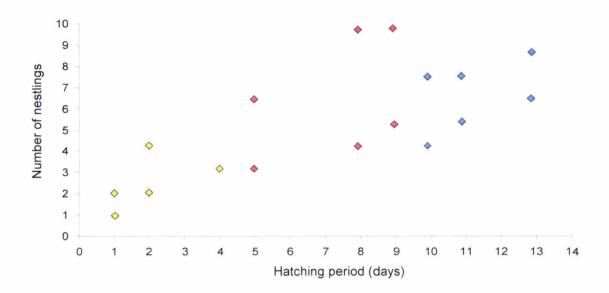


Figure 4.1 Hatching periods for broods of the red-crowned kakariki. Data points represent broods from 2004-2005 and 2005-2006. Data points may represent more than one brood. Low HA (yellow); medium HA (red); high HA (blue).

Table 4.1. Primary sex ratio of 11 clutches of the red-crowned kakariki on Tiritiri Matangi Island in relation to laying date and laying order. 2004-2005 breeding season. Statistic χ^2 refers to Wald Chi-square.

	Laying date/Laying order				
	Early	Middle	Late	Statistic	P
Proportion of males	0.52381	0.645833	0.303571	$\chi^{2}_{2} = 0.20$	P > 0.35
	First	Middle	Late	Statistic	P
Proportion of males	0.6	0.318182	0.578947	$\chi^2_2 = 0.53$	<i>P</i> > 0.46

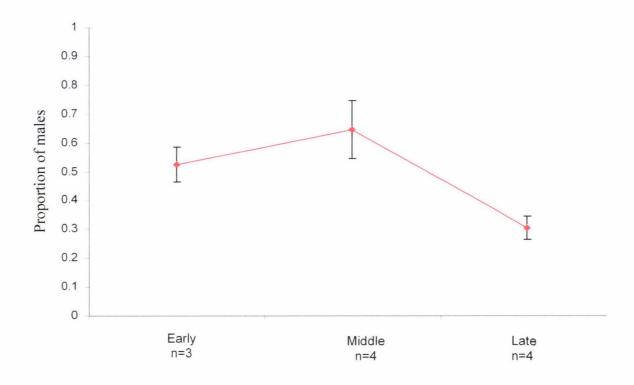


Figure 4.2 Proportion of males in a clutch according to laying date. Clutches laid in the 2004-2005 breeding season. Data points represent means \pm SE.

4.5.3 Nestling growth curves

The logistic model provided a good fit for mass increase and wing growth (mass increase r=0.96; wing growth r=0.98) (Figure 4.3). Body mass reached an asymptotic mean value of 92.24 ± 2.4 g. This mass was attained at an age of 31 ± 1.52 days. Maximum wing length was 151.46 ± 3.5 mm and was reached at an age of 37 ± 0.82 days (Table 4.2). After reaching asymptotic mass, nestlings showed mass recession (Table 4.3) and mass at fledging was approximately 90 to 95% of asymptotic mass.

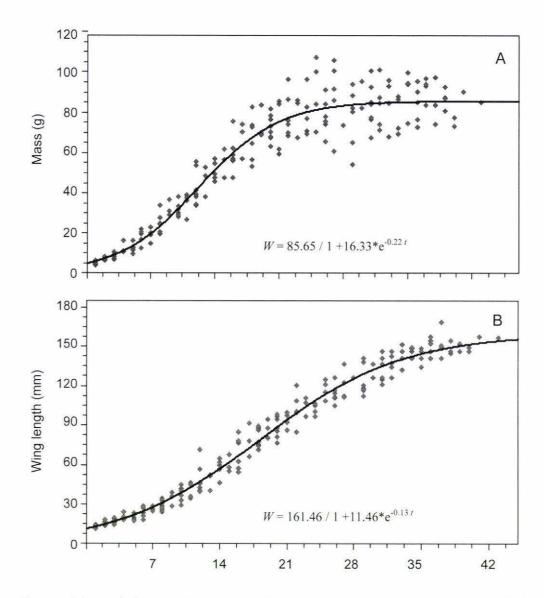


Figure 4.3. Logistic growth curves for 13 nestlings of the red-crowned kakariki. Sexes and hatching ranks combined. A) Mass gaining; B) Wing length.

4.5.4 Effects on nestling growth

Group A nestlings

For group A nestlings (13 fledglings from the 2004-2005 breeding season) there were no statistically significant differences between hatching ranks in asymptotic mass, final mass, mass increase, asymptotic wing length, growth rate for wing, mass loss after asymptote, time interval from 10 to 90% of mass asymptote or time interval from 10 to 90% of wing asymptote (Table 4.3). Regarding HA, nestlings from broods with medium HA seemed to have higher growth rates for wing than nestlings from broods with high HA (Growth rate for wing: broods with low HA = 4.78 ± 0.15 mm^{day} broods with high HA = 3.60 ± 0.11 mm^{day}), but the difference only approached significance (Two sample t-Test $t_2 = 2.16$, P = 0.053). No statistically significant differences were found in relation to HA and asymptotic mass, final mass, asymptotic wing length, mass loss after asymptote, time interval from 10 to 90% of mass asymptote or time interval from 10 to 90% of wing asymptote (Tables 4.4).

Table 4. 2. Variation in growth for 13 nestlings of the red-crowned kakariki on Tiritiri Matangi Island.

		Ran	ige
	Mean ± SE	Min.	Max.
Asymptotic mass (g)	92.24 ± 2.4	74.21	107.1
Time to attain asymptotic mass (g)	31 ± 1.52	22	38
Asymptotic wing length (mm)	151.46 ± 3.5	114	170
Time to attain asymptotic wing length (mm)	37.46 ± 0.82	32	43

Group B nestlings

For nestlings of group B (group A fledglings and fledglings from the 2005-2006 breeding season), the effects of HA, brood size, hatching rank, laying date and sex of nestlings were inconsistent across the chosen response variables: the degree of HA affected mass but no skeletal measurements. Nestlings from broods with low HA tended to have higher asymptotic values of mass than nestlings from broods with medium to high levels of HA, but the difference was only marginally significant (Kruskal-Wallis test χ^2 = 5.90, P = 0.052). In contrast, mass at fledgling of nestlings from broods with low HA was significantly higher than other HA classes (Kruskal-Wallis test χ^2 = 6.37, P < 0.05). No other measure of chick growth differed between HA classes (Table 4.5).

Hatching rank affected measures of mass and skeletal measurements. First hatched nestlings tended to have higher asymptotic and final masses. The differences however, only approached significance (Kruskal-Wallis test asymptotic mass $\chi^2_2 = 4.21$, P = 0.12; Kruskal-Wallis test final mass $\chi^2_2 = 5.32$, P = 0.06). Culmen and wing were larger in first hatched nestlings than other hatching ranks (Kruskal-Wallis culmen test $\chi^2_2 = 10.35$, P < 0.01; Kruskal-Wallis wing test $\chi^2_2 = 7.39$, P < 0.01) (Table 4.6).

Brood size affected only one skeletal measurement: wing length. Nestlings from small broods showed longer wings at fledgling than counterparts from medium or small broods (Kruskal-Wallis test $\chi^2_2 = 7.39$, P < 0.05). All other measures of nestling size and weight did not differ across brood sizes (Table 4.7).

Laying date did not affect either mass or skeletal measurements of nestlings (Table 4.8). In contrast, sex of nestlings had a significant effect in all measurements considered. Males showed higher asymptotic masses (Kruskal-Wallis wing test χ^2 ₁ =

4.67, P < 0.01), higher final masses (Kruskal-Wallis wing test $\chi^2_1 = 4.47$, P < 0.01), longer tarsus (Kruskal-Wallis wing test $\chi^2_1 = 4.07$, P < 0.01 and longer wings than females (Kruskal-Wallis wing test $\chi^2_1 = 2.93$, P < 0.01) (Table 4.9).

Table 4.3. Effects of hatching rank on variables describing growth for group A nestlings . Statistic χ^2 refers to Kruskal-Wallis tests; F statistic refers to one-way ANOVA. Values are means \pm SE.

		Hatching Rank			
	First hatched (n=4)	Middle hatched (n=4)	Last hatched (n=5)	Statistic	P
Asymptotic mass (g)	93.20 ± 1.13	90.58 ± 4.80	91.69 ± 5.47	$\chi^2_2 = 0.17$	P > 0.91
Final mass (g)	88.08 ± 1.33	86.67 ± 5.25	82.58 ± 7.74	$\chi^2_{2} = 0.11$	P > 0.94
Mass increase (g day)	3.94 ± 0.20	3.63 ± 0.37	4.06 ± 0.27	$\chi^2_{2} = 1.20$	P > 0.54
Asymptotic wing length (mm)	153.75 ± 2.78	159 ± 4.21	144 ± 7.92	$\chi^2_{2} = 0.34$	P > 0.34
Growth rate for wing (mm ^{day})	4.49 ± 0.23	4.63 ± 0.33	4.74 ± 0.26	$F_2 = 0.20$	P > 0.81
Mass loss after asymptote (g)	29. 57 ± 2.27	5.89 ± 1.49	13.08 ± 3.73	$\chi^2_{2} = 1.73$	<i>P</i> > 0.42
t ₁₀₋₉₀ mass (days)*	24.04 ± 3.19	25.63 ± 5.43	25.43 ± 2.97	$\chi^2_{2} = 0.17$	P > 0.91
$t_{10.90}$ wing (days)*	22.24 ± 1	26.72 ± 1.61	29.47 ± 1.72	$\chi^2_{2} = 0.79$	<i>P</i> > 0.67

^{*} Time interval from 10 to 90 % of asymptotic value

Table 4.4 Effects of levels of hatching asynchrony on variables describing growth for group A nestlings. Statistic Z refers to Wilcoxon-Mann-Whitney two sample test; t refers to Two sample t-test. Values are means \pm SE. P values less than 0.10 in bold.

	Hatching a	synchrony		
	Medium (n=2)	High (n=2)	Statistic	P
Asymptotic mass (g)	91.29 ± 0.67	95.06 ± 3.09	$Z_1 = 0.53$	P > 0.59
Final mass (g)	94.86 ± 2.31	82.73 ± 3.73	$Z_1 = 0.08$	P > 0.99
Mass increase (g day)	3.98 ± 0.18	3.60 ± 0.38	$Z_1 = 0.92$	P > 0.35
Asymptotic wing length (mm)	150 ± 2.90	153 ± 4.60	$Z_1 = 0.10$	P > 0.91
Growth rate for wing (mm day)	4.78 ± 0.15	3.60 ± 0.11	$t_1 = 2.16$	P = 0.053
Mass loss after asymptote	17.73 ± 3.79	12.04 ± 2.30	$Z_1 = 0.10$	P > 0.91
t ₁₀₋₉₀ mass (days)*	25.46 ± 3.16	22.83 ± 2.58	$Z_1 = 0.10$	P > 0.91
t ₁₀₋₉₀ wing (days)*	25.57 ± 1.06	30.38 ± 0.66	$Z_1 = 1.18$	<i>P</i> > 0.23

^{*} Time interval from 10 to 90 % of asymptotic value

Table 4.5. Effects of hatching asynchrony on nestling growth (group B nestlings). Statistic χ^2 refers to Kruskal-Wallis tests. Values are means \pm SE. P values less than 0.10 in bold.

	Low HA (n=7)	Medium HA (n=10)	High HA (n=8)	Statistic	P
Asymptotic mass (g)	105.59 ± 3.53	92.30 ± 1.85	95.25 ± 2.37	$\chi^2_2 = 5.90$	P = 0.052
Final mass (g)	99.94 ± 3.14	85.45 ± 2.23	85.90 ± 2.30	$\chi^2_2 = 6.37$	P < 0.05
Asymptotic culmen length (mm)	14.50 ± 0.28	12.86 ± 0.26	13.29 ± 0.28	$\chi^2_2 = 4.54$	<i>P</i> > 0.10
Asymptotic tarsus length (mm)	25.25 ± 0.28	24.36 ± 0.30	24.37 ± 0.24	$\chi^2_{2} = 2.22$	<i>P</i> > 0.32
Asymptotic wing length (mm)	142 ± 5.21	146.88 ± 2.59	138.53 ± 2.80	$\chi^2_2 = 4.92$	P > 0.08

Table 4.6. Effects of hatching rank on nestling growth (group B nestlings). Statistic χ^2 refers to Kruskal-Wallis tests. Values are means \pm SE. P values less than 0.10 in bold.

		Hatching Rank			
	First hatched (n=19)	Middle hatched (n=20)	Last hatched (n=20)	Statistic	P
Asymptotic mass (g)	99.20 ± 2.62	95.88 ± 2.29	89.25 ± 3.14	$\chi^2_2 = 4.21$	P >0.12
Final mass (g)	91.59 ± 2.48	86.74 ± 2.29	$81.89 \pm \ 3.13$	$\chi^2_2 = 5.32$	P > 0.06
Asymptotic culmen length (mm)	13.64 ± 0.33	13.63 ± 0.25	12.31 ± 0.33	$\chi^2_2 = 10.35$	P < 0.05
Asymptotic tarsus length (mm)	24.71 ± 0.26	24.64 ± 0.29	23.94 ± 0.34	$\chi^2_2 = 3.48$	P > 0.17
Asymptotic wing length (mm)	148.36 ± 2.37	147.80 ± 1.91	131.05 ± 3.65	$\chi^2_2 = 16.47$	P < 0.01

Table 4.7. Effects of brood size on variables describing growth for group B nestlings. Statistic χ^2 refers to Kruskal-Wallis tests. Values are means \pm SE. P values less than 0.10 in bold.

		Brood size			
	Small (n=4)	Medium (n=8)	Large (n=3)	Statistic	P
Asymptotic mass (g)	92.79 ± 3.09	93.24 ± 2.29	99.45 ± 2.56	$\chi^2_2 = 2.74$	P > 0.25
Final mass (g)	83.04 ± 3.23	86.94 ± 2.33	89.73 ± 2.83	$\chi^2_2 = 2.02$	P > 0.36
Asymptotic culmen length (mm)	13.09 ± 0.35	12.82 ± 0.26	14.01 ± 0.37	$\chi^2_2 = 4.93$	P > 0.08
Asymptotic tarsus length (mm)	24.38 ± 0.43	24.37 ± 0.26	24.59 ± 0.26	$\chi^2_{\ 2}=0.09$	P > 0.95
Asymptotic wing length (mm)	149 ± 3.46	139 ± 2.68	141.40 ± 3.52	$\chi^2_2 = 7.39$	P < 0.05

Table 4.8. Effects of laying date on growth for group B nestlings. Statistic Z refers to Wilcoxon-Mann-Whitney two sample test. Values are means \pm SE.

	Early (n=30)	Middle (n=29)	Statistic	P
Asymptotic mass (g)	95.81 ± 1.89	93.56 ± 2.51	$Z_1 = 0.78$	P > 0.43
Final mass (g)	87 ± 1.81	86 ± 2.69	$Z_1 = 0.24$	P > 0.80
Asymptotic culmen length (mm)	13.08 ± 0.27	13.30 ± 0.27	$Z_1 = 0.42$	P > 0.66
Asymptotic tarsus length (mm)	24.56 ± 0.25	24.28 ± 0.25	$Z_1 = 0.63$	<i>P</i> > 0.52
Asymptotic wing length (mm)	141.06 ± 2	143.58 ± 3.19	$Z_1 = 0.37$	P > 0.70

Table 4.9. Effects of nestling sex on growth for group B nestlings. Statistic Z refers to Wilcoxon-Mann-Whitney two sample test. Values are means \pm SE. *P* values less than 0.10 in bold.

	Se	ex			
	Male (n=26)	Female (n=33)	Statistic	P	
Asymptotic mass (g)	102.69 ± 1.76	88.41 ± 1.78	$Z_1 = 4.67$	P < 0.01	
Final mass (g)	94.23 ± 1.76	80.69 ± 1.96	$Z_1 = 4.47$	P < 0.01	
Asymptotic culmen length (mm)	14.60 ± 0.15	12.08 ± 0.14	$Z_1 = 6.57$	<i>P</i> < 0.01	
Asymptotic tarsus length (mm)	25.27 ± 0.18	23.76 ± 0.22	$Z_1 = 4.07$	P < 0.01	
Asymptotic wing length (mm)	148.92 ± 1.98	137.09 ± 2.68	$Z_1 = 2.93$	P < 0.01	

4.5.5 Nestling mortality and reproductive success

A total of 30 nestlings died (31%). Mortality was higher for males than females, however the difference was not statistically significant (dead males = 73%; dead females = 26%; Chi-square test χ^2 ₁ = 1.29, P > 0.25) (Figure 4.2a). Mortality was associated with hatching rank and was higher for last hatched nestlings, 73% of dead nestlings were last hatched in contrast to 23% middle hatched and only 0.03% first hatched nestling (Chi-square test χ^2 ₂ = 30.37, P < 0.01) (Figure 4.2b).

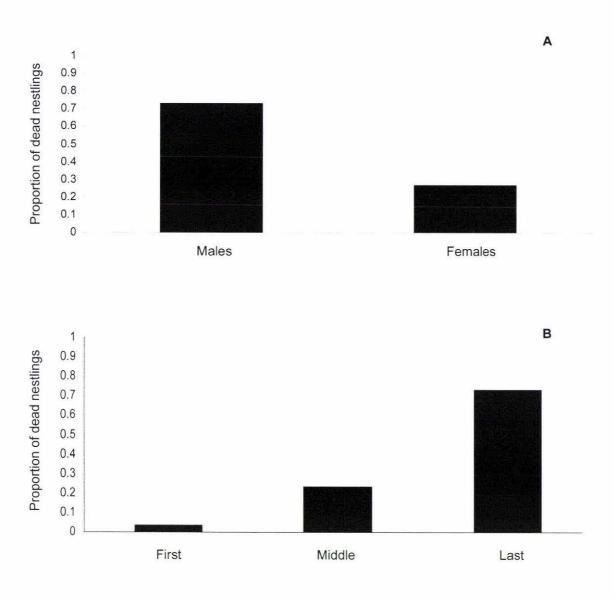


Figure 4.2. Mortality among nestlings of the red-crowned kakariki. A) Mortality according to sex. B) Mortality in relation to hatching rank.

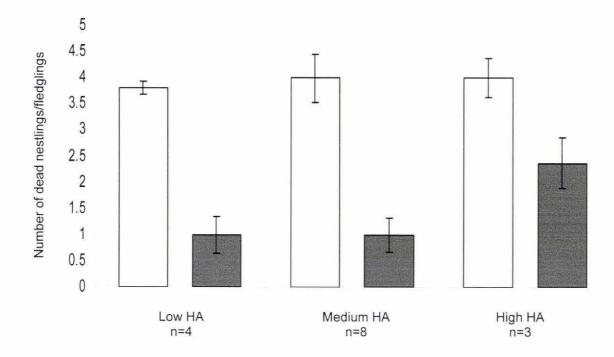


Figure 4.3. Relationship between levels of hatching asynchrony, mortality and number of fledglings in the red-crowned kakariki. White bars=number of fledglings; grey bars=number of dead nestlings. Values are means \pm SE.

Number of dead nestlings appeared to be higher for broods with high HA, however the difference did not reach significance (number of dead nestlings: broods with low HA = 1 ± 0.35 SE; broods with medium HA = 1 ± 0.33 SE; broods with high HA = 2.37 ± 0.48 SE; Kruskal-Wallis test χ^2 $_2$ = 1.75, P > 0.41). Likewise, broods with different degrees of HA produced a similar number of fledglings (number of fledglings: broods with low HA = 4 ± 0.12 SE; broods with medium HA = 4.14 ± 0.46 SE; broods with high HA = 3.87 ± 0.3 SE; Kruskal-Wallis χ^2 $_2$ = 0.29, P > 0.86) (Figure 3).

4.6 DISCUSSION

4.6.1 Hatching asynchrony and nestling growth

The results presented here reveal the following attributes of the breeding biology of red-crowned kakariki: variable degrees of hatching asynchrony, high nestling mortality associated with hatching rank, similar measures of growth and time to complete portions of the growth curve between nestlings of different hatching ranks, and a marked difference in mass and skeletal measurements between sexes. These characteristics partially agree with results from studies in other parrots. For example, in crimson rosellas there is constancy in measures of growth regardless of degree of hatching asynchrony and hatching rank of nestlings. However, in crimson rosellas mortality rates are similar between hatching ranks (Krebs, 1999), contrasting with the findings of the present study. For the red-crowned kakariki, mortality was higher for last hatched nestlings and only rarely occurred to first hatched nestlings. In green-rumped parrotlets, nestlings from

experimentally synchronised broods showed only slight differences in weight at fledging when compared with nestlings from asynchronous broods and weight at fledging varied little between hatching ranks (Stoleson and Beissinger, 1997). In the same species, mortality was higher for later hatched nestlings and these died due to starvation. These observations resemble the present study, where nestlings of different hatching ranks exhibited similar rates of growth for mass and wing (group A nestlings) and reached similar asymptotic mass and mass at fledging (group A and group B nestlings). Also, there was a clear trend in mortality towards later hatched nestlings and starvation was the main cause of death. However the sample size is limited and it would be necessary to sample a larger number of broods and to estimate growth rates across a more representative sample of nestlings between breeding seasons in order to make more conclusive statements.

There was a clear difference in nestling mass and skeletal measurements according to sex and these appear to be more significant than hatching position within the brood. Regardless of hatching rank, males attained higher asymptotic mass, final mass, tarsus, culmen and wing length. However, the interaction between hatching rank and sex could not be fully resolved with the tests applied in the present analysis and research is required to quantify the effect of sex and hatching rank within broods presenting different degrees of hatching asynchrony.

Reproductive success and the number of dead nestlings in broods of red-crowned kakariki did not change according to the degree of hatching asynchrony. However this may partially be due to limited data of breeding seasons and clearly monitoring over more breeding seasons is required to determine the influence of hatching asynchrony on

reproductive success. In American kestrels (*Falco sparverius*) changes in food availability between breeding seasons affect the degree of hatching asynchrony and influence reproductive success (Wiebe and Bortolotti, 1994). The data set for red-crowned kakariki included an unequal number of broods per breeding season. More broods from 2005-2006 were included and given that this was a year of higher reproductive success it is possible that the effect of hatching asynchrony was ameliorated. Furthermore, only three broods with high hatching asynchrony were available for analysis, limiting the explanatory power of the statistical tests performed.

Variability in the effects of hatching asynchrony between breeding seasons has been repeatedly reported in natural populations of parrots and in numerous passerine birds (Martin, 1987). In the temperate burrowing parrot (*Cyanoliseus patagonus*), nestlings exhibit variation in growth according to hatching rank and mortality is related to hatching rank (Masello and Quilfeldt, 2002) and the effects of hatching asynchrony are accentuated during years of low rainfall (Masello and Quilfeldt, 2004). Similarly, in *Calyptorhynchus* cockatoos parents can raise larger broods under favourable conditions of food supply, but fail to do so in adverse years (Garnett *et al.*, 1999; Saunders, 1986). Thus, it is reasonable to suggest that the observed similarity in growth parameters of redcrowned kakariki nestlings reflect a pattern of growth in a breeding season with high food availability. Given that nestlings of the breeding season with presumably lower food availability were under-represented in the analysis, the effects of hatching asynchrony and hatching rank may be underestimated and a more representative sampling is necessary prior to more conclusive statements.

4.6.2 Significance of brood reduction in red-crowned kakariki

The results presented here suggest a breeding strategy of adaptive brood reduction (Lack, 1968). This hypothesis regards food supply and parental ability for food provisioning as determinants of reproductive success. Under conditions of limited food supply, less competitive nestlings will starve and the brood will be "trimmed" to the optimum number that parents can successfully raise. This "trimming" of the brood most likely will start with the youngest nestling, given its inferior competitive abilities. In times of abundant food supply, the effects of hatching asynchrony are predicted to be lower given that parents might be more efficient foragers. As discussed in chapter 3, starvation of nestlings was higher in 2004-2005 than in 2005-2006. Furthermore, the number of fledglings produced in 2005-2006 increased suggesting that 2005-2006 was a breeding season with higher food supply.

There are numerous studies in favour of the brood reduction hypothesis (Clark and Wilson, 1981; Magrath, 1990), however support for this hypothesis is not unanimous (Stenning, 1996) given that other factors might be more crucial than food availability to determine reproductive success. For instance, inexperienced Brown thornbills (*Acanthiza pusilla*) are less likely to raise fledglings than individuals with previous breeding experience due to limited food provisioning skills (Green, 2001) rather than limited food availability. Differences in reproductive success of parrots associated to lack of breeding experience has been documented in the field and in experimental situations (Stone *et al.*, 1999; Wilson *et al.*, 1997) but has not been evaluated in New Zealand *Cyanoramphus* and clearly requires investigation.

4.6.3 Sex ratios

The data on nestling growth suggest that male red-crowned kakariki might be more costly to rise than females. Although I did not quantify the costs of raising nestlings of different sexes, males reached higher asymptotic mass, asymptotic tarsus and wing and it is reasonable to expect they would have higher energetic requirements than females (Stark and Ricklefs, 1998). In support of this view, adult red-crowned kakariki are slightly size dimorphic, with males being about 10% heavier than females and around 15% larger (Forshaw, 1989; Higgins, 1999). Furthermore, males suffered higher mortality, which possibly reflects higher energetic requirements and therefore higher susceptibility to food deprivation than females (Teather and Weatherhead, 1988; Weatherhead and Teather, 1991). Failure to reach significance of sex-biased mortality between nestlings was clearly an effect of limited sample size. A test carried out with hypothetical data reached significance when the sample size increased to 60 nestlings keeping proportion of dead males and females identical to the test presented in section 4.5.3. (Chi square test hypothetical data, $\chi^2_1 = 2.58$, P = 0.10, n = 60).

It has been proposed that in size dimorphic species, the costs of rearing males and females vary and that females will obtain greater benefits by adjusting reproductive effort to current conditions of resource availability (Trivers and Willard, 1973). Therefore, individuals of low condition or in years of low resource availability would maximise their reproductive effort by producing more individuals of the less costly sex (Tella, 2001; Trivers and Willard, 1973; Whittingham and Dunn, 2000) or by "trimming" the more costly sex (*i.e.* males) via brood reduction (Maynard-Smith, 1980).

In the current study this sex biased cost would predict a higher proportion of females during 2004-2005 given that presumably it was a breeding season of lower resource availability (Chapter 3). However, no bias was detected either at the clutch level or at the fledgling level. However, calculation of sex ratios was restricted to a group of clutches where sexing was successful and sample size is crucial in determining sex ratio biases (Ewen *et al.*, 2004; Ewen *et al.*, 2001; Hardy, 2002), thus sex ratio manipulation in red-crowned kakariki remains unresolved until a larger number of clutches is successfully sexed.

It is also possible that the fitness benefits to breeding females are of a different nature. For instance, in crimson rosellas there is a relationship between laying date, laying order and proportion of females in a clutch. Females are produced early in the breeding season and in the laying sequence (Krebs *et al.*, 2002). In contrast, males became more common towards the end of the breeding season. It has been proposed that this differential production of sexes maximizes fitness benefits for breeding pairs because females can reproduce as yearlings whereas males reproduce as two-year olds. Therefore, the pattern of sex allocation in crimson rosellas reflects a trade-off between costs and benefits of rising males and females at different stages of the breeding cycle (Krebs *et al.*, 2002).

It is not clear if breeding opportunities differ between male and female redcrowned kakariki. In captivity both sexes appear to breed at less than one year old (Higgins, 1999) but field data are missing. Although non-significant, there was a higher proportion of males in clutches laid early and middle in the breeding season. Of relevance is the observation that a male nestling born in January 2005 started breeding in December 2005 at 11 months of age (band combination ry-m, Appendix 5). Research is needed to resolve if age of first breeding differs between male and female red-crowned kakariki and if breeding pairs obtain greater fitness benefits by rising males at the beginning of the breeding season.

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CHAPTER 5: THE BREEDING ECOLOGY OF RED-CROWNED KAKARIKI IN
THE CONTEXT OF PARROT STUDIES, MANAGEMENT RELEVANCE AND
FUTURE DIRECTIONS FOR RESEARCH

5.1 ABSTRACT

The breeding ecology of red-crowned kakariki presents unique features among Psittaciformes. Even though some attributes are shared with related genera and members of Cyanoramphus, the combination of characteristics outlined in this study has not been documented for any other parrot species. In particular, red-crowned kakariki are remarkable in the diversity of nesting sites they use and in incubation being the main period of nesting loss. Results from this project and evidence from other studies suggest that red-crowned kakariki are a suitable candidate for translocation to fragmented areas or in early regeneration stages. Plant composition and abundance should also receive attention as it seems that food availability greatly influences reproductive success. Experience and health condition of breeding pairs may also be important predictors of reproductive success but additional research aimed to fully evaluate the role of these attributes into the reproductive performance of red-crowned kakariki is needed. A pilot study conducted using video cameras indicate differences in food allocation between males and females as shown for other parrot species. Due to the high theoretical relevance of this issue and its applicability into conservation research in this area must follow. It is also necessary to explore the possibility of nestling harvest for translocation purposes given the high death rate of later hatched nestlings. Finally research is required to further explore the relationship between laying date and sex allocation within clutches.

5.2 Breeding biology among Psittaciformes

The order Psittaciformes is a monophyletic, ancient and morphologically homogeneous group whose close living relatives are obscure (Dyke and Cooper, 2000; Harrison *et al.*, 2004; Miyaki *et al.*, 1998; Ribas *et al.*, 2005; Sibley and Alquist, 1990). Below the order level the systematics are unresolved and troublesome, although several efforts have clarified the position of particular sub-groups (Boon *et al.*, 2000; Joseph and Wilke, 2006; Rusello and Amato, 2004; Tavares *et al.*, 2004). In addition, various new taxa have been recently described (Gaban-Lima *et al.*, 2002; Maijer *et al.*, 1998; O'Neill *et al.*, 1991; Silveira *et al.*, 2005).

Even though the reproductive ecology of Psittaciformes remains insufficiently documented, studies to date provide an overview of the diversity of breeding patterns within the order. Most species studied in the wild have biparental care during the nesting cycle, and usually females are solely responsible for incubation, for example black and yellow-billed amazons (*Amazona agilis* and *A. collaria* respectively) (Koenig, 2001). However, in various cockatoo species, males alternate incubation with females, like in Major Mitchell Cockatoos (*Cacatua leadbeateri*) (Rowley and Chapman, 1991).

The majority of species form long-lasting pair bonds and the pair is the basic social unit, although there are some exceptions such as cooperatively breeding monk parakeets (*Myopsitta monachus*) (Eberhard, 1998a) and Eclectus parrots (*Eclectus roratus*) (Heinsohn and Legge, 2003) and communal breeders such as golden conures (*Guaruba guaruba*) (Oren and Novaes, 1986). Mating systems are also diverse within the order. Psittaciformes are mostly socially monogamous although cases of extra-pair paternity have been reported (*e.g.* golden conures (Becker *et al.*, 1997). However,

genetic monogamy has only rarely been assessed in wild populations (Masello and Quilfeldt, 2002) and thus the extent of extra-pair paternity remains unclear. Polygamy has been documented for kea (*Nestor notabilis*) and polyandry for Vasa parrots (*Coracopsis vasa*) (Wilkinson, 1994). The most extreme mating system documented to date is the lek system of kakapo (*Strigops habroptilus*) (Merton *et al.*, 1984).

As discussed in chapter 2, most parrots are cavity nesters and normally they make use of cavities excavated by other species or formed by insect and fungus activity (Forshaw, 1989). Secondary cavity use is the ancestral state of the order (Brightsmith, 2005b) and transitions to alternative nesting sites have occurred a number of times within the group (Eberhard, 1997). A few species construct nests such as monk parakeets and lovebirds (Agapornis sp.) (Eberhard, 1997; Eberhard, 1998b) and the Pesquet parrot (Psittrichas fulgidus) is unique in its habit of excavating its own nests (Igag, 2002). Not only dependence of hollows for nesting but also a high territoriality and guarding around the nest have been noticed. Female Eclectus parrots have been reported to guard a nest several months before the beginning of the breeding season (Heinsohn and Legge, 2003). Likewise, galahs (Eolophus roseicapillus) attend nesting hollows outside the breeding season (Rowley, 1990). Moreover, nest defence displays have been recorded outside the breeding season for Palm cockatoos (Probosciger aterrimus) (Murphy et al., 2003). As a consequence several studies have highlighted the importance of nesting sites as a key element in species conservation and recovery (Brightsmith, 2005c; Heinsohn and Legge, 2003; Igag, 2002; Marsden and Pilgrim, 2003; Monterrubio-Rico and Enkerlin-Hoeflich, 2004; Murphy et al., 2003; White and Vilella, 2004).

In general, the nestling stage is the main period of loss and predation has been identified as an important cause of loss for in Bahama parrots, *Amazona leucocephala* (Gnam, 1991); black-billed *A. agilis* and yellow-billed parrots *A. collaria* (Koenig, 2001); Lilac-crowned parrots *A. finschi* (Renton and Salinas-Melgoza, 2004). Less frequently, losses during the incubation have also been documented and include clutch failure due to environmental conditions in Blue-fronted parrots, *A. aestiva* (Fernandes Seixas and de Miranda Mouráo, 2002) or predation during incubation, for example in Glossy Black-cockatoos, *Calyptorhynchus lathami* (Garnett *et al.*, 1999).

5.3 Uniqueness of life-history traits of Cyanoramphus parakeets

The breeding system of red-crowned kakariki is assumed to be monogamous. Pairs remain together during successive breeding seasons (Higgins, 1999) and no instances of extra-pair paternity have been noticed. However the likelihood of extra-pair copulations exist given that females have been noticed soliciting and receiving food from males other than mates during the breeding season (Higgins, 1999). Red-crowned kakariki exhibit biparental care with female-only incubation and brooding (Higgins, 1999; Greene, 2003; this study).

Red-crowned kakariki stand out among parrots by the high diversity of nesting sites they use (Higgins, 1999; Greene, 2003; this study). This trait is likely to have evolved in relation to the absence of terrestrial mammalian predators before the arrival of humans into New Zealand. This characteristic is not however exclusive to red-crowned kakariki. Other New Zealand Psittaciformes also nest in a variety of sites (Chapter 2). Lower predation rates favour nest transitions in parrot communities in the Peruvian

Amazon (Brightsmith, 2005a) and it is thus likely that predator absence might have shaped the nesting site preferences of New Zealand Psittaciformes. Furthermore, in contrast to other studies, the incubation stage of red-crowned kakariki is the main period of loss. Causes of loss include hatching failure, or losses due to rain (Chapter 3).

Another noteworthy trait is the ability to raise large broods. It is not clear if this trait is common to all *Cyanoramphus* and further investigation is required to disentangle the ecological and phylogenetic components involved in this phenomenon. Information on the breeding ecology of other members is limited and insufficient to establish clear patterns. It has been reported that in Norfolk Island parakeets (*Cyanoramphus cooki*) clutch size range from four to eight, and up to four nestlings from a single brood have fledged from natural nests (Hicks and Greenwood, 1989). As in the red-crowned kakariki, males of Norfolk Island parakeet occasionally finish rearing a brood while the female move to another nest and start laying a second clutch. The nest is normally a hollow in a living tree or a cavity amongst root masses or crowns of tree-ferns (Hicks and Greenwood, 1989). Even less information is available for the New Caledonian parakeet (*Cyanoramphus saisseti*). No detailed studies on the breeding ecology of this species have been published but it is known that females lay two to four eggs in hollows or in a bed of leaves (Hannecart and Letocart, 1980; Juniper and Parr, 1998). No information on brood size and fledgling production has yet published.

Other Psittaciformes in the Pacific Region rear only small broods. The Ouvea parakeet (*Eunymphicus cornutus ouvaeensis*), lays two or three eggs and normally all hatch, however third hatched nestlings generally die due to starvation (Robinet and Salas, 1999). In the red-shinning parrot (*Prosopeia tabuensis*), the clutch is also composed of

two or three eggs and broods of three nestlings, however first hatched nestlings receive more food than last hatched nestlings and presumably grow slower. However high occurrence of poaching by locals has prevented a detailed estimation of nestling mortality before fledgling (Rinke, 1989; Saafi, 2002).

5.5 Seasonal variation in productivity

As discussed in chapters 2 and 3 there was a sharp contrast between measures of reproductive success in the first and second year of study and it is likely that food supply is a determinant factor in yearly reproductive output given the higher incidence of nestling starvation in the first breeding season and the occurrence of second clutches in the second breeding season. It is thus a priority to determine the causal factor behind drastic changes in productivity of kakariki. The effect of different levels of food supply on degree of hatching asynchrony is unclear because of the differences in hatchability between 2004-2005 and 2005-2006. Therefore, additional field studies are needed to document trends in productivity. This would be a useful tool in species management given that it may allow the outcome of a given breeding season to be anticipated and intervention to be planned.

In this study, I did not assess female body condition, another factor that has been reported to affect reproductive success (for instance in Great tits *Parus major*, Dufva, 1996). However, females of different condition do occur in this study population and research is required to quantify and evaluate female health and its effects on reproductive success. I noticed two females which can be classified as low-condition females given the extreme feather loss they exhibited. These females laid smaller eggs (Table 5.1) and had

very low reproductive success. Although these females were not banded, the female BWV26BN nested about three meters away from a nest she occupied in the previous breeding season and it is likely to be the same individual. She failed consistently showed signs of low condition (i.e. feather loss, dull plumage) and failed to fledge any young over the two years of study. The female LWV3N also exhibited extreme feather loss and dull plumage (Figure 5.1) and hatched only two nestlings out of seven fertile eggs (Table 5.1). Both nestlings died soon after hatching. Upon death of the second nestling the female was captured in the nest and banded to allow monitoring in subsequent breeding seasons. Red-crowned kakariki exhibit a yearly moult during December and April (Higgins, 1999) and feathers were commonly found in focal nests. However, the females referred to above presented an exceptional degree of feather loss when compared with other moulting breeding females and it is possibly related to health condition (Figure 5.2). Unfortunately, it was not possible to determine the cause as feather loss, and it could be due to stress, dietary deficiencies, age or disease (Koski, 2002).

Table 5.1. Reproductive parameters of females showing extreme feather loss. Refer to Table 1, Chapter 3 for average values of normal females.

Female No.	Season	Clutch Size	Egg Volume	Fertility	Hatchability	Fledglings
BWV26BN	2004-2005	4	5.12	50%	50%	0
BWV26BN?	2005-2006	4	5.16	100%	0%	0
LWV3N	2005-2006	7	4.97	57%	28%	0



Figure 5.1. Red-crowned kakariki females. A) Female LWV3N note the numerous feathers at the bottom of the nesting box; B) Close up of the head of female LWV3N, note the degree of baldness in the head; C) and D) females showing average feather loss. C) Female LVK16; D) Female LWV6N. Females in C and D produced an average of 4 fledglings whereas female in A produced none.

5.6 Parent-offspring interactions

The low reproductive success recorded in the first year of this study promoted the design and establishment of a pilot study aimed to evaluate the potential of infra-red cameras for the study of patterns of food allocation between nestlings. Four infra-red mini-cameras (Nature Cameras, UK) were mounted on nesting-box lids. When parents were away from the nest, the original nesting-box lid was replaced by a lid with a camera attached. Cameras were connected to an 8 V rechargeable battery. Camera signal was received by an antenna and receiver device connected to a portable computer; video and audio were recorded. After installation, continuous video recording started to assess behavioural changes in parent's behaviour as a result of camera installation and to document patterns of food allocation. Parents returned to the nest and called repeatedly (alarm call) from the nest entrance when confronted with the nest-camera for the first time. The calls usually lasted two to five minutes. However, after calling one member of the pair or both members entered the nesting box and started to feed the nestlings. Once inside the nest parents did not show signs of stress or abnormal behaviour due to camera installation. In two instances parents approached the camera for a few seconds but did not abandon the nest box. No instances of brood abandonment were recorded in the four chosen nests. Figure 5.2 show two stills obtained from the infra-red mini-cameras.

Male and female parents were easily identified by bill shape and size and occasionally by calling types. Males produce a soft call before entering the nest box, while females were mostly silent. A total of 29 feeding events were recorded on four clutches with broods of different ages. Even though this is a small sample size, some patterns were noticed and these require additional investigation. During the first one to

two weeks after hatching of the first nestling, females were solely responsible for brooding and feeding nestlings. Females received food from their mates and then transferred it to nestlings. It was noticed that newly hatched nestlings required "beak-to-beak" stimulation from females in order to posture and solicit food. This behaviour was not noticed in males. If a newly hatched nestling was present in a brood, it was ignored by males and in the two cases recorded such nestlings died shortly after. One pair (pair K21) was commonly seen entering the nesting box together and distributed food independently to the six nestlings brood, but in two instances the male was noticed transferring food to his mate inside the box where after she distributed the food to the brood.

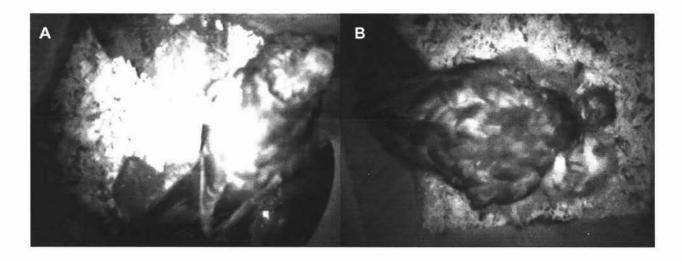


Figure 5.2. Infra-red images of brooding females. A) female from nest K21; B) female from nest K16. Note nestlings at the bottom of the nesting box.

Although these observations are limited, they indicate that parent-offspring interactions in red-crowned kakariki are diverse and might be related to age and

experience of parents. Age and experience are well documented phenomena in captive (Stone *et al.*, 1999) and free-ranging parrots (Wilson *et al.*, 1997) as well as several other bird species (Arnold et al., 2006; Green, 2001; Robertson and Rendell, 2001). It is thus promising to explore the relationship between patterns of food delivery between parents and offspring to factors that can explain hatching patterns, nestling growth and fledgling success.

5.7 Banded individuals

The consequences of hatching asynchrony can be expressed beyond the fledgling period and therefore, a better understanding of the consequences of hatching asynchrony and hatching ranks in the biology of red-crowned kakariki will benefit from future long-term studies targeting other life history traits. In the present study a total of 90 red-crowned kakariki were banded. These included 76 fledglings and 14 adults trapped with mist-nets. These banded individuals represent a good opportunity to explore survival and breeding performance of nestlings of known hatching rank and weight at fledgling.

Appendix 5 presents a list of all banded individuals, their band number and band combination.

5.8 Potential for translocations

As mentioned in chapters 1 and 2, the red-crowned kakariki has been subject to several translocations in New Zealand, however with mixed results. These releases have been inconsistently documented and therefore it is not clear which factors other than introduced mammalian predators are determinants of translocation success.

Independent lines of evidence suggest that red-crowned kakariki are a good candidate for translocation to fragmented or regenerating areas providing that introduced mammalian predators are absent (see Greene, 2003 and Elliot *et al.*, 1996a, 1996b for a discussion on predators). Red-crowned kakariki were first transferred to Tiritiri Matangi Island between 1974 and 1976, when more than 50% of the island's area was covered by grassland (Dawe, 1979). Since then no surplus translocations have taken place and no immigration from nearby populations (i.e. Little Barrier Island) has been confirmed, although it is a likely phenomenon that should not be ignored. The original number of birds was 84 birds (Dawe, 1979).

At present the red-crowned kakariki population on Tiritiri Matangi is estimated to be around 700 birds (D. Brunton and R. Stamps pers. comm. 2004). They nest successfully in the three main habitats on the island: grassland, replanted areas and remnant forests (Chapter 2) indicating that mature forest is not a prerequisite for the species. Similarly, tree cavities are not a necessity for translocation given the diversity of nesting places in which red-crowned kakariki nest successfully. Nevertheless, provision of nesting boxes is recommended because it facilitates monitoring of breeding pairs.

On Little Barrier Island, red-crowned kakariki are numerous in open areas (T. Greene pers. comm. 2004) and it has been suggested that the Chatham Islands subspecies (*Cyanoramphus n. chathamensis*) has expanded to cleared habitat (Greene, 2001). Furthermore, the Kermadec Islands subspecies (*C. n. cyanurus*) occurs in high densities on Macauley Island despite an apparent diminution in forested habitat (Greene *et al.*, 2004). Major changes in vegetation structure on Macauley island were caused by browsing goats (Veitch and Bell, 1990). Finally, on Little Barrier Island red-crowned

kakariki commonly forage at ground level in open areas (Greene, 1998). Ground foraging was also noticed during this study in all three habitat types.

Finally, it is necessary to investigate the possibility of using last hatched nestlings for translocation purposes. As discussed in chapter 4, breeding pairs experience numerous nestling losses, especially of last hatched nestlings. The potential exist to remove last hatched nestlings and to captive-rear those for future release. An alternative approach would be to cross-foster these nestlings to smaller broods. Intra-specific cross-fostering has been successful in the closely related Norfolk Island parakeet, *Cyanoramphus cooki* (Hicks and Greenwood, 1989).

A similar approach has been proposed to promote sustainable harvest of parrots for the pet market (Stoleson and Beissinger, 1997). The principal advantage of this approach in contrast to capture and translocation of adult caught birds would be a minimal effect on the source population since breeders are not removed for translocation. Hand-reared psittacines have been previously used for reintroduction and studies show that social interaction with conspecifics is a critical factor in the survival of hand-reared individuals (Brightsmith et al., 2005; Collazo et al., 2003; White et al., 2005). A mixed group of hand-reared and family-reared nestlings would provide a unique opportunity to explore differences in survival and breeding success allowing a direct assessment of the use of last hatched nestlings for translocation practices.

5.9 LITERATURE CITED

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Appendix 1. Research permit by the New Zealand Department of Conservation.



High Impact Research Permit

Research Permit Number: AK/15301/RES

Research Permit

Her Majesty the Queen, acting by and through the Minister of Conservation (the Grantor) GRANTS to LUIS ORTIZ CATEDRAL a Permit under Section 53 of the Wildlife Act 1953 and Section 49 of the Reserves Act 1977 for the purpose of

Reproductive Biology of Red Crowned Kakariki.

on the Site(s) specified in Schedule 1 of this Permit.

- The Permittee shall pay the Concession Fee (GST inclusive) of \$0, together with the application processing fee deposit in advance to the Grantor in the manner directed by the Grantor.
- The Permittee shall contact the local Area Manager prior to collecting in the area, in particular to ascertain any
 "no-go" areas, which may include areas of concern to tangata whenua. Permission to cross private land shall be
 obtained from the landowner prior to the conduct of this activity.
- This Permit does not confer on the Permittee any interest in the Site, nor does it derogate in any way from the rights of the public to use and enjoy the whole or any part of the Site.
- 4. The Permittee shall indemnify the Grantor against all claims by any person in respect of any injury, loss or damage (including tire damage) caused by or arising out of any act or omission of the Applicant, its servants, agents, contractors, clients or invitees, or otherwise caused as a consequence of its use of the Site or as a result of the conduct of the concession activity.
- The Permittee shall operate the research activity in a safe and reliable manner and shall comply with all statutes, bylaws and regulations, and all notices and requisitions of any component authority relating to the conduct of the collecting activity.
 - (a) The Concessionaire shall prepare a contingency plan for dealing with any mishap that may occur during the operation of collecting activities under this permit, including the recovery of sick or injured persons.
 - (b) The Permittee acknowledges that the Grantor accepts no responsibility for the safety of the Permittee.
- The Permittee shall not erect or bring onto the Site(s) (or any other land administered by the Grantor) any structure, install any facility, or alter the Site(s) in any way without the prior written consent of the Grantor).
- 7. The Permittee shall not, unless authorised in writing by the Grantor, interfere with, remove, damage, or endanger the natural features, animals, plants or historic resources in any area administered by the Grantor, or bring any plants or animals to the Landing Site(s), or deposit debris, rubbish, or other dangerous or unsightly matter, or contaminate any body of water. The Applicant shall ensure that its clients and invitees do not carry out any acts prohibited under this clause.
- The Permittee shall not transfer, sublet, assign or otherwise dispose of the interest granted by this Concession.
- The Grantor may terminate this Concession if the Permittee breaches any of the terms of this document or if the
 activity causes any unforeseen or unacceptable effects to the Grantor.
- 10. The Permittee shall comply with all reasonable notices and directions of the Grantor concerning the activities conducted by the Applicant on land administered by the Grantor. While conducting this activity, the Permittee shall carry this permit with them at all times.
- Use of aircraft in support of the Concession Activity is subject to separate approval. Vehicles shall only be operated on formed roads.
- 12. The Permittee shall take all waste and rubbish out of the Site and dispose of it in an environmentally sound manner away from public conservation lands. The Permittee must adhere to the Environmental and Water Care Code while conducting the activity, attached hereto.
- 13. Samples are to be collected away from tracks, huts, picnic areas or areas of high public use and as far as practicable, out of sight of the public. Wherever practicable, the Permittee shall use access routes to the collection areas that avoid damage to natural features.
- 14. The Permittee shall not collect samples from biologically sensitive areas, or in such quantities that the taking would unduly deplete the population or damage any other ecological associations.
- 15. All material collected shall remain the property of the Crown. The Permittee shall comply with any reasonable request from the Grantor or tangata whenua for access to any of the collected samples. Any surplus material is to be stored and the Department of Conservation is to be consulted on ultimate disposal of such material.

- 16. The Permittee shall not donate, sell or otherwise transfer to any third party any material, including any genetic material, or any material propagated or cloned from such material, collected under this permit, or any information obtained as a result of research done on such material or undertake any other activity with the sample not expressly approved herein; without the written permission of the Grantor in consultation with tangata whenua. Notwithstanding the preceding constraint, the Permittee may publish the results of such research results arising from the collection of the plants.
- 17. No material collected pursuant to this permit may be used for commercial purposes or patenting of plant varieties or registration of intellectual property rights on any derivatives.
- 18. Any taxon, which is new to science, shall have type specimens and a voucher specimen lodged with a registered New Zealand herbarium, recognised national invertebrate collection or equivalent appropriate collection. The Permittee shall notify forthwith the Grantor and local tangata whenua of any such finds.
- 19. Where obligations bind more than one person, those obligations shall bind those persons jointly and separately.
- 20. If requested, the Permittee shall keep the Grantor and tangata whenua informed on the progress of this research. Upon completion of the research, the Permittee shall forward a copy of the research findings, reports and published to the Grantor's office from where this permit was issued. The Permittee acknowledges that the Grantor may provide copies of these findings to tangata whenua.
- 21. The Permittee shall comply with the collection provisions on the attached schedule at all times.
- 22. Special Conditions
 - a) The permit holder(s) must arrange own transport to all sites listed in Schedule 1.
 - Any action under this authority may only be taken with the prior notification and consent of the Department of Conservation Area Manager Warkworth.
 - The permit holder must follow procedures that are advised by Department of Conservation Programme
 Managers, to prevent the introduction of disease, rodents, insect or weed species to the sites listed in
 Schedule 1. The Permittee will ensure that all field equipment is washed clean and sterilised with anti-viral
 solutions prior to entering sites. Equipment must also be sealed in containers so both the Permittee and
 DOC can be certain it is free of rodents and invertebrates. Boots and clothes must be free of mud and seeds.
 - d) The Permit Holder(s) must liaise with and follow advice provided by resident Department of Conservation Rangers of the sites listed in Schedule 1.
 - e) Approved Type of Research:
 - Artificial nest box provisioning and monitoring.
 - Handling of eggs and chicks from three days after hatching to fledging, to determine weight and
 other morphometric data.
 - Collection of tissue from dead birds and feather samples from adult and 14-20 day old nestling red crowned kakariki.
 - 4. Collection of any fertile but unviable eggs.
 - Extraction of DNA from tissue, feather and egg samples for the purpose of determine sex of birds.
 - Video recording of nests.
 - 7. Mist netting and hand netting at the nest to capture and mark individual red crowned kakariki.
 - All colour and metal banding must be carried out under a valid banding permit from the DOC banding office.
 - f) Only experienced people will be involved in the capture, handling and manipulation of birds.
 - All birds must be processed immediately on capture and released.
 - The study must be carried out as carefully as possible but if any adverse effects are observed the activity must be stopped and the Programme Manager, Island Biodiversity at the Warkworth Area Office must be advised immediately.
 - The kakariki must be handled as carefully as possible, but if any bird should die or is found dead, the body is to be given to a Department of Conservation Ranger.
 - The Permittee must not impact on any other absolutely protected wildlife, or other research or management activities at a site.

			Page 3 of 4
SIGNED by		SIGNED by	Jack Chile Calcal sel
Dated	27/10/04	Dated	October 21st 2009
Rob McCa	dlum, Auckland Conservator	Dr. Luis Or	tiz Catedral
	ND THROUGH THE MINISTER OF ON ("The Grantor")	AS APPLICANT	
In the presence of	of Mulistant	In the presence of	RKStamp.
Witness	From Olighant	Witness	Rosalie Stam
Occupation	DOC office	Occupation	Doc Officer
Address	Andeland Convers	Address	Auckland Consensatery
Schedule O	ne		
(1) Approved	Site(s)		
Tiritiri M	atangi Island		
(2) Approved	Date(s)		
15th Septe	ember 2004 to 30th May 2006		

Appendix 2. Banding permit by the New Zealand, Department of Conservation,

New Zealand Banding Scheme



NEW ZEALAND NATIONAL BANDING SCHEME

INSTITUTIONAL PERMIT TO BAND BIRDS NO. 0297

Dr Mr Ms Mrs

Sandra Anderson

School of Biological Sciences University of Auckland Private Bag 92019

Auckland

Is hereby authorised pursuant to the provisions of the Wildlife Regulations 1955 to band birds (species and localities stated below only) for ornithological studies, using bands supplied by the Department of Conservation.

The operator must comply with the banding rules set out overleaf, and any special conditions appended as a schedule to this permit.

Permission to catch and handle protected birds and to re-release them into the wild is hereby granted by the Director-General of Conservation.

Dated this 21st day of September 2004.

SPECIES

LOCALITIES

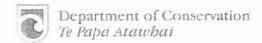
Red-crowned Parakeet

Tiritiri Matangi Island

Valid until	Colour bands	Mist nets	Other special catching devices or markers	Signed by/on behalf of Director-General of Conservation	Date
31/8/2006	YES	YES	NO	Rusinicou	23/9/4

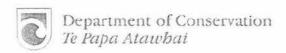
NOTE. If an extension of this permit is required, this permit should be sent to the Banding Office before the expiry date.

THIS PERMIT MAY BE REVOKED AT ANY TIME.



CONDITIONS OF ISSUE

- The operator will adhere to the rules and instructions as laid down from time to time by the banding office.
- (a) The operator acts for him/herself in trapping birds under the scheme, and no resposibility
 or liability can attach to the Department of Conservation, the Banding Office or any other
 member through failure to adhere to authorised instructions.
 - (b) The Department of Conservation nor the Banding Office accept any resposibility or liability for any accident or harm occurring to any operator while carrying out work under the Banding Scheme.
- 3. The operator is to band only those species and at those localities stipulated on this permit.
- Colour bands, tags or any other markers may not be used except for schemes approved by the Banding Office and shown on this permit.
- Mist nets, cannon nets and other special catching devices may not be used unless shown on this permit.
- Operators must always first obtain permission for purposes of entry from the owner, occupies or controlling authority of the land on which the birds are to be banded.
- Birds are to be trapped and bands used only by the authorised operator or under the operator, direct supervision.
- Birds are to be released immediately after banding, and every care taken to prevent harm or injury.
- 9. The operator will exercise due care in trapping and placing or replacing bands on birds.
- 10. The type of trap used must in no way harm the bird.
- The band sizes for various species of birds as stipulated by the Banding Office are to be strictly adhered to.
- The bands are to be closed round by means of a pair of pliers so that the butt ends meet completely and do not overlap.
- If a band is for any reason taken off a bird, it is NEVER to be used on another bird, but must be returned to the Banding Office.
- The operator is to keep, and return, proper records as stipulated on forms supplied by the Banding Office.
- 15. If revoked at any time, this permit is to be returned to the Banding Office immediately.



NEW ZEALAND NATIONAL BANDING SCHEME

INSTITUTIONAL PERMITS

Conditions of Issue

- Institutional Banding Permits are vested in the name of a single person, the permit holder, who
 is responsible for all banding matters pertaining the permit.
- The permit holder may authorise, in writing, other persons to carry out banding activities
 covered by the permit, provided these persons are suitably trained for the work. A copy of the
 permit must be attached to the written authorisation.
- The permit holder will ensure that the sub-permittee adheres to the rules and regulations as set out on the permit and in the Bird Banders Manual, as well as to any other conditions set by the Banding Office.
- The permit holder is responsible for the actions of the sub-permittee.
- There shall be no contact between the sub-permittee and the Banding Office. All
 communications, including orders for equipment and forms, must come through the permit
 holder.

Appendix 3. Permission by the Animal Ethics Committees of Massey University and The University of Auckland

APPLICATION FORM TO USE ANIMALS IN RESEARCH

	()r	accordance with the	Animal Welfare Act 1	999.)	
Please give a Project Tit (which may be released the Official Information A	under	Reproductive biology novaezelandieae) on	of red-crowned kaka Tiritiri Matangi Island	riki (<i>Cyanoramphus</i> , New Zealand	
Responsible Investigator		Luis Ortiz Catedral	Department	or School of Biological Sciences, University of Auckland	
	***	Dianne Brunton	Organisation	School of Biological Sciences, University of Auckland	
If appropriate indicate the investigator reports).	ne person	stacted <u>at any time</u> by the Anim g this study.	is project (This should not be	the investigator, but the person to whom the Animal Welfare Officer in the event of animal Mobile:n/a	
submission will be considered	by the Co	completed by the Head of Demmittee.	partment (or CEO of outside	e Organisation or Institution), before the	
Tick √ (copy and paste this √ symbol) if relevant, then add any Head of Department This project can be accommodated within the curre staff, equipment) in my Department / Organisation.			the current resources (budget, nisation.		
		This project requires	the following addition	al resources:	
Peer reviewed? Yes		This proposal has already been reviewed as part of a successful funding application. The following granting body has allocated funds specifically for work covered by this proposal -			
Peer reviewed? No		The following (University of Auckland) colleague(s) not named as personnel in this application could provide local expert comment, if required, in the absence of peer review prior to this application being submitted -			
Please indicate ratio		Commercially funded activities.	contract P	ublic good or academic activities.	
	at	id in this protocol will follow Missey Univ. / Organisation	the procedures as defined Name:David	Lambert	
		FOR USE OF ETHIC	CS COMMITTEE ONLY	App. sent out 25-11-05	
	RE	CEIVED		orlar	
Date received:	17	NOV 2005	Application No.	051.14	
	Rese	arch Ethics			
Biological Safety Comm approval also required? Yes / No	ittee	MASSEY UNIV	e the reference numb	er.	

FACULTY SERVICES Faculty of Medical and Health Sciences

Chris Thoreau Secretary, Animal Ethics Committee



Grafton Campus 85 Park Road, Grafton Auckland, New Zealand Telephone 64 9 373 7599 ext. 88731 Facsimile 64 9 373 7569 or ex 85569 email c thoreau@auckland ac nz

The University of Auckland Private Bag 92019

11 October 2004,

Dr D. Brunton. School of Biological Sciences,

Dear Dianne and Luis,

AEC/08/2004/R281 - APPROVAL NOTICE

Reproductive biology of red-crowned kakariki (Cyanoramphus novaezelandieae) on Tiritiri Matangi Island, New Zealand.

This application was discussed by the committee. The response received in reply to the AEC request for further detail has been assessed.

Herewith confirmation that the application is approved for three years.

Approval date 24 September 2004

Expiry date

24 September 2007

Please note the requirement regarding reporting of animal use brought about by the Animal Welfare Act 1999.

As Principal Investigator it is your statutory responsibility to provide usage statistics to the AEC for incorporation into the University consolidated return to MAF. This is required on an annual basis. I will be asking for an animal usage return at the end of every calendar year of the approval period for every current protocol. These returns are required by me by the middle of January, but may be filed as soon as the number used in any one calendar

Forms for Animal Ethics Committee use can be found at: http://www.health.auckland.ac.nz/research/forms/ethics/animal.

Regards, Chris

Chris Thoreau Secretary

Animal Ethics Committee

Animal usage return forms, one per calendar year of approval period. MAF animal type codes

Appendix 4. Food items of red-crowned kakariki (*Cyanoramphus novaezelandiae*) on Tiritiri Matangi Island. November

Species	Common/ maori name	Food type	Feeding bouts
Plantago laceolata		Seeds/Flowers	5
Unidentified grass		Seeds	23
Cordyline australis	Ti Kouka	Flowers/ Fruits	15
Metrosideros excelsa	Pohutukawa	Flower buds	10
Solanum americanum		Flowers	1
Phormium tenax	Flax/Harakeke	Flower buds/ Seeds	10
Myrsine australis	Mapou	Fruits	5
Unidentified Compositae		Flowers/Seeds	6
Muehlenbeckia axillaris	Pohuehue	Stems/Fruits	2
Pseudopanax arboreus	Five finger/Puahou	Fruits	5
Geranium macrophyllum		Fruits	6
Coprosma sp.	Karamu	Leaves	2
Leptospermum scoparium	Manuka	Seeds	1
Raphanus aff raphanistrum		Seeds	2
Modiola caroliniana		Seeds	6

Appendix 5. List of banded red-crowned kakariki during the present study on Tiritiri Matangi Island. "0" indicates no color band.

Band No.	Sex	Band combination	Band No.	Sex	Band combinatio
106601	Male	yb-m	116840	Male	b-mg
106602	Male	yr-m	116839	Male	g-my
106603	Female	m-wb	116838	Female	y-mb
106604	Male	wr-m	116837	Female	y-mw
106605	Male	wb-m	106647	Female	y-mr
106606	Male	rb-m	106648	Male	w-mr
106607	Female	m-rw	116885	Female	mg-wb
106608	Male	y-m	116886	Male	w-mg
106609	Male	m-r	116887	Female	m-rg
106610	Male	w-m	116888	Female	mb-wb
106611	Male	b-m	116889	Female	mb-wg
106612	Male	g-m	116847	Male	b-my
106613	Male	r-m	116845	Female	b-mw
106614	Female	m-y	116846	Female	b-mr
106615	Male	ry-m	116844	Male	g-mb
106616	Male	m-g	116843	Female	m-bg
106617	Female	m-w	116842	Female	m-by
106618	Female	m-b	116832	Male	g-mg
106619	Male	m-ry	116834	Male	yw-mb
106620	Female	wg-m	116833	Male	by-m
106621	Female	m-wy	116835	Male	g-mb
106622	Male	wy-m	116831	Male	bg-m
106623	Female	m-wr	116830	Male	gy-mw
106624	Male	rg-m	116828	Male	gr-m
106625	Female	0-ym	116827	Female	m-gw
106626	Female	0-gm	116826	Female	m-gb
106627	Male	0-wm	116879	Female	gy-m
106628	Female	m-yw	116880	Female	mg-gw
106629	Male	w-my	116881	Female	mb-gw
106630	Male	yg-m	116882	Female	mb-gb
106632	Male	yw-m	116883	Female	bg-mg
106633	Female	m-wg	116884	Female	bg-mb
106634	Female	m-yr	116836	Female	mr-rr
106635	Male	gb-m	116892	Female	m-yb
106636	Male	rw-m	116893	Female	g-mr
106637	Male	y-my	116891	Female	r-mb
106638	Male	w-yw	116849	Male	m-br
106639	Female	m-yg	116848	Male	bw-m
106641	Female	r-mg	116896	Male	br-m
106642	Female	r-my	116895	Male	m-gr
106643	Female	m-rb	116894	Male	g-mw
116890	Female	mb-ww	116819	Female	mr-wr
116850	Male	bg-m	116818	Male	rb-mg
116841	Male	m-gy	116817	Female	wy-my