Copyright is owned by the Author of the thesis. Permission is given for a copy to be downloaded by an individual for the purpose of research and private study only. The thesis may not be reproduced elsewhere without the permission of the Author. Effects of food availability and predation on reproductive success and behaviour of *Petroica longipes* in a fragmented landscape



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ABSTRACT

Declines of avian populations in fragmented landscapes are well documented. However, the underlying factors causing these declines are often poorly understood. Two key habitat variables that negatively impact species persistence in small forest fragments are predator abundance and food availability, both crucial determinants of avian reproductive success. I examined the effect of fragment size, isolation and disturbance on these two habitat variables, and the influence of these habitat variables on reproductive success and behaviour of North Island robins (*Petroica longipes*). The study was carried out in 15 forest fragments (1.6 - 1625 ha) in an agricultural forestry landscape in the central North Island of New Zealand from 2002 to 2005.

I found no association between a measure of relative predator abundance (proportion of tunnels tracked by *Rattus rattus*) and either fragment size or isolation. Domestic livestock grazing appeared to have a negative impact on rat abundance. However, the lack of a relationship between rat tracking rate and robin nest survival suggests that rat tracking rates may not be well correlated with predator abundance in small fragments. Nest survival increased with food availability (invertebrate biomass) as expected, but decreased with fragment size. Overall daily nest survival was 0.315 (*SE* 0.003).

I also determined whether food availability was associated with incubation behaviour or foraging efficiency. Female nest attentiveness was expected to increase with increasing frequency of male incubation feeding, which was in turn expected to increase with food availability. The rate of male incubation feeding did alter the female's incubation rhythm (shorter on- and off-bouts), but was negatively associated with the overall proportion of time females spent on their nests. Male incubation feeding rates were not significantly associated with food availability. In addition, measures of foraging efficiency (proportion of time spent foraging, prey capture rate) were not significantly associated with food availability in either males or females.

This study did not support recent predictions related to incubation behaviour or habitat fragmentation, and this may reflect current theory being largely based on results from north-temperate ecosystems. In particular, there was no evidence that the small or disturbed fragments had inferior habitat for robins. I recommend that conservation managers in New Zealand not overlook the value of small habitat fragments.

TABLE OF CONTENTS

ABSTRACT							
TABLE OF CONTENTSIII							
LIST OI	GURES	VI					
LIST OI	ABLES	VIII					
ACKNO	LEDGMENTS	X					
1.0 EFF LAI	TS OF HABITAT QUALITY IN FRAGMENTEI SCAPES)					
	Study species and area Aims	6 10					
2.0 ABU TO FRA	DANCE OF NEST PREDATORS AND FOOD WITH RESPECTIZE, ISOLATION AND DISTURBANCE OF FORESTMENTS	Г Г 13					
2.1 N	nods	15					
	 Study species and area Food availability Predator abundance Statistical Analyses 	15 15 16 17					
2.2 R	lts	19					
	 Pitfall biomass Rat tracking rates 	19 21					
2.3 E	ussion	23					
3.0 NES FRA	SURVIVAL, PRODUCTIVITY AND PREDATION IN FORES' MENTS	Г 27					
3.1 N	rods	29					
	 Study species and area Nest Monitoring Food availability Predator abundance Statistical Analyses 	29 29 30 30 30					
3.2 F	llts	33					
	 Estimates of nest survival Random effects 	33 38					

47

68

82

3.3	Discussion		40
	3.2.3	Fledgling number	39
	3.2.4	Productivity	39

4.0 INCUBATION RHYTHM, NEST ATTENTIVENESS AND TIMING OF BREEDING IN THE NORTH ISLAND ROBIN

4.1	Method	5	50
	4.1.1	Study species and area	50
	4.1.2	Incubation attendance	50
	4.1.3	Food availability	51
	4.1.4	Statistical analyses	52
4.2	Results		53
	4.2.1	Timing of breeding	53
	4.2.2	Nesting behaviour and incubation feeding	54
4.3	Discussi	on	57
5.0	TIME BU ANNUAL	DGETS OF NORTH ISLAND ROBINS DURING THEIR CYCLE	63
5.1	Method	5	65
	5.1.1	Study species and area	65
	5.1.2	Behavioural observations	65
	5.1.3	Data collection	66
	5.1.4	Food availability	67

	5	
5.1.5	Statistical Analyses	

Results 5.2

5.2	Results		69
	5.2.1	Seasonal variation in time allocation	69
5.2.2 Sex-related		Sex-related differences in time allocation	72
	5.2.3	Pre-breeding period	73
	5.2.4	Breeding season	75
	5.2.5	Post-breeding period	75
5.3	Discussi	on	78

6.0 AN INEXPENSIVE METHOD FOR IDENTIFYING PASSERINE **NEST PREDATORS**

6.1	Method	S	8-
	6.1.1	Study species and area	84
	6.1.2	Clay egg construction	84
	6.1.3	Artificial clay egg attachment	8.
	6.1.4	Predator identification	80
6.2	Results		8'
	6.2.1	Artificial clay egg acceptance	8
	6.2.2	Predator identification	83

6.3	Discussion	89
7.0	FINAL DISCUSSION	93
RE	FERENCES	101

LIST OF FIGURES

Figure 1.1.	Map of study area showing fragments of native forest surrounded by
	exotic forest and agricultural matrix. The 15 fragments filled in red
	are those containing robin pairs that were intensively monitoring
	during three breeding seasons (2002-2005)
Figure 2.1.	Mean (± 1 SE) invertebrate biomass per collection period (six weeks)
	over the three-year sampling period, across all pitfall traps19
Figure 2.2.	The probability $(\pm 1 SE)$ of tunnels being tracked by rats in fragments
	of different size and in the presence (\circ) or absence (\blacklozenge) of domestic
	livestock grazing in the Benneydale region, New Zealand, 2002-
	2005
Figure 3.1.	Estimated daily survival rates (DSR) for North Island robin nests
	during a) 2002-2003, b) 2003-2004 and c) 2004-2005 breeding
	seasons in the Benneydale region, New Zealand
Figure 3.2.	The effect of fragment size (a, b & c) and invertebrate biomass (d, e
	& f) on the overall survival of robin nests during 2002-2003 (a & d),
	2003-2004 (b & e) and 2004-2005 (c & f)
Figure 3.3.	Mean (± 1 SE) number of fledglings and independent juveniles
	produced per female across the three breeding seasons40
Figure 4.1.	Relationship between invertebrate biomass on robin territories and
	laying dates of first clutches by pairs on those territories54
Figure 4.2.	Scatter plot of mean on-bout (cube root scale) and off-bout (log
	scale) duration versus the male incubation feeding rate for all 114
	nest watches
Figure 5.1.	Proportion (± 1 SE) of time budget female (\blacksquare) and male (\Box) robins
	spent foraging, resting and undertaking body maintenance activities
	during (a) pre-breeding 2004, (b) males only during the breeding
	season of 2004-2005 and (c) post-breeding 2003-2005
Figure 5.2.	Proportion $(\pm 1 SE)$ of time budget males spent foraging during the
	2004-2005 breeding season while they had no nest or fledglings

	(MF), while female is nest building and incubating, and while
	feeding nestlings or juveniles70
Figure 5.3.	(a) For aging attack rates (± 1 SE) for female (\blacksquare) and male (\Box) robins
	during pre-breeding 2004, the 2004-2005 breeding season and post-
	breeding 2003-2005 period and (b) Foraging attack rates (± 1 SE) for
	males during the 2004-2005 breeding season while he has no nest or
	fledglings (MF), while female is nest building and incubating, and
	while feeding nestlings and juveniles71
Figure 6.1.	Photograph of an artificial clay egg in an active (a) song thrush (top
	left egg) and (b) greenfinch (middle egg) nest. (c) Artificial
	greenfinch egg, with harrier beak imprint, hanging outside nest after
	a predation event
Figure 7.1.	a) Male incubation feeding rates relative to nest predation rate (%
	nests lost during incubation) for open-nesting and hole-nesting
	northern-hemisphere species in comparison to North Island robin
	feeding and predation rates and b) Nest attentiveness relative to the
	rate of male incubation feeding for the same open and hole-nesting
	species plus North Island robin for comparison. This graph is
	reproduced from Figures 1 & 2 in Martin and Ghalambor (1999)

LIST OF TABLES

- Table 2.2.Correlation (r s) between invertebrate biomass on each robin territory
during the three sampling years, across the different sampling
months in the Benneydale region, New Zealand, 2002-2005.21

- Table 4.1.Diagrammatic illustration of the predicted influence (see above) thatincreased food availability, ambient temperature, nest predation andmale incubation feeding (MIF) has on incubation behaviour.50
- Table 4.2.Summary of generalized linear mixed model selection for incubation
behaviour and incubation nest survival of North Island robins in the
Benneydale region, New Zealand for 2002-2005.55

Table 4.3.	The results of nest watch data from robins in the Benneydale region
	from 2002-2005 with the corresponding predictions outlined in the
	introduction in Table 4.1
Table 5.1.	Difference of least square means (DLSM) between pre-breeding,
	breeding (male only) and post-breeding in the proportion of time
	robins allocated to foraging70
Table 5.2.	The average foraging attack rate calculated from each observation
	period (total time budget) for the pre-breeding, breeding season and
	post-breeding periods for male and female robins72
Table 5.3.	Effect of sex, temperature, time of day, and invertebrate biomass of
	foraging time and foraging attack rates of North Island robins during
	the 2004 pre-breeding period. Effects of these factors on foraging
	time and foraging attack rate are analysed using general linear mixed
	modelling, results are for univariate models74
Table 5.4.	Effect of temperature, time of day, and invertebrate biomass of
	foraging time and foraging attack rates of male North Island robins
	during the 2004-2005 breeding season. Effects of these factors on
	foraging time and foraging attack rate were analysed using general
	linear mixed modelling, results are for univariate models75
Table 5.5.	Effect of temperature sex, time of day, and invertebrate biomass of
	foraging time and foraging attack rates of North Island robins during
	the post-breeding period (2003-2005). Effects of these factors on
	foraging time and foraging attack rate are analysed using general
	linear mixed modelling, results are for univariate models77
Table 6.1.	The individual response of five European passerine species after the
	addition of an artificial clay egg to their own clutch
Table 6.2.	Predator identification at the 30 active bird nests preyed on while
	containing artificial eggs. Numbers are given for nests where
	predator sign was left at the nest site and where partial predation
	occurred (one or more eggs from a clutch disappearing before
	complete predation)

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For Johnno, a sheep.



1.0 Effects of habitat quality in fragmented landscapes

Habitat fragmentation converts areas of continuous habitat into small, isolated remnants. Together with total loss of habitat, this land transformation is widely inferred as the primary cause of the recent decline in biodiversity worldwide (Vitousek et al., 1997). Species distributed across fragmented landscapes frequently experience local extinction (Saunders, 1989). Whether such extinctions result in global extinction of the species or a reduction in local biodiversity is of great concern to conservation biologists. Conserving species in fragmented landscapes requires an understanding of the factors that cause declines of populations and therefore accounts for their current distributions.

Declines of species in fragmented landscapes can occur through metapopulation dynamics, because local extinction rates increase as fragment sizes decrease and recolonisation rates decrease as fragments becomes more isolated (i.e. metapopulation dynamics *sensu* Hanski, 1994; Hanski and Gilpin, 1997). However, the quality of habitat fragments may also decrease as those fragments become small and isolated, producing similar patterns of local extinction (Saunders et al., 1991). Theoretical approaches for understanding patterns of population declines at a broad-spatial scale tend to emphasise either habitat or metapopulation factors, and these two approaches have recently been described as separate paradigms (Armstrong, 2005). While I present no data on metapopulation dynamics, my work is part of a collaborative project assessing both the role of habitat quality (this thesis) and metapopulation factors (Y. Richard in prep.) in the distribution of a native passerine in a fragmented New Zealand landscape.

Following fragmentation, remaining habitat fragments vary in size, isolation and habitat quality (Saunders et al., 1991). This variability in the connectivity and quality of the habitat may affect abundance and availability of resources, predator density and behaviour, and ultimately influence the reproductive success of bird species. Because of the potential importance of nest survival in avian population dynamics, it is not surprising that fragmentation studies have endeavoured to measure nest survival rates between fragmented and continuous forest habitats (e.g. Wilcove, 1985; Robinson et al., 1995; Friesen et al., 1999). Reduced survival has generally been associated with increased nest predation and brood parasitism or a decrease in food abundance (Brittingham and Temple, 1983; Wilcove, 1985; Robinson et al., 1995; Burke and Nol, 1998; Zanette et al., 2000). Despite support for these factors underlying the decline of forest fragment species, we must be careful when interpreting and extrapolating these results, particularly to other geographical regions. Current knowledge is largely based in the eastern United States (Cavitt and Martin, 2002; Chalfoun et al., 2002b; Stephens et al., 2003), and often from artificial nest studies, which may not reflect predation rates or patterns on natural nests (e.g. Zanette, 2002; Mezquida et al., 2004; Skagen et al., 2005).

Impacts of habitat fragmentation on the demographic processes of New Zealand's avifauna are presently unstudied. Extensive fragmentation has occurred over the space of 650-750 years, with humans (both Polynesian and European) reducing the indigenous forest cover from approximately 85 percent of the land area to about 23 percent (Ministry for the Environment 1997). Much of the remaining forest is restricted to remote mountainous areas or to lowland fragments, while "... the main pressures now come from the degenerative effects of fragmentation and the impacts of alien plants and animals" (Ministry for the Environment 1997). Whilst forest clearing is considered to reduce the available habitat for native species, it is not generally considered to reduce the habitat quality of the remaining forest in New Zealand (Atkinson, 2002). This seems presumptuous considering the negative impact that habitat fragmentation has been shown to have on avian demographics in the northern hemisphere due to changes in habitat quality (Small and Hunter, 1988; Robinson et al., 1995; Fenske-Crawford and Niemi, 1997; Hartley and Hunter, 1998).

2

The lack of fragmentation studies in New Zealand almost certainly stems from the imminent problem that currently confronts wildlife conservation managers. That is, the detrimental impact of introduced mammalian predators on the extinction, and severe decline, of the country's unique and endemic avifauna (Duncan and Blackburn, 2004). Evolving in the complete absence of mammalian predators, New Zealand's birds are naïve and extremely vulnerable to both nest and adult predation by mammalian predators (James and Clout, 1996; Innes et al., 1999; Powlesland et al., 1999; Moorhouse et al., 2003; Innes et al., 2004). Because introduced mammalian predators are still causing continued population declines of several species, intensive predator control is necessary for the conservation of many New Zealand birds (Clout et al., 1995: McLennan et al., 1996; O'Donnell, 1996). Species are moved to predator free offshore islands or areas on the mainland ("mainland islands") where predators are either controlled through intensive poisoning and trapping or excluded by predator-proof fences (Armstrong, 1995; Armstrong and McLean, 1995; see the Reintroduction Specialist Group Oceania Website at: http://www.massey.ac.nz/~darmstro/rsg.htm). Although research and conservation programs in New Zealand focus on nest predation, one of the key factors affecting avian survival in forest fragments, the role habitat fragmentation plays in these population extinctions/declines remains untested. Do populations in small fragments suffer additional costs for living in a fragmented environment, such as even higher rates of nest predation due to an influx of nest predators from the surrounding matrix (review in Chalfoun et al., 2002b) or perhaps reduced food availability? These are important questions that need to be promptly addressed in New Zealand for future persistence of populations in what is now a highly modified environment. Such studies will also add valuable information to the fragmentation literature in regards to a different geographical region within a unique evolutionary system.

The New Zealand robins, *Petroica longipes* (North Island robin) and *P. australis* (South Island robin, Holdaway et al., 2001), are commonly used as indicator species throughout New Zealand (Powlesland, 1997). Robin nest survival is used to compare mainland populations with and without management (Powlesland et al., 1999), and robins are often reintroduced into areas where long-term, intensive predator control is being undertaken to test the adequacy of these control programs (Armstrong, 2000). Robins make an ideal species to study the effects of habitat fragmentation because,

despite their decline since human colonisation (Oliver, 1955), they can still be found in large continuous forests and some forest fragments on mainland New Zealand.

To accurately measure the habitat quality of forest fragments, it is important to directly measure demographic performances of individual populations, specifically birth and death rates (Breininger et al., 1995; Armstrong, 2005). In addition to this information, it is also important to determine which habitat characteristics may be key factors in affecting population dynamics. Two crucial determinants of avian reproductive success are (i) food availability and (ii) nest survival rates. It is well recognized that food abundance and availability affect the reproductive success of birds (Lack, 1968; Martin, 1987), and that nest predators are accountable for up to 80% of avian nest losses (Ricklefs, 1969; Martin, 1993). This makes food and predator abundance key habitat variables to measure when assessing habitat quality.

Food availability has generally been ignored in previous habitat fragmentation studies, largely because invertebrate sampling is enormously labour-intensive, and statistical differences can be difficult to obtain because of the high variation around mean estimates (Cooper and Whitmore, 1990). The emergence of Burke and Nol's (1998) study demonstrating that invertebrate biomass per area was 10 to 36 times greater in large compared with small forest fragments has sparked a number of studies investigating food and forest fragments. However, to date only Burke and Nol (1998) and Zanette et al. (2000) have found evidence linking a measure of food availability and forest fragmentation with negative implications for avian species, whereas no noticeable food limitation was found in three other studies (Nour et al., 1998; Buehler et al., 2002; Sekercioglu et al., 2002).

Both Burke and Nol (1998) and Zanette et al. (2000) studied insectivorous species that, like New Zealand robins, feed predominately on the forest floor. These surface dwelling insects may be prone to increased desiccation at habitat edges, where the environment is warmer and drier (Didham et al., 1996). Such edge effects have been found to penetrate at least 50 m within New Zealand fragments with altered microclimate and vegetation associations (Young and Mitchell, 1994). Studies on the effect of habitat edges on invertebrate abundance are equivocal, with invertebrate abundance increasing towards the forest edge (Roland and Taylor, 1997; Rothman and Roland, 1998), decreasing

along forest edges and within small fragments (Burke and Nol, 1998; Zanette et al., 2000; Van Wilgenburg et al., 2001) or showing no difference between edges and small fragments (Buehler et al., 2002; Sekercioglu et al., 2002; Major et al., 2003). Insect assemblages can also be altered by livestock grazing (Abensperg-Traun et al., 1996; Bromham et al., 1999), another potentially negative impact in small forest fragments. Habitat fragments distributed in agricultural landscapes are often on privately owned land, without adequate fencing from domestic livestock.

It is difficult to determine the true extent to which food is limiting avian species, as it can be misleading to rely solely on measures of food abundance to assess food availability (Hutto, 1990). It is extremely difficult to know whether food availability has been measured adequately as researchers will perceive the environment differently to their study species. Hutto (1990) suggested studies use quantitative measures of behaviour and reproduction that vary with food supply to confirm that a given measure of food availability is appropriate. For example, Zanette et al. (2000) found that invertebrate biomass per area in small fragments was about half that in larger fragments, and was able to verify this measure of food abundance by recording shorter breeding seasons, lighter eggs and smaller nestlings in small fragments for eastern yellow robins (Eopsaltria australis). Fortunately the effect of food availability on behaviour and reproduction in passerines is quite well known. Birds' mean temporal attack rates (number of attacks/unit time) decrease when food availability is reduced (see Hutto, 1990). Food supplementation experiments and correlative studies have both shown that birds in food-rich areas spend a shorter proportion of time foraging than birds in areas of low food availability (Davies and Lundberg, 1985; see Hutto, 1990). During the breeding season, food availability has been shown to directly affect most aspects of reproductive life-history in birds (review in Martin, 1987), such as timing of breeding, hatching success, length of the incubation period, productivity, female nest attentiveness and male incubation feeding rates (Lyon and Montgomerie, 1985; Lifjeld and Slagsvold, 1986: Martin, 1987: Nilsson and Smith, 1988: Rauter and Reyer, 1997: Zanette et al., 2000; Eikenaar et al., 2003; Pearse et al., 2004). These life-history characteristics can be used to help verify a measure of food abundance.

Unlike food availability, nest survival has been extensively studied in the fragmentation literature. Nest survival is often reduced along habitat edges (e.g. Gates and Gysel,

1978; Yahner and Scott, 1988), within small habitat fragments (e.g. Wilcove, 1985; Small and Hunter, 1988) and fragmented landscapes (e.g. Robinson et al., 1995; Zanette and Jenkins, 2000). Although there appears to be considerable support for reduction in nest survival with fragmentation, there are undeniably inconsistencies (e.g. Gale et al., 1997; Friesen et al., 1999). In addition, the underlying mechanisms for such patterns via direct studies of nest predators and fragmentation are lacking (Chalfoun et al., 2002b). Concluding their paper on the abundance and species richness of a wide range of nest predator taxa, Chalfoun et al. (2002a) stated "*A crucial link that still needs to be rigorously tested is whether nest predation rates are directly correlated to predator abundance*". Thus, it appears to be important to concurrently measure the effect of fragmentation on nest predators and nest survival across a number of forest fragments.

In New Zealand mainland systems, where predators are the critical factor affecting both nest and adult survival, the abundance of nest predators is especially important to measure (James and Clout, 1996; Innes et al., 1999; Powlesland et al., 1999; Moorhouse et al., 2003; Innes et al., 2004). One of the most destructive predators is the ship rat (*Rattus rattus*), accidentally introduced in the second half of the 19th century and now found throughout the country (Atkinson, 1973). These are agile climbers who eat a wide range of fruits, invertebrates and birds and are known to be major predators of robin nests (Brown, 1997; Brown et al., 1998; Innes, 2001). In general footprint tracking tunnels are used to estimate the relative density of ships rats, with tunnels using ink-pad and paper to record the presence of rats (Innes et al., 1995; Ward-Smith et al., 2004). Such a method requires far less time and effort than attempting to measure absolute density, and encouragingly tracking rates have been found to correlate with estimates of absolute density in rat removal experiments (Brown et al., 1996; Blackwell et al., 2002).

1.1 Study species and area

I studied North Island robins in the Benneydale region ($175^{\circ}22$ 'E, $38^{\circ}32$ 'S) in the central North Island of New Zealand. Over three breeding seasons between August 2002 and February 2005 I monitored 72 different pairs (n = 30, 36, 34 for each consecutive year) across 15 fragments ranging in size from 1.6 - 1 626 ha (Table 1.1). I initially searched for robins in over 55 forest fragments in a 14 000 ha area of remnant podocarp-broadleaf forest. Most fragments less than 50 ha contained few if any robin pairs, so all small fragments with robins were included in the study. In fragments #1-11

(see Table 1.1) all robin pairs were monitored as they contained relatively few robins. Study plots were established with flagging tape at 50 m intervals over a 150 x 150 m grid (girds used for tracking tunnels *see* 2.1.3). Pairs situated outside this grid in the smaller fragments were still monitored e.g. Mangarruhel's three pairs in the third year were situated > 500 m from each other. In fragments #12 and #13 pairs were monitored around the central study plot. I chose two larger fragments (#14 and #15) that were close to the occupied small fragments and established study plots > 200 m from the forest/pasture edge. While these two large fragments contained many robins a maximum of five pairs were monitored in each, these pairs were centred near the study plots (Table 1.1 & Fig. 1.1).

The forest remnants in this study were originally part of a continuous podocarpbroadleaf forest, now restricted to Pureora Forest Park, situated 20 km east of the study area. Pureora is one of the largest podocarp-broadleaf forests remaining in the North Island, covering approximately 78 000 ha. The landscape between Pureora and the study area is now dominated by pasture used for sheep and cattle grazing and large tracts of exotic plantations (*Pinus radiata*). The canopy within my forest fragments retains some of the relic forest species, with scattered to locally dense emergent podocarps including rimu (Dacrycarpus dacrydioides), matai (Prumnopitys taxifolia), miro (P. ferruginea), and totara (Podocarpus totara). The canopy is now dominated by the broadleaf species tawa (Beilschmiedia tawa), with areas of hinau (Elaeocarpus dentatus) and rewarewa (Knightia excelsa). Common understorey species included mahoe (Melicvtus ramiflorus), kamahi (Weinmannia racemosa), pigeonwood (Hedycaryo arborea), kanono (Coprosma grandifolia), putaputaweta (Carpodetus serratus), tree fuchsia (Fuchsia excorticata) and soft treefern (Cvathea smithii). All fragments were logged in the past, the most obvious signs being the scarcity of large podocarps and the presence of large tree stumps.

Table 1.1. The 15 forest fragments and their individual sizes and isolation index (see Chapter 2, p.16 for description, the smaller the number the more isolated the fragment), plus the number of robin pairs monitored in each fragment during the three breeding seasons (2002-2005). Numbers in parenthesis indicate how many females died during the breeding season or were not present during the following breeding season. Numbers in the first column correspond to the fragments' positions on Figure 1.1.

		Size	Isolation		Year	
#	Fragment	(ha)	(log)	1	2	3
1	12 th patch [*]	1.6	3.9	1	1	1
2	Little Tutu	2.0	3.1	0	0	1(1)
3	T37 [*]	2.9	3.7	1(1)	0	0
4	Benneydale [*]	3.7	2.9	1(1)	0	0
5	Tutu	4.9	2.8	2	2	2
6	Dennis	14.0	3.3	1	2 (2)	1
7	T74 [*]	14.4	3.3	2 (2)	2	3
8	B86	17.3	3.2	0	1	1(1)
9	Mangaaruhel	33.7	3.2	1	2	3
10	Te Hape [*]	46.8	3.4	2(1)	3(1)	2
11	Mangaaruhe2	71.9	2.9	2 (2)	1	1
12	Т38	72.1	3.6	4(1)	5 (3)	4 (2)
13	T91	147.1	3.4	3(1)	4 (2)	4(1)
14	Herekawe	316.2	3.7	5 (3)	6(1)	6(1)
15	Mangapehi	1625.7	4.9	5 (2)	7(4)	5

* Grazed fragments- no fencing adequate to exclude domestic livestock.



Figure 1.1. Map of study area showing fragments of native forest surrounded by exotic forest and agricultural matrix. The 15 fragments filled in red are those containing robin pairs that were intensively monitoring during three breeding seasons (2002-2005). The numbers correspond to individual fragments detailed in Table 1.1.

North Island robins are small (ca. 28 g), socially and genetically monogamous passerines (Ardern et al., 1997), with pair bonds usually retained throughout the breeding season and subsequent years until the death of the partner. Territory sizes varied considerably depending on the size of the forest fragment, but were typically between 0.5–2.0 ha and actively defended year-round. Outside the breeding season pairs subdivide the territory and have little interaction, with contact usually resulting in aggressive chases. Robins are extremely inquisitive, by clearing leaf litter robins can be

encouraged onto the ground to feed on the uncovered invertebrates. While on the ground it was relatively easily to train robins to take mealworm (*Tenebrio molitor*) larvae. After 'training', robins were lured into claptraps and individually colour banded for identification. All work for the project was conducted under a research permit from the New Zealand Department of Conservation and had animal ethics approval from Massey University Animal Ethics Committee.

Robins start breeding at one year of age, with males exhibiting delayed-plumage maturation (Armstrong et al., 2000). Females generally built their first nest in late August or early September, with a clutch of 2-3 eggs (*mean* 2.60, *range* 2-3, n = 78; Powlesland et al., 2000) laid in successive days after nest completion. The male feeds the female frequently during the building and egg-laying periods (courtship feeding). The female alone incubates the clutch for about 19 days, during which she receives a considerable amount of food from the male (male incubation feeding). Both adults feed nestlings for about 21 days until fledging and juveniles for 4-6 weeks post-fledging. Juveniles remain on the natal territory for 7-10 weeks (Armstrong et al., 2000). Females are multi-brooded and are capable of three successful broods or up to five failed nesting attempts in one breeding season (pers. obs.). The mean interval from fledging to laying of the subsequent clutch is 3.9 weeks (SE = 0.46, n = 15), minimum 10-16 days (Armstrong et al., 2000). While the mean interval between failed nesting attempts is 2.0 weeks (SE = 0.69, n = 3), minimum 6-9 days (Armstrong et al., 2000). The last young are usually fledged in late February.

1.2 Aims

My study aims to improve our understanding of the relationship between habitat fragmentation, food availability and predator abundance, and their influence on robin nest survival and productivity. This study is particularly significant, as it will be the first fragmentation study of this kind to be conducted in New Zealand. Not only will this broaden our knowledge of the processes that occur through habitat fragmentation but it will add information for another geographical region, within a system whose evolutionary history is especially unique, and where avian species are currently besieged by an array of introduced mammalian predators.

10

I collected food availability (invertebrate biomass) and predator abundance (rat tracking rates) data across a range of forest fragments differing in size, isolation and disturbance in an agricultural, forestry landscape in the central North Island of New Zealand (Chapter 2; Table 1.1 & Fig. 1.1). Currently, information pertaining to the response of New Zealand's invertebrate community and introduced mammalian predators to the effects of habitat fragmentation is lacking. These two key determinants of habitat quality are particularly important to measure as they both have the potential to impact the reproductive performance of avian populations (Martin, 1987; 1993; 1995). These habitat variables are generally expected to respond negatively (food) and positively (nest predators) to the process of habitat fragmentation. While collecting food availability and predator abundance data. I simultaneously monitored the reproductive success (nest survival and productivity) of robin pairs throughout the same study fragments (Chapter 3; Table 1.1). I first aimed to determine if there was a difference in reproductive success between the forest fragments differing in size, isolation and disturbance. I then aimed to test whether the observed patterns in reproductive success could be related to the two key habitat variables, determining the value of these variables as predictor indices in the future reproductive performance of robin populations.

Whereas the first two chapters focus specifically on the effects of habitat fragmentation, **Chapter's 4 and 5** assess behavioural responses of robins to food availability. By undertaking observations during female incubation and collecting time budget data during different periods of the robin's annual cycle. I further assess whether robins are food limited in the study area. Because perspectives and tests of life-history evolution have generally been based on north-temperate systems (see review Martin, 2004), these data on robin behaviour offer a unique opportunity to assess the impact of both predation pressure and food availability on a life-history system that evolved with a different predator assemblage that it currently experiences. I specifically test whether robin's incubation strategies conform to theory developed in north-temperate ecosystems.

The identification of individual species responsible for the high nest predation rates observed in fragmented landscapes is often only circumstantial, and generally relies on evidence obtained either through (i) artificial nests and model eggs, a well recognised method, with well recognised weaknesses (e.g. Zanette, 2002; Mezquida et al., 2004) or (ii) surveys of the abundance of potential nest predators along forest edges and from within forest interiors. In an attempt to better understand the impact of nest predation, it is important that we are able to accurately identify major predators within a system. Therefore, in **Chapter 6** I advocate a method of using artificial clay eggs in active passerine nests to identify nest predators. Due to the inaccessibility of robin nests I undertook this pilot study using nests from introduced European species whose nests were plentiful in the study area. I believe this method would be valuable to future nest predation studies, particularly those carried out in New Zealand.



2.0 Abundance of nest predators and food with respect to size, isolation and disturbance of forest fragments

Concern about the decline of avian populations, and the apparent link to forest fragmentation, has lead to studies attempting to unravel the relationship between fragmentation and the demographics of avian populations (e.g. Wilcove, 1985; Robinson et al., 1995; Donovan et al., 1997; Cooper and Walters, 2002; Lampila et al., 2005). Unquestionably fragmentation can negatively impact individuals through the direct loss of breeding, migratory or stopover habitats. However, three key findings have emerged from research on the avifauna living in small forest fragments (i) reduced nest survival (see recent review Chalfoun et al., 2002b; Stephens et al., 2003; Lampila et al., 2005), (ii) increased rates of brood parasitism (Brittingham and Temple, 1983; Robinson et al., 1995) and (iii) more recently the possible effect of food limitation (Burke and Nol, 1998; Zanette et al., 2000).

In an attempt to limit the number of habitat characteristics I measured, I chose two key variables from the fragmentation literature, nest predator abundance and food availability. My goal was to determine if predator abundance and food availability varied across forest fragments and to use these data in subsequent chapters to assess if this variation was correlated with the nest survival, productivity and breeding behaviour of robins (*Petroica longipes*). Robins are not a host for the two cuckoo species within New Zealand (long-tailed cuckoo, *Eudynamys taitensis*; shining cuckoo *Chrysococcyx*

lucidus) and for that reason brood parasitism was not considered (Gill, 1983; Briskie, 2003).

Previous research had shown that North Island robins were strongly affected by predation on eggs, nestlings, and nesting females during the breeding season (Brown, 1997; Powlesland et al., 1999; Armstrong et al., in press), and that the main nest predator in mainland broadleaf-podocarp forest is the ship rat (*Rattus rattus*) (Brown, 1997; Brown et al., 1998). I therefore indexed the abundance of ship rats using tracking tunnels, the standard technique for monitoring rodents in New Zealand forests (Innes et al., 1995). Previous research had also indicated that North Island robins were largely ground-feeding insectivores, and consumed most invertebrates encountered while foraging (Raeburn, 2001). I therefore indexed food availability for robins using pitfall traps, the standard method for monitoring ground invertebrates in New Zealand (Green, 2000).

With a high influx of nest predators into small forest fragments in other fragmentation studies (Hoover et al., 1995; Donovan et al., 1997) and findings of increases in abundance of ship rats in small and disturbed fragments (Dunstan and Fox, 1996), I predicted rat tracking rates to be higher in smaller fragments, with an associated decrease in nest survival among the robins breeding within these fragments. I also predicted invertebrate biomass to be reduced in smaller fragments, given findings in other studies showing reduced biomass on birds' territories in small compared to large forest fragments (Burke and Nol, 1998; Zanette et al., 2000), with an associated reduction in foraging efficiency and reproduction among the robins breeding within these fragments.

In addition to fragment size, I assessed the effects of two other variables: isolation and grazing regime. Isolation of fragments is an important component of habitat fragmentation, as reduction in dispersal and re-colonisation rates are predicted to cause declines in distributions of populations and species (Hanski, 1994; Hanski and Gilpin, 1997). When considering such effects, it is important to know whether isolation of fragments is also correlated with habitat quality, for example due to differences in soil type, topography, microclimate (Saunders et al., 1991). In New Zealand it is known that the historical pattern of forest fragmentation is not random with respect to habitat

14

landscape features (Ministry for the Environment 1997). Assuming that a reduction in the survival or reproductive output of a species in an isolated fragment is due solely to rates of dispersal (i.e. metapopulation dynamics) may therefore be unjustified (Armstrong, 2005). This is particularly likely, for example, if isolation is correlated with features of habitat quality because fragments persist as non-random areas within a modified environment (e.g. southern facing remnants in particularly steep terrain). I therefore assessed whether rat tracking or invertebrate biomass among fragments was correlated with isolation. Grazing by domestic livestock is a key factor affecting habitat quality of forest fragments, as it is well known to affect vegetation cover, litter cover, soil and the microclimate (Yates et al., 2000). I therefore tested whether variation in rat tracking rates or invertebrate biomass among fragments were correlated with grazing intensity and fragment isolation as well as fragment size.

2.1 Methods

2.1.1 Study species and area

See section 1.1 for details. I measured food availability and predator abundance in 15 forest fragments (Table 1.1) over three robin breeding seasons (2002-03, 2003-04, and 2004-05).

2.1.2 Food availability

The following is a general description of the invertebrate sampling method used to index food availability within each robin territory. Results from this sampling are used throughout the remainder of the thesis, so this section will be cited in the methods sections of subsequent chapters.

To index food availability I set up grids of continuous-kill pitfall traps, a common method used throughout the world for sampling surface-active invertebrates (Southwood, 1994). I indexed food availability on the territory of each robin pair being monitored (Table 1.1), hence the sample of territories in each fragment was used to assess food availability for the fragment. To ensure I centred the pitfall grids on each territory, I used the location of each pair's first nesting attempt to situate a grid of 6 (3 x 2) pitfall traps, with inter-trap spacing of 10 m. Pitfall sites were created using sleeves of PVC pipe (76 x 150 mm) inserted into the ground until the lip was flush with the

forest floor. A plastic cup (75 x 85 mm) was placed within each sleeve and filled twothirds with ethylene glycol to preserve the invertebrates caught. Each trap was covered by a piece of 30 x 30 cm aluminium to prevent rainfall, leaves and twigs from falling into the trap. The cover was approximately 2 cm above the ground's surface. Because it was clearly evident that leaf litter was severely impacted by livestock grazing and I was interested in the invertebrates living within the leaf litter, I recorded the litter depth (mm) at each pitfall trap and averaged across the six traps. Pitfall contents were collected every six weeks. During the first breeding season there were three sampling periods between 15 November 2002 and 22 March 2003. During the second season pitfalls were opened earlier and collected four times between 31 August 2003 and 17 February 2004. During the final season pitfalls were collected five times between 20 July 2004 and 16 February 2005. All invertebrates collected, except Carabid beetles, were dried at 60°C for 36 h and weighed on an electronic balance to the nearest 0.001 g. carabid beetles were excluded from the samples because both South Island robins (P. australis) (Powlesland, 1981) and North Island robins (Raeburn, 2001, and this study) avoided eating these beetles. The contents of the six pitfalls in each grid were summed, resulting in one dry biomass measurement per territory every six weeks.

2.1.3 Predator abundance

The following is a general description of the tracking tunnel method used to index the abundance/activity of ship rats within each forest fragment. Results from these tracking tunnels are used throughout the remainder of the thesis, so this section will be cited in subsequent chapters.

I used the proportion of baited tracking tunnels with rat footprints (tracking rate) to provide an index of relative rat abundance. Although standard protocols have been developed for the use of tracking tunnels. allowing conservation managers and researchers to compare tracking indexes across studies and sites (Gillies and Williams 2003 unpublished), it was impossible to use this standard spacing due to our fragment sizes. I used the standard inter-tunnel interval of 50 m, but placed tunnels in grids rather than transects. I put a 4 x 4 grid in all fragments large enough to fit such a grid (>3 ha) and a 3 x 3 grid in fragments between 1.5-3 ha. The smallest fragments had five tunnels, consisting of one central tunnel and four tunnels 50 m at right angles. Grids were centred in small fragments, whereas grids in larger fragments were positioned on the

main robin study area > 200 m from the forest/farmland boundary. All grids were orientated on an east-west and north-south bearing.

All tracking tunnels consisted of a wooden base with a plastic 'coreflute' cover (500 x 100 x 100 mm). The tracking papers and central ink-pad (covered with food dye) were placed in a separate plastic tray inside the tunnel. Tunnels were baited with peanut butter every four to six weeks and the papers left for 24 h on each tracking occasion. As an animal passed through the tunnel it picked up food colouring on its feet, leaving footprints on the papers as it departed. I used this data to obtain a tracking rate per fragment for each of the tracking occasion across the three years 2002-2005 (tracking rate = tunnels tracked in 24 hr / tunnels available).

2.1.4 Statistical Analyses

Invertebrate biomass for the six pitfall traps per robin territory were summed and square root transformed prior to analysis to normalize the distribution of the data (tested with Shapiro-Wilks' statistic). The response variable pitfall biomass was then analysed using PROC MIXED (Version 8.02 SAS Institute, 1999) to fit a general linear mixed model. Predictor variables used in the analyses included fragment size (ha) and isolation (both variables log-transformed prior to analysis), the mean rat tracking rate for each biomass collection period, leaf litter depth and grazing regime within the fragment (ungrazed = no domestic livestock; grazed = no fencing adequate to exclude domestic livestock). The univariate models for each predictor variable were run with year and month (month collection began) included in the model and robin territory as a random effect. The random effect accounted for the significant variation between robin territories (territory $F_{78, 316} = 4.57$, P < 0.001). This was necessary as each territory was the sampling unit in the analysis, with multiple samples collected across years and months.

After taking into account the variation across years, months and among individual territories the relationship between invertebrate biomass and the predictor variables could be assessed. The most parsimonious model was obtained by sequentially adding and deleting significant terms (univariate significance $\alpha < 0.10$). Both forwards and backwards elimination were used to test for model robustness. For the significant temporal trends in invertebrate biomass I calculated the difference of least square means (DLSM) to make pairwise comparisons between different months and years. The

Bonferroni procedure was used to adjust significance levels to control for Type I error when conducting multiple pairwise comparisons.

I calculated an index of fragment isolation based on radio-tracking data for dispersing juvenile robins within my fragmented landscape (Y. Richard in prep.). This index differs from the conventional measurement of fragment isolation which only considers the straight line distance to the nearest forest area of a particular size or greater (e.g. Watson et al., 2005). Instead, two measurements were needed to calculate this index; the sum area of the surrounding fragments within a 3 km radius from the focal fragment, divided by the "cost distance" to each of these fragments. The cost distance not only takes into account the actual distance between the fragments but also the habitat matrix a dispersing robin would need to cross to reach each fragment. A low cost distance would indicate a short dispersal distance and an easier matrix for a robin to use (e.g. suitable habitat corridor), a larger value indicates a long dispersal distance and a harder matrix to cross (e.g. pasture). The smaller the isolation index, the more isolated the fragment.

Spearman correlation analyses (SAS PROC CORR) were used to assess the relative ranking (ordinal data low-high biomass) of the robin territories across the biomass collection periods, using the Bonferroni correction to adjust the significance levels to control for Type I error.

The response variable rat tracking rate was analysed as proportional data (tracked tunnels / total), using the SAS GLIMMIX macro, fitting a generalized linear mixed model. The error distribution and link function were specified as binomial and logit with fragment included as a random effect as tracking tunnels were run over multiple years and months within the same fragments. Predictor variables used in the analyses included year, month, grazing regime and fragment size and isolation, both of these variables were log-transformed prior to analysis to normalize data. The most parsimonious model was obtained by sequentially adding and deleting significant terms (univariate significance $\alpha < 0.10$). Both forwards and backwards elimination were used to test for model robustness. All tests are two-tailed and the assumed level of significance for all tests is $\alpha < 0.05$.

2.2 Results

2.2.1 Pitfall biomass

There was a marked seasonal effect on the mean pitfall biomass, with a significant difference between months (Month $F_{5, 318} = 88.77$, P < 0.001). Biomass was lowest for collection periods starting in September (end of winter), and was highest during the summer months of January, February and the early autumn month of March (Fig. 2.1).

The year 2003-2004 recorded the highest mean pitfall biomass for January compared to the other two years, and for February compared to 2002-2003 (Fig. 2.1). There were no other significant differences between years for the months I could directly compare (Fig. 2.1).



Figure 2.1. Mean ($\pm 1 SE$) invertebrate biomass per collection period (six weeks) over the three-year sampling period, across all pitfall traps. The months are when the six-week collection periods started (not necessarily the start of each month). All months were significantly different from each other (P < 0.006), except January and March (DLSM = -0.075, SE = 0.044, P > 0.100) and October and November (DLSM = 0.062, SE = 0.034, P > 0.100). Asterisks indicate that biomass was higher in 2003-2004 than one or both of the other years for the months indicated (** P < 0.01, ***P < 0.001).

Individual analysis of the predictor variables revealed the significant effect sampling year and month have on invertebrate biomass (Table 2.1). Because of this effect they were both included in the analysis for each predictor variable. None of the variables I measured had a significant effect on invertebrate biomass (Table 2.1), with the final model only including year ($F_{2, 316} = 26.06$, P < 0.001) and month ($F_{5, 316} = 86.50$, P < 0.001). Although leaf litter depth did not help predict invertebrate biomass there was a significant reduction in leaf litter in grazed (*mean* 22.3 mm, *SE* = 0.772) compared with ungrazed fragments (*mean* = 36.1 mm, *SE* = 0.436; *t* = -5.330, *DF* = 13, *P* < 0.001).

Table 2.1. Generalized linear mixed models (binomial error, logit link) examining the influence of year, month, grazing regime, fragment size and isolation, leaf litter depth and mean rat tracking rate on the variation in invertebrate biomass (\sqrt{g}) after controlling for variation between indivudual robin territories (territory included as a random effect).* Individaul univariate estimates controlling for the effect of year and sampling month. Estimate for year, month and grazing are differences in the logit with respect to the intercept value (2002-2003, September and grazed).

Variable		Univariate Models			*Month & year controlled		
		Estimate	SE	t	Estimate	SE	t
Year [2002-2003]	2004-05	-0.261	0.046	-5.67***			
	2003-04	0.001	0.044	0.03			
Month [Sept]	October	0.146	0.041	3.57***			
	November	0.209	0.041	5.11***			
	January	0.408	0.039	10.28***			
	February	0.662	0.039	16.66***			
	March	0.483	0.053	9.10***			
Grazing [grazed]		-0.051	0.063	-0.82	-0.022	0.053	-0.42
Fragment size Log ₁₀ (ha)		-0.013	0.029	-0.45	-0.009	0.024	-0.40
Isolation Log ₁₀		-0.015	0.038	-0.38	-0.014	0.032	-0.44
Leaf litter depth (mm)		-0.001	0.002	-0.29	0.002	0.002	0.99
Rat tracking rate		-0.077	0.091	-0.85	-0.111	0.077	-1.44

*P < 0.10, **P < 0.05, ***P < 0.01

One problem when sampling invertebrates is the large variation around mean estimates of invertebrate abundance (and biomass). In particular it is useful to establish whether the variability between territories is consistent across collection periods. If during a collection a territory is ranked high (high biomass), but then during the next collection period it is ranked low (low biomass) this would indicate large variation within a single territory. Alternately, if the relative ranking of the robin territories remained stable over the collection periods this would provide support for the pitfall data to be useful in the analysis of reproductive success and behavioural observations (Chapters 3-5). Indeed, in 14 out of 19 cases, territory rankings were significantly correlated between pairs of months in the same breeding season (Table 2.2). Territory rankings, therefore, generally stay consistent. That is, territories that collect high invertebrate biomass one month appear to collect high biomass all months, and vice versa for low biomass territories.

Table 2.2. Correlation (r s) between invertebrate biomass on each robin territory during the three sampling years, across the different sampling months in the Benneydale region, New Zealand, 2002-2005. Correlation coefficients in bold retain their statistical significance after sequential Bonferroni correction ($\alpha = 0.05$; Quinn and Keough 2002).

	Ост04	n	NOV04	n	JAN05	n	Feb05	n
SEP04	0.598***	32	0.637***	25	0.738***	21	0.491*	21
Ост04			0.659***	29	0.363	25	0.180	25
Nov04					0.276	32	0.317	32
JAN05							0.514**	32
	Nov03		Jan04		FEB04			
Ост03	0.799***	26	0.675***	24	0.672***	24	XXXXXX ()	
Nov03			0.673***	35	0.617***	35		
Jan04					0.689***	36		
	Feb03		MAR03				-	
JAN03	0.563**	28	0.010	28				
FEB03			0.409*	28				

*P < 0.05; **P < 0.01; ***P < 0.001

2.2.2 Rat tracking rates

Rat tracking rates were lower during 2002-2003 (mean tracking rate = 0.573, SE = 0.043, n = 71) compared with the other two years (Table 2.3; 2003-04, mean tracking rate = 0.686, SE = 0.047, n = 60; 2004-05, mean tracking rate = 0.643, SE = 0.044, n = 0.643, SE = 0.044, SE = 0.044, n = 0.643, SE = 0.044, SE = 0.044, n = 0.643, SE = 0.044, N =

61). No seasonal effects were detected or any effect of fragment isolation (Table 2.3). Tracking rates were lower in fragments grazed by domestic livestock and in smaller fragments (Fig 2.2, Table 2.3). However, when fragment size, grazing and year were entered into the model, fragment size was no longer significant, resulting in a reduced model. That is, the variation observed in rat tracking rates could be explained by the low tracking rates reported in 2002-2003 and the presence or absence of domestic livestock grazing (Table 2.3).

Table 2.3. Generalized linear mixed models (binomial error, logit link, with fragment included as a random effect) relating rat tracking rate to year, month, fragment size, isolation and grazing regime. Estimate for year, month and grazing are differences in the logit with respect to the intercept value (2002-2003, March and grazed).

.,	Univaria	te Mod	els	Reduced Model			
Variable		Estimate	SE	Т	Estimate SE		t
Year	2004-05	0.517	0.245	2.11**	0.437	0.245	1.78*
	2003-04	0.995	0.251	3.96***	0.958	0.253	3.79***
Month	September	-0.381	0.494	-0.77			
	October	-0.046	0.474	-0.10			
	November	0.586	0.484	1.21			
	December	-0.075	0.578	-0.13			
	January	0.114	0.476	0.24			
	February	0.202	0.477	0.42			
Grazing		2.211	0.517	4.28***	2.202	0.591	3.73***
Fragment size Log	0.959	0.404	2.38**				
Isolation		0.046	0.823	< 0.0			

*P < 0.10, **P < 0.05, ***P < 0.01



Figure 2.2. The probability $(\pm 1 SE)$ of tunnels being tracked by rats in fragments of different size and in the presence (\circ) or absence (\blacklozenge) of domestic livestock grazing in the Benneydale region, New Zealand, 2002-2005. Tracking tunnels were baited with peanut butter and left for 24 h.

2.3 Discussion

I found no evidence to suggest rats increased in relative abundance/activity in small forest fragments. These results are contrary to the predictions in the forest fragmentation literature whereby, predator abundance and activity have been found to increase with decreasing fragment size. However, in a recent review by Chalfoun et al. (2002b) over half of the studies (57%) testing predator abundance in respect to fragment size did not find a significant relationship. Of the remaining studies, 26% found an increase in nest predator abundance in small forest fragments, while 17% found they were less abundant in smaller fragments (Chalfoun et al., 2002b).

With the relatively recent discovery of the negative impact reduced invertebrate biomass in forest fragments has on avian insectivores (Burke and Nol, 1998; Zanette et al., 2000), food availability is beginning to be implemented in fragmentation studies. The role of food limitation in other fragmented systems is still relatively untested. I did not find any relationship between invertebrate biomass and forest fragment size, even

when invertebrate collection was >200 m from the forest edge in two larger fragments, presumably far enough to escape microclimatic edge effects (Young and Mitchell, 1994).

Although invertebrate biomass was variable among robin territories, there was very little variation between the different forest fragments and no trend with respect to fragment size. These results indicate that robins in small fragments have similar availability to food to those living in larger fragments. Taxonomic differences between invertebrate samples may have been detected if I had detailed the composition and diversity of the invertebrate community between fragments (Van Wilgenburg et al., 2001). However, this study was primarily focused on the food available to foraging robins, not the change in the invertebrate diversity or structure. Changes in invertebrate diversity would be more likely to affect a species that exhibits specialized foraging behaviour or prey type than the generalist foraging behaviour displayed by robins (Powlesland, 1981; Raeburn, 2001, pers. obs.).

I also did not find a difference in invertebrate abundance between grazed and ungrazed fragments, even though the grazed fragments contained significantly less leaf litter. Studies examining the effects of grazing and habitat fragmentation on invertebrate communities have found complex relationships between species, woodland types and disturbance levels (Abensperg-Traun et al., 1996; Bromham et al., 1999). The structural complexity and diversity of the understorey and leaf litter habitat can influence the complexity of the invertebrate community (Andersen, 1986; Bromham et al., 1999). Although 1 do not know whether taxonomic differences exist between invertebrate communities in grazed and ungrazed fragments, this study showed that highly disturbed fragments are capable of supplying robins with similar invertebrate biomass to that found in less disturbed fragments.

Although the measure of invertebrate biomass did not differ significantly among fragments, there were significant differences among robin territories. Hutto (1990) warned that one trap on a territory could not represent conditions over the whole territory unless variation within a territory was less than between territories. It appears that the number of traps was sufficient to average variation across a territory, as territory rankings remained relatively constant over the collection periods. This is an important

24

result as it means comparisons between food availability and territories can be made with respect to nest survival, productivity and behavioural observations.

In general, fragmentation studies propose hypotheses about nest predators to explain the elevated nest-predation rates without directly studying the response of nest predators to fragmentation (see review Chalfoun et al., 2002b). Understanding the response of important nest predators to habitat fragmentation in New Zealand is critical, as nest predation is a significant process affecting the local demography of native species (e.g. Clout et al., 1995; James and Clout, 1996; Powlesland et al., 1999; Moorhouse et al., 2003; Innes et al., 2004). Throughout New Zealand, management and conservation agencies follow standard protocols when running tracking tunnels to assess management practices. However, no appropriate technique has been implemented in small forest fragments. While the method used in this study retained the 50 m interval between tunnels, the grid system is not comparable to other studies. A grid system risks increased contagion (one rat tracking a large number of tunnels), resulting in a potentially inflated and misleading tracking rate. Rat mark-recapture studies in small forest fragments would help address this if indeed there is a problem with such a system, highlighting an area of relatively little research within New Zealand.

Studies of the introduced ship rat in Australia and Madagascar have found higher abundances associated with disturbed, secondary forest types and roadside corridors where native rodents are less abundant (Dunstan and Fox, 1996: Downes et al., 1997; Lehtonen et al., 2001). Therefore, it was surprising that in my study I found rat tracking rates were significantly lower in highly disturbed, grazed fragments. The lack of native rodent competitors could explain the increased rat abundance in the less disturbed forest types in this study. This notion is supported by a study on the oceanic island of Tenerife (Canary Islands) with no native rodents. On Tenerife, ship rat predation on artificial nests was greater within the forest interior and a preserved forest remnant than along road edges and within a disturbed remnant (Garcia et al., 2005). It seems more likely that intensively grazed fragments provide unsuitable habitat for foraging rats. Little is known about the amount of time ship rats spend foraging on the ground, while two studies from New Zealand have found contrary results with ship rats spending 73% of foraging time >2 m above the ground (Hooker and Innes, 1995) and 93% on the ground (Dowding and Murphy, 1994). In Australia, ship rats spent large periods on the ground,

25
presumably foraging for some of this time (Cox et al., 2000). Cox et al. (2000) found that rats preferred microhabitats with a deep cover of leaf litter, and dense understorey with numerous vertical stems. A structurally complex and dense microhabitat not only provides plentiful food but it also offers protection from potential predators. In addition to the average leaf litter depth being reduced in grazed fragments, the understorey also tended to be completely removed (eaten) or trampled. Even where the presence of ship rats increased with the level of habitat disturbance, Lehtonen et al. (2001) still found a positive association with the amount of herbaceous cover. The lack of cover in grazed fragments may result in reduced protection from potential predators such as stoats (*Mustela erminea*) and cats (*Felis catus*), preventing rats from moving easily along the forest floor.

The similar invertebrate biomass between the grazed and ungrazed sites adds support for the suggestion that rats are avoiding the forest floor in grazed fragments due to a lack of cover, not lack of food. Invertebrates can make up a large component of ship rats' diets in New Zealand (Gales, 1982; Miller and Miller, 1995) and are abundant in the broadleaf-podocarp forest leaf litter (this study, Moeed and Meads, 1986). Therefore, we might expect rats to spend some time foraging on the ground, even in the grazed fragments. The lower rat tracking rates in grazed fragments could indicate avoidance in foraging on the forest floor, where tracking tunnels were located, but not a reduction in rat abundance. The underlying behaviour of the rats in such a modified environment requires further investigation.

Invertebrate biomass and rat tracking rates were not correlated with fragment size or isolation in this study. In the following chapters, I assess whether any of these variables are correlated with robin nest survival and productivity, incubation and foraging behaviour.



3.0 Nest survival, productivity and predation in forest fragments

Forest fragmentation has been cited as the cause of decline in many avian species in the northern hemisphere (Hagan and Johnston, 1992), with analogous evidence of "area sensitive" species now emerging from the southern hemisphere (Ford et al., 2001; Zanette, 2001). One hypothesis for population declines is reduced reproductive output in these highly fragmented landscapes caused by increased nest predation and brood parasitism (Brittingham and Temple, 1983; Wilcove, 1985; Hoover et al., 1995; Robinson et al., 1995; Hartley and Hunter, 1998; Burke and Nol, 2000). However, the response of nest predators to fragmentation appears to depend on the taxa, landscape scale and matrix studied (Chalfoun et al., 2002b). With nest predation already accounting for up to 80% of avian nest losses (Martin, 1993), any evidence that suggests that species are subject to even greater risks of predation in small fragments could account for the apparent "area sensitivity".

While numerous studies have examined the effects of habitat fragmentation on nest survival (see reviews in Chalfoun et al., 2002b; Stephens et al., 2003), no studies have addressed this issue within New Zealand, even though extensive forest fragmentation has taken place over the last 150 years. Mammalian predators introduced to New Zealand have caused the extinction and severe decline of the country's unique and endemic avifauna (Duncan and Blackburn, 2004) and are believed to be the main cause of ongoing population declines of several species (Clout et al., 1995; McLennan et al., 1996; O'Donnell, 1996). Consequently, conservation management and research is aimed

towards eradication of these introduced predators. The role of fragmentation in these population declines is unknown.

Recently, strong evidence has emerged concerning another threat posed by forest fragmentation, the availability of food (Robinson, 1998), with detectable food shortages observed in small fragments (Burke and Nol, 1998; Zanette, 2000; Luck, 2002; Luck, 2003). Food abundance and availability, like nest predation, are important factors affecting the reproductive success of birds (Lack, 1968; Martin, 1987). Higher reproductive output is generally associated with years (or areas) with greater food availability (see review, Newton, 1998). Nestling starvation during adverse weather conditions has been associated with a decrease in invertebrate abundance (Högstedt, 1981), as has fledgling number per nest (Strong et al., 2004). As nest survival is one of the key parameters affecting population viability, a reduction in survival caused by low food availability, higher nest predation or the synergistic effect of both (Zanette et al., 2003) would obviously be detrimental for the remaining mainland species of New Zealand.

Nest survival is an extremely important component of many avian studies, and used when assessing conservation management performance. It is often reported as "apparent success", the number of successful nests divided by the total number found. As early as the 1950s, it was recognised that apparent nest survival overestimated the true success rate because of the under-representation of early failed nests (Snow, 1955; Hammond and Forward, 1956) and a method was developed to overcome this problem (Mayfield, 1961; Mayfield, 1975). Many variations of Mayfield's original method are currently used in bird demographic studies (Johnson, 1979; Bart and Robson, 1982; Rotella et al., 2000; Stanley, 2000; Armstrong et al., 2002; Dinsmore et al., 2002; Jehle et al., 2004; Rotella et al., 2004; Stanley, 2004). Fortunately for current researchers, recent developments made it possible to incorporate a range of biologically relevant variables into nest survival models and to rigorously evaluate the importance of those variables (Dinsmore et al., 2002; Stephens, 2003; Rotella et al., 2004; Shaffer, 2004).

My goal was to test the possible effects of fragmentation on nest survival and productivity (2002-2005) of the North Island robin (*Petroica longipes*), formerly common throughout the North Island (Oliver, 1955). Unlike many other native species,

28

robins still occur in a number of forest fragments on the mainland, allowing me to evaluate the variation in daily nest survival rates across a range of forest fragment sizes. I used the program MARK (White and Burnham, 1999) to analyse whether nest survival varied with (1) fragment size and isolation, (2) predator abundance/activity or (3) food availability. Productivity was analysed using a nonlinear mixed model. I also provide data on the number of fledglings produced per successful nesting attempt and the relationship between fledging success and food availability, testing for the possible effect of nestling starvation.

3.1 Methods

3.1.1 Study species and area

See section 1.1.

3.1.2 Nest Monitoring

l monitored nest attempts by all pairs studied in each of the three breeding seasons (See section 1.1), i.e., 30 pairs in 2002/2003, 36 pairs in 2003/2004, and 34 pairs in 2004/2005. All pairs were checked weekly for nests, starting from the last week in August or the first week in September. Nests were typically found by following the females after the males called them off the nests to feed them. If no nest was found during the check, I continued until I had observed the female for at least 30 minutes, ensuring that she had no nest. I could therefore determine the laying date within one week, and could often/usually determine it more precisely from known dates of nest building, start of incubation, hatching dates and nest failure. All nests, once located, were monitored every week until they failed or successfully fledged at least one young. I determined the status (incubating, brooding or failed) of the nest by observing the behaviour of the parents. Most nests were too high (> 10 m) to easily observe the contents, and such checks could have attracted predators. I visited each nest as close to the day of fledgling as possible (1-4 days) to observe the parental feeding by the pair to determine the number of young (1-3) fledged. When juveniles were approximately four weeks post-fledging parental birds begin to reduce feeding and aggressively chase juveniles (pers. obs.). During this stage I would spend 1-2 days on the territory locating and banding all juveniles present when they could still be reliably detected due to their mobility and loud begging. After this stage juveniles were much harder to detect as they began to move outside their parents territory boundaries and were no longer regularly

fed (Y. Richards pers. com.). Hence I defined the juveniles as independent at four weeks of age. I therefore defined productivity as the number of independent young produced by a female over the breeding season, and checked each pair four weeks after fledging to count the number of juveniles present.

3.1.3 Food availability

See section 2.1.2.

3.1.4 Predator abundance

See section 2.1.3.

3.1.5 Statistical Analyses

Program MARK offers a flexible interface to build detailed models of daily nest survival using individual, group and time-specific covariates. Initially nests were coded similar to Dinsmore (2002) in MARK (Version 4.2), with years entered as groups and 29 August standardized as day 1 of the 180 day nesting season. Dinsmore et al. (2002) used a covariate for each day of the nesting season to incorporate the daily age of the nest on each of the days in the nesting season. I simply entered a nest's age on the first day of the nesting season, a single and often negative value instead of 180 covariates, and used the special functions available in MARK to calculate ages on all other days (see Rotella et al., 2004).

While MARK is a powerful tool in evaluating time-specific survival, I found no evidence that daily nest survival varied in a linear or quadratic trend across the breeding season. I therefore simplified the encounter history in MARK by treating all nests as laid on the same day and coded days according to the age of the nest rather than the laying date.

An example of MARK encounter history showing laying date

/*MGRR, 2002-01*/ 82 91 97 1 1 -80;

This nest was found on day 82 of the breeding season when it was two days old, last known to be active on day 91 and failed sometime between day 91 and day 97, the final nest check.

An example of a MARK encounter showing nest age

/*MGRR, 2002-01*/ 2 11 17 1 1;

This nest was two days old when found and failed somewhere between 11-17 days of age. This second method for coding the data allowed easier manipulation of the design matrix, and made it possible to include interactions between nest age and other factors.

I developed a set of *a priori* hypotheses to evaluate the variation in daily survival probabilities of robin nests relative to a number of ecological factors:

- Year: Nest survival rates often vary across study years. The source of this annual variation is frequently unknown as a large number of factors are potentially responsible (e.g. weather). I assessed annual variation across three breeding seasons, and tested whether any such variation could be accounted for by food availability or predator abundance and the following factors (see below). The three years were entered as groups in MARK.
- Nest age: In altricial species adults make increasingly frequent visits as a nest increases in age to feed growing nestlings. This increased activity is purported to increase the risk of nest predation (Skutch, 1949; Martin et al., 2000).
- 3) *Fragment size*: I tested the well-documented hypotheses that nest survival declines with decreasing fragment size (see review, Stephens et al., 2003).
- 4) Isolation index: Isolated fragments may tend to have higher or lower quality habitat due to differences in soil type, topography, microclimate (Saunders et al., 1991). Assuming that a reduction in the survival or reproductive output of a species in an isolated fragment is due solely to rates of dispersal (i.e. metapopulation dynamics) may therefore be unjustified (Armstrong 2005). In addition, isolated fragments may tend to have lower quality birds that were unable to acquire territories in more accessible fragments. See section 2.1.4 for description of isolation index (Y. Richard in prep.).
- 5) *Food availability (invertebrate biomass)*: Food availability is an important factor affecting the reproductive success of birds (Lack, 1968; Martin, 1987). Limited food can result in reduced nestling provisioning (Luck, 2003), fewer fledglings per nest (Strong et al., 2004), smaller nestlings, lighter eggs and shorter breeding seasons (Zanette et al., 2000). The index of food availability for each nesting attempt was the invertebrate biomass collected on the territory (see Chapter 2) during the 6-week period that best corresponded to the time of the nesting attempt.

6) *Predator abundance*: I hypothesized that nest survival would decrease with ship rat (*Rattus rattus*) tracking indices, as robin vital rates (annual adult survival and productivity) have been found to be negatively correlated with rat tracking rates (Armstrong et al., in press). Each nesting attempt was assigned the yearly mean rat tracking rate for the fragment (Chapter 2) as there was little variation between months.

I first considered the simplest model in which there is a constant daily nest survival. I then considered models in which each of the above six variables were added independently, and discarded any variable that did not improve the model. I considered a model with an interaction between nest age and year, as I suspected there was an usually high rate of nest predation during the incubation stage during the first breeding season. I then added other variables to that model.

Program MARK evaluates model support using Akaike's Information Criterion (AIC). The best model is that with the lowest AIC, indicating the best compromise between fit to the data (higher for more complex models) and simplicity (fewer parameters). The relative support for each model is indicated by their Akaike weights (Burnham and Anderson, 1998), calculated from the differences in AIC (Δ AIC) values between each candidate model and the best model. Fragment size, isolation and invertebrate biomass were log-transformed prior to model fitting because these variables had skewed distributions.

After selecting the best model, I derived estimates for daily survival rate and nest survival based on the parameter estimates produced by that model (see results). Nest survival is defined as the probability of a nest surviving from clutch completion to fledging, hence was estimated as the probability of a nest surviving for 40 days, the approximate time from the end of laying to fledging in North Island robins. Following Seber (1982), the delta method was used to obtain approximate standard errors and confidence intervals for these derived estimates.

In addition, using the approach of Shaffer (2004) I used PROC NLMIXED (Version 8.02 SAS Institute, 1999) to fit a logistic-exposure model to the nest survival data, specifying a binomial error distribution and a logit-link function. This approach can fit

similar models to those obtained using MARK, and also allows the inclusion of a single random effect. I used female as a random effect to test for variation among females and to assess whether predictor variables still had explanatory power when variation among females was included. The method could therefore be used to assess whether the apparent effects of any predictor variable were due to pseudoreplication, i.e., confounding effects of the same individual being associated multiple times with similar values of a predictor variable. However, I found that I could not fit models with more than one predictor variable in addition to the random effect, hence I used this approach to complement my MARK analysis rather than replace it. I ran all univariate models both with and without the random effect to ensure that the results for the latter group of models were the same as those obtained using MARK.

1 analysed the response variable number of fledglings (number of fledglings per successful nest) and productivity (number of independent young per female per year) using PROC NLMIXED, specifying a Poisson error distribution and a log-link function. The number of fledglings per successful nest was transformed by subtracting one, allowing an approximate fit to the Poisson distribution. Female was included as a random effect. The predictor variables used for both analyses were the same as those used in the nest survival analysis. However, each pair was assigned a single index of food availability for each breeding season rather than for each nesting attempt for the productivity analysis. These values were obtaining by fitting a general linear model to the food availability data for each year (Chapter 2) with respect to pair and food, and using the effect size for each pair as the index.

3.2 Results

3.2.1 Estimates of nest survival

A total of 203 robin nests were monitored over the three years, with daily nest survival 0.199 (*SE* 0.007) for 2002-2003, 0.336 (*SE* 0.004) for 2003-2004, and 0.363 (*SE* 0.004) for 2004-2005 based on the {year} model. Overall daily nest survival for the three breeding seasons was 0.315 (*SE* 0.003) based on the {constant} model.

Of the models considered, only two models received substantial support with both Δ_i values ≤ 1 and Akaike weights >0.20 (Table 3.1). Under the best model, the daily survival of robin nests was a function of the interaction between year and nest age plus fragment size and invertebrate biomass.

Daily nest survival rate increased substantially with nest age in 2002-2003, whereas a much smaller increase occurred in the other two years (Fig. 3.1). Consequently, models excluding the interaction between year and nest age received negligible support (Table 3.1).

Table 3.1. Summary of model selection results analysing daily survival rates of North Island robin nests during 2002-2005 in the Benneydale region, New Zealand using the program MARK. A logit link was used for all models. Prior to analysis, invertebrate biomass (food availability), fragment size and isolation were log-transformed.

Nest survival model ¹	K ²	AIC ³	Δ_i^4	wi ⁵
Nest age*Year + Fragment size + Biomass	8	592.637	0.000	0.407
Nest age*Year + Biomass	7	593.189	0.552	0.309
Nest age*Year + Fragment size	7	594.558	1.921	0.156
Nest age*Year	6	595.355	2.718	0.104
Nest age	2	599.095	6.458	0.016
Fragment size + Biomass	3	603.252	10.615	0.002
Fragment size	2	603.823	11.186	0.002
Biomass	2	604.030	11.393	0.001
Mean rat tracking rate	2	604.424	11.787	0.001
Year	3	604.727	12.090	0.001
Constant	1	604.743	12.107	0.001
Isolation	2	605.754	13.117	0.001

¹Candidate models for factors affecting daily nest survival.

²Number of parameters in model.

³Akaike's Information Criterion.

⁴Difference in AIC values from that of the best model.

⁵Akaike weights, indicating the relative support for the models.



Figure 3.1. Estimated daily survival rates (DSR) for North Island robin nests during a) 2002-2003, b) 2003-2004 and c) 2004-2005 breeding seasons in the Benneydale region, New Zealand. These estimates are derived from parameters estimated for model {Nest age*Year + Fragment size + Biomass} (Table 3.1) using Program MARK. The estimated DSRs shown here assume average values for fragment size and invertebrate biomass. 95% confidence intervals were estimated using the delta method (Seber, 1982).

When invertebrate biomass was added to the model {year*nest age}, it improved the model considerably (Table 3.1). The slope estimate on a logit scale for invertebrate biomass was positive (in the best model $\beta_{\text{biomass}} = 0.884$, SE = 0.444, CI = 0.009, 1.758), meaning nest survival increased with invertebrate biomass. The addition of fragment size to the best model also improved the model (an increase of $0.552 \text{ }\Delta\text{AIC}_{\text{c}}$ units), with a negative slope estimate (in the best model $\beta_{\text{fragment size}} = -0.184$, SE = 0.115, CI = -0.409, 0.043), meaning reduced nest survival in larger forest fragments.

The logistic regression equations for estimating daily survival probabilities under the best model were:

Logit (\hat{S}_i) for

2002-03 = 2.215 + 0.074 (nest age) - 0.184 (fragment size) + 0.884 (biomass) 2003-04 = 3.574 + 0.012 (nest age) - 0.184 (fragment size) + 0.884 (biomass) 2004-05 = 3.934 + 0.002 (nest age) - 0.184 (fragment size) + 0.884 (biomass)

To evaluate the effect of fragment size and invertebrate biomass on nest survival, I first derived estimates of daily survival probability from the above equations across a range of fragment sizes and biomass measurements (in the range recorded within the study). The estimated nest survival (probability of surviving 40 days) was then obtained from the product of the 40 daily survival rates. Figure 3.2 shows the estimated effects of fragment size and invertebrate biomass on nest survival for each of the three breeding seasons.



Figure 3.2. The effect of fragment size (a, b & c) and invertebrate biomass (d, e & f) on the overall survival of robin nests during 2002-2003 (a & d), 2003-2004 (b & e) and 2004-2005 (c & f). Estimates were calculated from the logistic regression equation from the best model {Nest age*Year + Fragment size + Biomass}, using an average biomass measurement in the fragment size calculations and an average fragment size for the biomass calculations. The biomass measurements represent the typical range over the three years. 95% confidence intervals were estimated using the delta method (Seber, 1982). Estimates are plotted on a log-scale. Black arrows in graph (a) indicate actual fragment sizes used in the study during 2002-2003, additional black arrows in the following two years represent new fragments, while the white arrow indicates a fragment where robins were no longer breeding after the first season.

3.2.2 Random effects

In PROC NLMIXED I used the univariate terms from the nest survival models under consideration in the MARK program, adding female as a random effect to consider the possible effects among individual females. The best model from this analysis was identical to the best univariate model {nest age} obtained using MARK (Table 3.1, Table 3.2). The addition of female as a random effect reduced the support of this model (Δ AIC = 1.693). In other cases, adding the random effect increased the support of univariate models (Δ AIC was 1.112 for biomass) or had little effect. The important result is that nest age, invertebrate biomass, and fragment size are still shown to affect daily nest survival when variation among individual females is accounted for (Table 3.2).

Table 3.2. Summary of generalized linear model selection (binomial error, logit link) with female included as a random effect for North Island robin nest survival in the Benneydale region, New Zealand, 2002-2005. Prior to analysis, invertebrate biomass, fragment size and isolation were log-transformed.

Nest survival model	К	AIC	Δ_{i}	Wi
Nest age	2	599.095	0.000	0.420
Nest age*	3	600.788	1.693	0.180
Biomass*	3	602.918	3.823	0.062
Fragment size*	3	603.570	4.475	0.045
Constant*	2	603.740	4.645	0.041
Fragment size	2	603.823	4.728	0.040
Biomass	2	604.030	4.935	0.036
Mean rat tracking rate*	3	604.352	5.257	0.030
Mean rat tracking rate	2	604.424	5.329	0.029
Year*	4	604.466	5.371	0.029
Year	3	604.727	5.632	0.025
Constant	1	604.743	5.648	0.025
Isolation*	3	604.969	5.874	0.022
Isolation	2	605.754	6.659	0.015

* female included as a random effect in model.

3.2.3 Fledgling number

On average, the 88 successful nests fledged 1.86 (SE = 0.698) nestlings. This value could be slightly underestimated, as fledglings that died very quickly following fledging may not have been located before their disappearance. Fledgling number did not vary between years ($F_{2.35} = 0.90$, P = 0.415) and was not related to the two variables important to nest survival; fragment size (*estimate* = -0.016, SE = 0.144, P = 0.909) or invertebrate biomass (*estimate* = -0.423, SE = 0.510, P = 0.409), nor was it related to mean rat tracking tunnel rate (*estimate* = 0.138, SE = 0.413, P = 0.738) or isolation (*estimate* = 0.085, SE = 0.196, P = 0.664).

3.2.4 Productivity

On average, females produced 1.20 independent juveniles per breeding season (n = 100, SE = 0.110, range 0-4), with little support for differences between the three breeding seasons (Table 3.3, Fig. 3.3). None of the models received strong support in the analyses of productivity, with {fragment size} the only model better than the {constant}. The slope estimated for fragment size was negative ($\beta_{\text{fragment size}} = -0.186$, SE = 0.123, Cl = -0.427, 0.055), a qualitatively similar result to that obtained for nest survival.

Table 3.3. Summary of generalized linear model selection (Poisson error, log-link) with female included as a random effect for productivity in the Benneydale region, New Zealand, 2002-2005. Prior to analysis, invertebrate biomass, fragment size and isolation were log-transformed.

Productivity model	К	AIC	Δ_{i}	Wi
Fragment size	3	288.699	0.000	0.253
Constant	2	288.817	0.117	0.239
Isolation	3	289.233	0.534	0.194
Mean rat tracking rate	3	289.741	1.041	0.151
Biomass	3	290.618	1.919	0.097
Year	4	291.384	2.684	0.066

I also calculated the number of fledglings produced per female calculated 1-3 days after successfully fledging. This is different from fledgling number (as above) as it takes into account all nesting attempts (including failed nests). This is similar to productivity except calculated immediately after fledging (1-3 days), not four weeks after fledging as in the productivity analysis. On average females produced 1.64 fledglings per breeding season (Fig. 3.3; n = 100, SE = 0.143, range = 0-5). This slightly higher result compared to productivity indicates a reduction in fledgling numbers during the four week postfledging period.



Figure 3.3. Mean $(\pm 1 SE)$ number of fledglings and independent juveniles produced per female across the three breeding seasons.

3.3 Discussion

My results suggest that North Island robins experienced relative food shortages throughout the breeding season, with lower nest survival correlated with low invertebrate biomass. Nest survival was higher in smaller fragments, contrary to my prediction that nest survival would be lower in such fragments due to higher predation. Although there is strong evidence from the northern hemisphere that smaller forest fragments tend to have higher nest predation (see review, Stephens et al., 2003), there is little evidence from Australasia (i.e. continental Australia and mainland New Zealand). The previous studies assessing nest survival as a function of fragment size have all been conducted in Australia. Only two of these studies found negative effects of fragments (Major et al., 1999) and an unfragmented compared to a fragmented landscape (Luck, 2003). One study found higher nest survival in smaller fragments, consistent with my results (Brooker and Brooker, 2001), and five found no apparent

effect (Taylor and Ford, 1998; Matthews et al., 1999; Walters et al., 1999; Zanette and Jenkins, 2000; Cooper et al., 2002). My results demonstrate the complexity of drawing similar conclusions between fragmented environments across different species and ecological systems.

In a recent review of nest predators and forest fragmentation, Chalfoun et al. (2002b) concluded that avian, but not mammalian, nests predators were more likely to respond in a positive manner to fragmentation, increasing in abundance, activity, and species richness. Chalfoun's avian predators refer to the larger carnivorous members of the Corvidae family, which are absent from the native New Zealand avifauna. Only two potential avian predators were seen regularly in my study area, morepork (Ninox novaeseelandiae) and the Australian magpie (*Gymnorhina tibicen*). Although morepork are known to prev on robin nestlings (Brown, 1997), the occurrence is unlikely to be common as a detailed study on morepork diet in Pureora Forest revealed 99% of their diet was invertebrates (Haw et al., 2001). The importance of magpies as major nest predators is questionable (Morgan et al., in press) and they were never located within any forest fragment. This scarcity of avian predators within this system may account for the lack of a negative effect of forest fragmentation on nest survival. The other major cause of reduced nest survival in forest fragments is caused by brood parasitism (Brittingham and Temple, 1983; Robinson et al., 1995). Neither of New Zealand's cuckoos species (long-tailed Eudynamys taitensis; shining cuckoo Chrysococcyx lucidus) parasitise robin nests (Gill, 1983; Briskie, 2003), although they have the potential to be diurnal nest predators (J. Briskie pers. obs.). While both species were present within this system, they were relatively uncommon, all but eliminating this potentially negative impact on nest survival.

Ship rats are major predators of robin nests within New Zealand (Brown, 1997; Brown et al., 1998), yet rat tracking indices were poor predictors of nest survival in this study. Tracking indices have been shown to be well correlated with actual rat population densities in some situations (Brown et al., 1996; Blackwell et al., 2002). However, Blackwell et al. (2002) were only able to demonstrate a significant correlation between rat tracking rates and estimated density (based on residual trap catch) at moderate to high population densities, not at low rat population densities. Indeed, many of the fragments in my study recorded 80-100% rat tracking indices, with little variation

between months or years. This is substantially higher than in the tawa-podocarp forest in Blackwell et al. (2002) study. I suggest that high tracking indices, like low, make this method inappropriate at accurately estimating relative rodent abundance. Complete saturation (i.e. 100% indices) is unable to detect slight reductions or increases in rat abundance, which may be necessary for correlation with nest survival rates. Also, the grid system required in small fragments has a higher risk of contagion through multiple tracking of tunnels by one individual rat. Therefore this method is very susceptible to rodent activity levels and home range sizes. Information about the home range size of ship rats in small fragments is currently unknown, although in general they appear variable and adaptive (Innes and Skipworth, 1983; Hooker and Innes, 1995; Innes, 2001). Variation in tracking rates was only recorded in fragments intensively grazed by domestic livestock (Chapter 2), with grazed fragments recording lower tracking rates, similar to a previous study on the North Island (Innes et al., 2004). Even with lower indices, I was unable to detect a correlation with nest survival. It is possible that rats are still abundant within these fragments, but are behaving differently, whereby they avoid descending to the ground because of reduced understorey cover caused by domestic livestock grazing (Cox et al., 2000).

Robin nest survival increased considerably with nest age during the first breeding season. Generally, this is unexpected for altricial species, as Skutch (1949) hypothesized increased activity by adults feeding young should attract nest predators, causing a proximate decrease in nest survival during this period. High predation levels during the incubation period have resulted in a lack of support for Skutch's hypothesis in the past (Martin, 1992; Roper and Goldstein, 1997). However, Martin et al. (2000) demonstrated that this effect was caused by poor nest sites incurring rapid predation. Once nest-site effects were taken into account, predation showed a strong proximate increase with parental activity during the nestling stage. Martin et al.'s (2000) results suggest that vulnerable robin nest sites may have indeed sustained rapid predation during the first season when 1 recorded the highest nest predation levels. However, if vulnerable nest sites were suffering rapid predation, resulting in the different survival rates between nesting stages, I would have expected to see similar patterns during all breeding seasons. Following Martin et al. (2000), I surmise two alternative reasons why I lacked any nest age effect during 2003-2004 and 2004-2005.

First, no nest site or parental activity effects may have occurred during the last two years. Second, both nest site and parental activity influenced predation, causing them to offset each other resulting in no differences in observed survival rates between nesting stages. The first reason seems unlikely, as vulnerable nest sites are almost certainly located quickly, as demonstrated by Brown (1997) when ship rats depredated 49% of North Island robin and tomtit (P. toitoi) nests within five days of clutch completion. Although the New Zealand avifauna evolved with a suite of avian predators (Holdaway, 1989; Holdaway and Worthy, 1996) the complete absence of mammalian predators means that robins may be naive to choosing 'safe' nest sites from mammalian predators. Increased parental activity at nest sites during daylight hours seems unlikely to influence robin nest predators as they are predominantly nocturnal or olfactory/auditory searching predators (rats, mustelids, morepork; although the impact of Australasian Harriers Circus approximans as nest predators on native forest species is unknown). Although activity at robin nests may not be important, robin nestlings are extremely noisy, making them vulnerable to mustelids, especially stoats (Mustela erminea). Stoats are known to be active during the day and were regularly seen in the forest fragments (Murphy and Dowding, 1994; Alterio and Moller, 1997). My inconsistent predation levels between nesting stages is replicated throughout the North Island, with high predation rates found both during the incubation and nestling stages or constant across the nesting period depending on the robin population, year or type of nest predator (Armstrong et al., 2002). This implies a complex interaction between nest predator abundance and assemblages between sites and years.

If robins were food limited. I would predict nestling starvation to be higher on those territories with low biomass, resulting in a positive correlation between the number of nestlings fledged and invertebrate biomass (Strong et al., 2004). This relationship was not detected in my study, seemingly inconsistent with limited food availability. Ideally, the number of nestlings hatched and surviving to fledgling would be a better indicator of nestling starvation. Unfortunately due to the inaccessibility of robin nests this was not possible. However, for five nests where I knew the clutch size and number of nestlings hatched, three experienced brood reductions before failing or fledging, adding qualitative support for low food availability. There are three reasons why low invertebrate biomass might result in complete nest failure, thus creating low nest survival rather than reducing the number of young fledged from successful nests.

Firstly, due to the small clutch size of 2.60 for North Island robins (Powlesland et al., 2000), a reduction due to starvation could result in complete nest failure (Luck, 2002). Secondly, the risk of nest predation may be increased when food supply is low because of begging by nestlings (Leech and Leonard, 1997), with hungry nestlings begging for food more vigorously than satisfied nestlings (Price and Ydenberg, 1995). Stoats were observed tracking begging nestlings within the study area. Therefore, if hungry nestlings created greater noise we could expect complete nest failure, rather than witnessing a brood reduction. Thirdly, adults foraging on low biomass territories may need to leave nests unattended more frequently (Zanette et al., 2000), potentially increasing the risk of nest predation (Arcese and Smith, 1988).

The combined effects of food and predation on nest survival appear complex. Recently, Zanette et al. (2003) experimentally demonstrated a synergistic effect of food and nest predators on the annual reproductive success of song sparrows (Melospiza melodia). Compared to controls (high predation, low food) sparrows produced nearly twice as many extra young when experiencing low predation pressure while being supplied with ad libitum food. In comparison pairs experiencing low predation (and low food) produced 1.3 extra young and those supplied with supplementary food (and high predation) produced 1.1 extra young relative to controls. Although I did not experimentally test this synergistic effect, comparative data from robins within predator-free and predator controlled areas demonstrate this possible effect. Pureora Forest Park, situated 20 km east of my study, is one of the largest intact podocarpbroadleaf forests remaining in the North Island, covering approximately 78 000 ha. Within this site I would not expect low food availability. The critical factor affecting robin nest survival within this forest is nest predation, with nest survival of 60% (CI 44-74%) with predator control and 25% (CI 17-35%) without predator control (Powlesland et al., 1999; Armstrong et al., 2002). In comparison, nest survival for a reintroduced population on Tiritiri Matangi island where mammalian predators are absent (potentially much lower predation levels by native avian predators), was only 37% (CI 26-49%), significantly lower than the level achieved at Pureora after predator control (Armstrong et al., 2002). Such a marked increase in nest survival after predator control at Pureora may be explained by the synergistic effect of reduced nest predation and high food availability.

Annual productivity was not reduced by forest fragmentation. In fact I found a negative effect between juvenile survival to independence (approximately four weeks after fledging) and fragment size. Not surprisingly this follows the same trend observed in the robins' nest survival rates. The highest value that productivity could attain would be 1.64, if all fledglings were to reach independence. There was a slight reduction in the number of nestlings fledged to those that reached independence. However, this was not as dramatic as I would have thought considering how extremely noisy begging fledglings were during their first few weeks. Direct comparison of these results to other studies within New Zealand is difficult as they measure productivity in terms of fledglings rather than independent juveniles. We can probably assume the number of independent young to be slightly lower than the number fledged as seen in this study. The number of fledglings produced per female in this study was higher than the 0.9 attained by the robin population in Pureora forest without predator control, but noticeably fewer than the 3.7 produced during intensive predator control (Powlesland et al., 1999). Whether this increase in fledgling production compared to the non-control site is a result of a negative impact of fragmentation on predator abundance/activity is unknown. Further comparison between the Pureora sites and the forest fragments could help address these question. Either way these results are encouraging for small-scale poison operations and robin persistence in small fragments.

Habitat fragmentation does not appear to be negatively impacting nest survival or productivity, potentially because of the already high impact that mammalian nest predation have in this unique system. Although introduced mammalian predators undeniably have detrimental impacts on oceanic islands, the associated decrease in nest survival caused by habitat fragmentation may not be applicable in situations where mammalian predators have filled the role of generalist predators. Food availability appeared to be limiting nest survival within this study, but distinguishing between nest failures caused by predation or nestling starvation was not possible. Nestling starvation can lead to predation, with the two sources of mortality operating simultaneously (Högstedt, 1981), while complete brood failures due to starvation would be indistinguishable from predation for inaccessible nests (Luck, 2002). These results highlight the possible need for food limitation to be consideration in habitat restoration projects. Food supplementation experiments could provide valuable information about

the processes underlying food limitation within this system, and reveal the potential reproductive output achievable by these birds.



4.0 Incubation rhythm, nest attentiveness and timing of breeding in the North Island robin

Incubation has been shown to be an extremely costly component of reproduction (reviewed in Williams, 1996), especially in the Passeriformes where over 60% of whole families exhibit female-only incubation (Deeming, 2002). These females face a trade-off between time allocated to foraging for maintaining their own energy requirements and the thermal needs of the developing embryos. Females must intermittingly divide the day into periods for foraging (off-bouts), where the clutch is left unattended and begins to equilibrate with ambient temperature, and incubation periods (on-bouts), where females use energy re-warming the eggs on their return to the nest (Williams, 1996). The optimal incubation rhythm (on- and off-bouts) can potentially be influenced by a large number of ecological factors including climatic conditions, food availability, stage of incubation, time of day, mate feeding rates and nest predation (Skutch, 1962; Davis, 1984; Conway and Martin, 2000a; Conway and Martin, 2000b; Deeming, 2002). With such a large number of factors influencing incubation behaviour it is not surprising that we see large variation in avian incubation strategies (see Conway and Martin, 2000b).

To hatch successfully, avian eggs must be maintained at temperatures that facilitate embryonic development, the optimal temperature falling somewhere between 34-38°C (Webb, 1987; Williams, 1996). Prolonged exposure to temperatures above this optimum is often fatal (Williams and Ricklefs, 1984), while embryonic development ceases or

slows as temperatures drop below this optimum (Webb, 1987). Therefore, the ambient temperature a bird is exposed to while incubating is expected to be a primary determinant influencing its incubation behaviour. For example, a female in a cold environment is selectively driven to take shorter off-bouts to minimize the risk of the eggs falling below optimal temperatures. With less time to forage the female must make more trips per hour, consequently shortening her on-bouts (Conway and Martin, 2000b). Surprisingly, studies investigating the relationship between temperature and on- and offbout duration have had inconsistent results, with positive, negative and no correlations reported (see review in Conway and Martin, 2000a). A nonlinear relationship between temperature and bout duration across a wide range of temperatures. Their model still only explains a small proportion of the variation seen in bout duration, highlighting the obvious importance of numerous additional energetic and ecological factors that may constrain incubation behaviour.

Energetic or ecological factors that reduce nest attentiveness (proportion of time spent on the nest) can result in negative effects on reproductive success, by reducing hatchability and increasing the incubation period (Lyon and Montgomerie, 1985; Lifjeld and Slagsvold, 1986; Nilsson and Smith, 1988). For example, this increase in incubation period can escalate the risk of predation by exposing nests for longer periods (Ricklefs, 1969; Bosque and Bosque, 1995). When the cost of failure for a nesting bird is complete clutch loss, it is not surprising that incubation behaviour has evolved to reduce nest predation, with species suffering high nest predation reducing activity at their nests (Conway and Martin, 2000b). Food availability is another factor that likely constrains female incubation behaviour. Abundant evidence shows increased food availability can increase a female's nest attentiveness (Rauter and Reyer, 1997; Eikenaar et al., 2003; Pearse et al., 2004) and even induce earlier breeding in a large number of species (Davies and Lundberg, 1985; Fleischer et al., 2003). However, Conway and Martin's (2000b) analyses failed to find a relationship between food and interspecific variation in incubation behaviour. This was possibly due to the lack of a direct quantitative measure of relative food availability across species.

In many species where females incubate alone, the male can supplement the female's energetic costs by supplying food to her throughout the laying and incubation periods

48

(Ricklefs, 1974). Royama (1966) suggested that the food was of essential nutritional value to the female and subsequently improved her reproductive success, i.e. the female nutrition hypothesis. This hypothesis is supported by studies showing that male incubation feeding increases a female's nest attentiveness (Lyon and Montgomerie, 1985; Lifjeld and Slagsvold, 1986; Halupka, 1994). However, the benefits of increased feeding rates by males could be reduced if nest predators are attracted through the increased number of nest visits (Skutch, 1949; Martin and Ghalambor, 1999).

Here, I examine whether incubation behaviour is correlated with the probability of nest failure during incubation for North Island robins (*Petroica longipes*). This species exhibits male incubation feeding and also suffers high nest predation levels (Powlesland et al., 1999). Therefore, I predict that increased activity at nest sites (female foraging trips and male incubation feeding) would increase the likelihood of predator detection and hence the risk of nest failure. Because females should increase nest attentiveness in the presence of high predation, a conflict arises between male incubation feeding rates and predation (see Table 4.1).

In addition to nest survival, I also looked at the influence of food availability, ambient temperature and male incubation feeding on incubation behaviour (Table 4.1). The robins in this study were located in a highly fragmented and modified habitat where they may experience reduced food availability (Burke and Nol, 1998; Zanette et al., 2000). To test the relationship between food availability and incubation behaviour. I measured invertebrate biomass on each territory and analysed the subsequent measurement in relation to robins' incubation behaviour. I predicted that robins on highbiomass territories would begin breeding earlier and exhibit increased nest attentiveness because of reduced foraging effort during off-bouts. Evidence suggests that incubation feeding is costly to the male, as males decrease their feeding rates when supplied with extra food or when handicapped (removed tail feathers) (Lifjeld and Slagsvold, 1986; Smith et al., 1989). Therefore I expect males on high biomass territories to reduce their feeding rates as females can attain their own food requirements, while males should attempt to increase their incubation feeding rates on low biomass territories. Nest attentiveness should be positively associated with male incubation feeding in support of the female nutrition hypothesis. Robins in this region experience temperate conditions during breeding, with mild-cold spring temperatures creating high-energy demands of

49

the female. Thus, male incubation feeding and nest attentiveness should be negatively correlated with ambient temperature, causing a change in incubation rhythm with shorter on- and off-bouts (see Table 4.1).

Table 4.1. Diagrammatic illustration of the predicted influence (see above) that increased food availability, ambient temperature, nest predation and male incubation feeding (MIF) has on incubation behaviour. Signs (-/+) represent negative or positive direction of relationship.

Inaukation habauiour	Increased						
Incubation behaviour	Food	Food Temperature		MIF			
Nest attentiveness	+	_	+	+			
(on-bout)	+	_	+	+			
(off-bout)	_	+	Ξ.	-			
MIF	-	_	_/+				

4.1 Methods

4.1.1 Study species and area

See section 1.1.

4.1.2 Incubation attendance

Data on female nest attentiveness were collected by observing nests from a distance of 25-30 m using binoculars between the hours of 0900 and 1730 during fine weather. Nest watches were conducted in all fragments except T37 and Little Tutu (Table 1.1). During 2002-2003 and 2003-2004 it was intended that each nest was watched twice, but nest failure prevented this for most nests, resulting in only 18 nests observed twice. Therefore during 2004-2005 nests were only watched once. Due to their inquisitive nature and training, robins usually visited the observer on arrival near the nest-site, so nest watches only commenced when females were on the nest and the males had disappeared. In most cases the observer could begin an hour-long nest watch within 10 min of arrival. During the third year, the observer waited 20 min before commencing the nest watch. If the female was off the nest at the end of the hour nest watch, the

observer waited until she returned to record the length of her last off-bout. This meant nest watches could be over one hour long.

Over the three breeding seasons nest watches were conducted for 51 different robin pairs, with 11 pairs in 2002-2003 (17 nest watches), 32 pairs in 2003-2004 (66 nest watches) and 25 pairs in 2004-2005 (31 nest watches). From each nest watch the following variables were recorded: nest attentiveness (proportion of total time female spent on the nest); on-bout duration (average time female spent on nest per bout); offbout duration (average time female spent off nest per bout); nest trips (number of times female left the nest) and incubation feeding (number of times the male fed the female). The male would call the female from the nest and generally feed her within sight of the observer, with males very rarely feeding females on the nest. Incubation feedings were probably slightly underestimated, as males may have fed females multiple times once she left the nest area, although generally these feedings were still in view of the observer and included in the analysis. Ambient temperature (°C) was recorded during all nest watches, and generally changed by no more than one degree over the hour. I also recorded the clutch age, with nests considered "early" in the first ten days of incubation and "late" after that. Due to regular nest checks, clutch age could easily be determined from nest building behaviour, from known hatching, fledgling or previous failure dates.

4.1.3 Food availability

See section 2.1.2.

I opened the invertebrate pitfall traps earlier during 2004, 20th July before the start of breeding to investigate the influence of food availability on the timing of breeding. During August-September 2004, females were checked every 5-6 days until their first nesting attempt was located, allowing me to accurately assign a laying date to each pair.

Because there were multiple pitfall collections per territory, assigning a biomass measurement to each nest depended on the duration of the nesting attempt and the collection date. The longest pitfall collection period each nest was active throughout was assigned to a nest. Therefore, the same biomass measurement could be used for more than one nesting attempt since concurrent failed nesting attempts could be within the same six-week collection period.

4.1.4 Statistical analyses

Correlation analysis (SAS PROC CORR: Version 8.02 SAS Institute, 1999) was used to examine the relationship between invertebrate biomass and timing of breeding, and between nest attentiveness and bout duration. Laying dates were log-transformed to normalize the data distribution (tested with Shapiro-Wilks' statistic). All tests are two-tailed and the level of significance for all tests is $\alpha = 0.05$.

Female robins tended to only leave nests when males called to feed them, resulting in a strong correlation between female nest trips and male incubation feeding rates. Therefore, the frequency at which females left the nest per hour was not included in the analyses of incubation behaviour, resulting in four response variables: nest attentiveness, average on- and off-bout duration and male incubation feeding. Transformation of three response variables was necessary to normalize their distributions, following the transformations suggested by Quinn and Keough (2002); nest attentiveness (arcsine transformed), on-bout (cube root transformed) and off-bout (log transformed) duration. The four response variables were analysed using the SAS GLIMMIX macro (Littell et al., 1996), fitting a generalized linear mixed model with pair and nest watch number included as random effects. The error distribution and link function were specified as normal and identity for nest attentiveness, on-bout and offbout duration, while a Poisson distribution and log-link function were specified for male incubation feeding due to the distribution of the response variable (count data 0-8). Random effects were included in the analyses due to multiple nest watches preformed across pairs and two nest watches conducted at 18 nests. After taking into account the variation among individual pairs and nests the relationship between the four response variables and the following predictor variables could be examined; Temperature (°C), food availability (invertebrate biomass), time of day (hour) and clutch age (early or late). Ambient temperatures did not range widely among nest watches (8-21°C) in contrast to 2-38°C in Conway and Martin's (2000a) study. I therefore used linear models to explain the relationship between temperature and incubation behaviour. The effect of male incubation feeding was included as a predictor variable in the nest

attentiveness, on- and off-bout analysis. During model selection the most parsimonious models were obtained by sequentially adding and deleting significant terms (univariate significance $\alpha < 0.10$). Both forwards and backwards elimination were used to test for model robustness. I present pooled results across years as no differences were detected between the four incubation behaviours across the three years (all *P* > 0.491).

I also looked at the effect the previous on- (cube root transformed) and off-bout (logtransformed) duration had on the subsequent bout duration. Because multiple on- and off-bout durations were used per nest, I used nest as a random effect in the GLIMMIX macro along with nest watch number.

I calculated daily nest survival during the incubation period (19 days) for the 96 nests for which nest watches were undertaken, and tested the cause of variation in survival using the generalized linear modelling approach by Shaffer (2004). Logistic-exposure models were fit using PROC NLMIXED with a binomial distribution and logit-link specified by Shaffer (2004). Nest attentiveness, on- and off-bout duration, male incubation feeding and the number of female nest visits during each nest watch were used as predictor variables.

4.2 Results

4.2.1 Timing of breeding

I was able to assign laying dates for the first clutches of 34 pairs during the 2004 breeding season, and 23 of these pairs had pitfall grids set-up during the July-September 2004 collection period. Females initiated first clutches earlier when located on higher biomass territories (Fig. 4.1).





4.2.2 Nesting behaviour and incubation feeding

I conducted 114 nest watches over the three-year observation period, with females exhibiting an average of 72.6% nest attentiveness (SE = 0.97, range 43.5-93.5%) during these observations. Females left the nest on average 3.2 times per h (SE = 0.15, range 1-12), with off-bouts averaging 6.5 min (SE = 0.38, range 1.9-22.1), and on-bouts averaging 18.6 min (SE = 1.15, range 2.6-56.9).

Nest attentiveness tended to be lower at higher temperatures, and when the male incubation feeding rate was high (Table 4.2). When temperature and male incubation feeding rate were included in the model, the strength of both their trends was improved and noticeably approached statistical significance (temperature = -0.009, SE = 0.005, P = 0.065; male feeding = -0.017, SE = 0.008, P = 0.053). No other variables explained a significant amount of variation in female nest attentiveness (Table 4.2). Males fed females 2.8 times per h on average (SE = 0.2, range 0-8), and this feeding rate was not significantly associated with temperature, invertebrate biomass, time of day or clutch age (Table 4.2).

Table 4.2. Summary of generalized linear mixed model selection for incubation behaviour and incubation nest survival of North Island robins in the Benneydale region, New Zealand for 2002-2005. Identity-link function used for nest attentiveness, on-bout and off-bout, log-link for male incubation feeding and logit-link for the nest survival models.

	Univariate models		Reduced Models			
	Estimate	SE	t	Estimate	SE	t
Nest attentiveness						
Temperature	-0.008	0.005	-1.74*			
Food availability	0.001	0.027	0.03			
Male feeding	-0.016	0.008	-1.83*			
Time	< 0.001	< 0.001	0.41			
Clutch age [late]	-0.029	0.029	-1.02			
Male feeding						
Temperature	-0.017	0.019	-0.90			
Food availability	-0.026	0.097	-0.26			
Time	< 0.001	< 0.001	0.11			
Clutch age [late]	0.107	0.108	0.99			
On-bout						
Temperature	0.015	0.009	1.72*			
Food availability	0.111	0.050	2.20**	0.083	0.041	2.03**
Male feeding	-0.104	0.013	-8.04***	-0.106	0.014	-7.56***
Time	< 0.001	< 0.001	0.26			
Clutch age [late]	-0.064	0.049	-1.30			
Off-bout						
Temperature	0.023	0.007	3.22***	0.020	0.006	3.17***
Food availability	0.042	0.039	1.08			
Male feeding	-0.068	0.012	-5.67***	-0.064	0.011	-5.57***
Time	< 0.001	< 0.00 l	0.04			
Clutch age [late]	0.008	0.043	0.18			
Nest survival						
Nest attentiveness	1.493	0.914	1.32			
Male feeding	-0.023	0.105	-0.22			
On-bout	0.011	0.016	0.69			
Off-bout	-0.030	0.039	-0.75			
Female nest visits	-0.091	0.096	-0.95			

*p<0.10, **p<0.05 ***p<0.01

Nest attentiveness was highly correlated with the duration of on-bouts (r = 0.486) and off-bouts (r = -0.512), and the effect of incubation feeding on nest attentiveness was associated with changes in these durations. On-bout and off-bout were highly correlated (r = 0.478). A partial correlation measuring the strength of this linear relationship, adjusting for the effect of male incubation feeding reveals the strong influence male feeding has on female bout duration (r = 0.265). The duration of on- and off-bouts both decreased as the incubation feeding rate increased (Table 4.2 & Fig. 4.2), meaning females left the nest more times per hour. However, the effect of male incubation

feeding was larger for on-bout duration, meaning females spent less time on the nest when the feeding rate was high.



Figure 4.2. Scatter plot of mean on-bout (cube root scale) and off-bout (log scale) duration versus the male incubation feeding rate for all 114 nest watches.

Ambient temperature recorded during nest watches did not explain significant variation in on-bout duration (Table 4.2). However, it did explain significant variation in off-bout duration (Table 4.2), with females leaving the nests for longer periods as temperatures increased. Female on-bout duration had a positive relationship with food availability, with females on high biomass territories having longer on-bout periods (Table 4.2). Offbout duration was not related to food availability (Table 4.2). The overall incubation survival for the 96 nests where nest watches were conducted was $60\% \pm 10\%$. None of the incubation behaviours I recorded significantly affected the rate of nest survival during the incubation stage (Table 4.2).

The durations of on-bouts were not affected by previous off-bout duration (*estimate* = 0.002, SE = 0.007, P = 0.802), whereas off-bout durations were positively correlated with the duration of the previous on-bout (*estimate* = 0.029, SE = 0.003, P < 0.001).

4.3 Discussion

Of the predictions outlined in Table 4.1, I found support for a negative relationship between nest attentiveness and ambient temperature and between male incubation feeding and female off-bout duration (Table 4.3). A positive relationship between on-bout duration and food availability and off-bout duration and temperature is consistent with the hypothesis that females are resolving the conflict between their own foraging needs and the thermal requirements of the developing embryos via their incubation rhythm (on- and off-bout). In all other respects the results did not support the predictions (Table 4.3). In fact, male incubation feeding deviated from the prediction by shortening both the overall nest attentiveness and female on-bout duration.

Table 4.3. The results of nest watch data from robins in the Benneydale region from 2002-2005 with the corresponding predictions outlined in the introduction in Table 4.1. Signs (-/+) represent negative or positive directions of the individual relationships. NO = no relationship found; YES = predicted relationship found; OPPOSITE = opposite relationship to the prediction; SLIGHT = a trend for the predicted relationship (P < 0.10). MIF = male incubation feeding.

Incubation behaviour	Increased				
	Food	Temperature	Predation	MIF	
Nest attentiveness	+ NO	– SLIGHT	+ NO	+ OPPOSITE	
(on-bout)	+ YES	- NO	+ NO	+ OPPOSITE	
(off-bout)	- NO	+ YES	– NO	– YES	
MIF	– NO	– NO	- / + NO		

57

When assessing the relationship between ambient temperature and nest attentiveness, I used linear models based on Conway and Martin's (2000a) conclusion that relationships will only be non-linear if temperatures range from less than 9°C to greater than 26°C. I found a slight negative relationship between nest attentiveness and temperature, and this was due to off-bouts being longer at higher temperatures. This result suggests that females avoided taking long off-bouts at low temperatures due to potentially detrimental effects on the developing embryos. The lack of on-bout duration and temperature dependence supports the suggestion of Conway and Martin (2000a) that their model would be weaker for species that exhibit male incubation feeding. Male incubation feeding strongly affected on-bout duration, and was not correlated with temperature, possibly due to the limited range of ambient temperatures recorded in the study.

Food abundance and availability are important factors affecting the reproductive success of birds (Lack, 1968; Martin, 1987). When females are supplied with extra food during incubation, either by male incubation feeding or supplementary food, they often exhibit an increase in nest attentiveness, hatchability and a reduced incubation period (Högstedt, 1981; Lyon and Montgomerie, 1985; Nilsson and Smith, 1988; Smith et al., 1989; Sanz, 1996; Rauter and Reyer, 1997; Eikenaar et al., 2003). In my study, if I had only examined nest attentiveness I would not have revealed any influence of food availability on female incubation behaviour. In fact, females were responding to food availability by spending longer periods on the nest (on-bout) on high-biomass territories, supporting the idea that incubation is energetically expensive and influenced by the females' energy requirements. Reid et al. (1999) found that starlings' (Sturnus vulgaris) foraging success cued the end of each foraging bout, and that parental energy levels cued the end of each incubation bout. Female energy levels also appeared to be a cue used to terminate on-bouts in my study, assuming females were able to forage more efficiently on high-biomass territories and therefore had higher energy levels at the start of on-bouts. However, there is no evidence that females had shorter off-bouts on richer territories, and indeed it was temperature that influenced off-bout duration.

Although nest attentiveness was not associated with invertebrate biomass, the overall low rate of attentiveness (72.6%) and the positive relationship with on-bout duration indicates food limitation within the study area, potentially even on territories of higher biomass. Further support comes from studies of the closely related South Island robin

58

(*P. australis*) where females exhibit higher nest attentiveness (77.7-81.0%) than recorded in the present study (Powlesland, 1983; Mackintosh and Briskie, 2005). Mackintosh and Briskie (2005) concluded that their population was not limited by food and demonstrated this via supplementary feeding experiments, detecting no difference in the nest attentiveness for control (78.9%) and experimentally fed females (80.0%). Unfortunately, male incubation feeding rates were not reported in Mackintosh and Briskie's (2005) study. If the males were not food limited we might have expected to see a decrease in feeding rates. Food-supplementation experiments to test if we could increase nest attentiveness and decrease male feeding rates would help answer whether all robins in this study area were food limited.

Food availability appeared to determine timing of breeding, with females on high biomass territories nesting earlier than low biomass territories. Similar effects have been shown experimentally, with many species breeding earlier when extra food is supplied (Högstedt, 1981; Davies and Lundberg, 1985, references within). I also interpret my observed correlation as evidence of food limitation on low biomass territories, as I would otherwise expect all females to start breeding as early as possible to increase their reproductive output through multiple nesting attempts. It is unknown whether the start of breeding is directly constrained by nutrient requirements for egg formation, or whether cueing breeding to food supply functions to ensure a food supply for later nesting (Perrins, 1996; Siikamaki, 1998). Courtship feeding could play an important role in supplying females with the extra food necessary to produce eggs (Krebs, 1970), so it would be interesting to investigate the relationship between male courtship feeding, biomass and timing of breeding.

Nest predation can influence the evolution of passerine life-history traits by placing constraints on parental activity at the nest (Martin, 1995; Conway and Martin, 2000b). To reduce predator detection, some north American species have evolved an incubation strategy of longer on- and off-bouts, reducing the frequency of nest visits (Conway and Martin, 2000b). However, species nesting in colder environments are forced to take shorter off-bouts, as long off-bouts can cause decreased hatchability and extend the incubation period (Lyon and Montgomerie, 1985). Therefore, the duration of on- and off-bouts may be expected to evolve to an optimal compromise depending on the relative risks of predation and chilling. Although robins suffer high nest predation rates

during incubation I found no evidence to suggest that incubation behaviour influenced nest predation in anyway. Activity at robin nest sites during the day is unlikely to influence nest predators within this system, as the primary predators are predominantly nocturnal or olfactory/auditory searching (*Rattus rattus*, mustelids, morepork *Ninox novaeseelandiae*).

The results of my study did not support the female nutrition hypothesis, whereby male incubation feeding is believed to be an important source of energy for the female, allowing her to spend longer on the nest (Lyon and Montgomerie, 1985; Lifjeld and Slagsvold, 1986; Halupka, 1994). Contrary to this hypothesis, I found that high incubation feeding rates tended to reduce female nest attentiveness by changing the females nesting rhythm, with shorter on- and off-bouts. Rauter and Reyer's (1997) study on water pipits (Anthus spinoletta), found similar results, with male incubation feeding changing the temporal pattern of on- and off-bouts from a few long to several short bouts. I found that male incubation feeding reduced females' off-bout durations. However, off-bouts were reduced less than on-bouts, resulting in the net decrease in nest attentiveness. During short off-bouts, mean egg temperatures may in fact remain higher than for eggs where females take one long off-bout. Robin nests are insulated and placed in what appear to be well-protected microclimates (pers. obs.), and I suggest that robin embryos very rarely face unfavourable or lethal temperatures. Although males did not help reduce females' nest attentiveness, females with high rates of male incubation feeding may need to use less energy after each foraging bout to re-warm their eggs as their eggs have had less time to cool. There was no evidence that the incubation feeding rate was food limited, as there was no relationship between incubation feeding rates and invertebrate biomass. However, it remains possible that the amount of food provided by males was higher on high-biomass territories or that all males were food limited to some extent.

Conway and Martin (2000a) found that previous bout duration explained variation in both the subsequent on- and off-bout durations, demonstrating behavioural decisions attempting to balance time budgets over short time frames. My results suggested that off-bout duration was strongly affected by the previous on-bout duration. Females presumably deplete their energy reserves after long on-bouts, and therefore need to take longer off-bouts to help restore these reserves. In addition, because short on-bouts were

60

associated with high incubation feeding rates, females may have had to do less foraging due to the energy supplied by the male's food. The relationship between the previous off-bout duration and the following on-bout was not significant as it was confounded by the strong influence of male incubation feeding on on-bout duration. While these results are not consistent with Conway and Martin's (2000a), incubation feeding was extremely rare in their study, suggesting populations with different male incubation feeding rates will differ between their incubation strategies.

The lack of support, especially for the predictions involving nest predation and male incubating feeding in Table 4.3, highlights the unusual incubation strategy displayed by the robins in this study. In a review of 19 northern hemisphere species Martin and Ghalambor (1999) demonstrated that while incubation feeding was beneficial (i.e. increased nest attentiveness) it was constrained among open-nesting, compared to cavity-nesting species because of higher predation levels and the risk of attracting nest predators. Robin incubation feeding rates in this study fall between the open-nesting and cavity-nesting species in Martin and Ghalambor's study (1999, see Figure 1). Robins, however, suffer much higher predation levels than the open-nesting species reported by Martin and Ghalambor (1999). This likely reflects the unique evolutionary history of the New Zealand avifauna, which evolved with a restricted suite of arboreal predatory birds (Holdaway, 1989; Holdaway and Worthy, 1996). Robins on the New Zealand mainland now suffer nest predation predominately by introduced mammalian predators, and at a much higher rate than would have occurred in the past. The female incubation strategies we observe, resulting from the influence of both nest predation and male incubation feeding, do not fit the predictions generated largely from life-history theory in northtemperate systems (see review Martin, 2004). The proximate response to food and temperature shown by the females indicates plasticity in incubation behaviour, but the lack of variation in male incubating feeding rates may indicate a relatively constrained trait for this species.

In summary, females appeared to behave in response to their own energy levels with respect to on-bout duration, while they appeared to avoid the risk of egg chilling during off-bout periods. This variation in avian incubation behaviour demonstrates different strategies utilized by species to deal with their own energetic needs and the thermal requirements of the developing embryos. Although ambient temperature and food
availability explained some of the variation I observed in incubation behaviour, future work on this species under different conditions (i.e. food-supplementation, mammalian predator control) may reveal further insight into the incubation strategies employed in differing environments. Whether the lack of support for the nest predation and male incubation feeding predictions is related to past evolutionary strategies or inappropriate predictions for a southern hemisphere species is unknown, but gives rise to interesting questions regarding why robins have such high incubation feeding rates but low nest attentiveness.



5.0 Time budgets of North Island robins during their annual cycle

Organisms, especially those living in temperate zones, face an array of seasonal changes in their environments. These seasonal changes can result in large variation in resource availability, restricting the time organisms are able to utilize these resources for particular processes in their life cycles. For example, birds in temperate zones usually have limited time to carry out breeding and moult, as these processes are generally restricted to times when conditions are favourable (see review Murton and Westwood, 1977). Once breeding and moult are completed, temperatures begin to decrease and birds experience increased thermoregulatory costs at the same time food availability and the time available for foraging are also decreasing. Resident bird species of the northtemperate zone have been shown to modify diet composition and exhibit some physiological adaptations to balance their time budgets during winter (Calder and King, 1974; Swanson, 1990). However, birds generally have been found to change their time budget strategies in relation to seasonal conditions and the phases of their annual cycles (Hickey and Titman, 1983; Lundberg, 1985; Bryant and Tatner, 1988; Enoksson, 1990; Lill, 1991).

Foraging and resting make up the majority of time budget activities for many avian species (Herbers, 1981; Hickey and Titman, 1983; Lundberg, 1985; Bryant and Tatner, 1988; Enoksson, 1990; Lill, 1991). Because foraging time reflects direct energy gain, it is not surprising that substantial research has examined the effect of different

- (1) Foraging included searching, capturing, eating and the occasional caching of prey items. The number of prey items captured during each foraging bout was recorded, and these data converted into a *temporal foraging attack rate* (number of attacks per time foraging min⁻¹) for the observation session. Prey items were often too small to see, so I assumed that every peck at the foraging substrate resulted in capture; this *may* have overestimated prey capture rate, but is unlikely to influence comparisons between seasons or sexes.
- (2) Resting was recorded when robins assumed the resting posture with head withdrawn onto the body, feathers fluffed, and tail slightly depressed (Powlesland, 1981). They often perched on one leg while resting.
- (3) Body maintenance activities including stretching, shaking, preening, oiling, toenibbling, beak-wiping, scratching, anting and sunning.
- (4) Males sang frequently during pre-breeding, occasionally during breeding, and rarely during the post-breeding periods. Females also occasionally sung. Vocalizations during aggressive encounters were recorded as territorial-defence activities.
- (5) Interspecific aggression was generally towards smaller avian species such as tomtits (*P. toitoi*), grey warblers (*Gerygone igata*) and fantails (*Rhipidura fuliginosa*). Robins displayed their white frontal spots before chasing and bill snapping (Flack, 1976).
- (6) Territorial defence included chasing and display by wing lifting, elevating the crown feathers, puffing out breast feathers and bill snapping towards neighbouring robins (Flack, 1976).
- (7) Partner interactions during pre- and post-breeding periods were usually aggressive. Males were usually dominant over females, but when males encroached on female non-breeding territories, the females aggressively displaced them.

5.1.3 Data collection

Time budget observations were undertaken during three periods, pre-breeding (July-August), breeding (September-January) and post-breeding (February-April). All prebreeding data were collected from 24 July to 1 September 2004, and this period was considered to end when courtship feeding began. I obtained time budgets from 30 male and 19 female robins during the pre-breeding period, with each bird observed once. All breeding season data were collected from September 2004 to January 2005. I divided the breeding season into four six-week periods during which invertebrates were sampled (see below), and observed each male once during each period. Sample sizes changed during breeding as new pairs were located and added to the study, while some pairs were removed when their partner (usually the female) disappeared. Hence, all males were paired, and I recorded the male's stage of breeding (no nest, building, incubation, nestlings, and fledged young) during each observation session. Females were not observed during the breeding period because of the difficulty in observing them for more than a few minutes while incubating or brooding. Post-breeding data were collected from 5 February to 7 April in 2003, 2004 and 2005. These observations were undertaken once individuals finished nesting and were no longer feeding juveniles. I collected post-breeding data from a total of 51 males and 41 females, with 22 males and 15 females observed in 2003, 28 males and 17 females observed in 2004 and for 31 males and 27 females observed in 2005. Although only one observation was obtained per individual during post-breeding time budgets each year, some individuals could be sampled two or three times over the three observation periods depending on the length of time they were present in the study.

I collected time budget data between the hours of 0830 and 1630 during fine weather. I observed the robins from a distance of 5-20 m using binoculars, recording data onto a mini-cassette tape. Due to their inquisitive nature and training, robins usually visited the observer on arrival at their territory. Therefore, time budgets only commenced when the focal individual began normal foraging away from the observer, typically 10-15 minutes after arrival. Time budgets were focused on either the male or female, depending on which bird was first located on a territory. I continued each observation session until the robin was lost from sight for more than five seconds or until I had observed it continuously for 60 minutes. If the robin was lost from sight, 1 re-started the observation session unless 1 had already observed it continuously for at least 5 minutes. Robins were generally lost when they flew through dense vegetation or foraged extremely high. 1 recorded the ambient temperature and time each time budget commenced.

5.1.4 Food availability

See section 2.1.2.

For each time budget observation, a single invertebrate biomass measurement for each territory was used to assess food availability and foraging behaviour. Since pitfall

contents were cleared every six weeks, the collection period closest to each time budget period was used.

5.1.5 Statistical Analyses

The response variables foraging time and foraging attack rate were analysed separately for each of the three periods during the robin's annual cycle (pre-breeding, breeding and post-breeding) using PROC MIXED (Version 8.02 SAS Institute, 1999) to fit a general linear mixed model. Values for foraging time (a proportion) were arsine transformed prior to analysis, and values for foraging attack rate were log transformed to normalize distributions. Individual robins were included as a random effect to account for the multiple time budgets preformed for individuals during the breeding and post-breeding periods. After taking into account the variation among individuals the relationship between the response variables and the following predictor variables could be examined: sex (pre- and post- breeding only), temperature (°C), invertebrate biomass (grams, log-transformed), time of day (hour), and stage of breeding (for the breedingseason observations only). During model selection the most parsimonious models were obtained by sequentially adding the significant terms, P < 0.10, although both forwards and backwards elimination were used to test for model robustness. If significant differences were found between male and female foraging behaviour, 1 performed separate analyses. I calculated the difference of least square means (DLSM) to compare effects of categorical explanatory variables. The Bonferroni procedure was used to adjust significance levels to control for Type I error in these multiple comparisons.

Vocalization, inter- and intraspecific encounters and partner interactions were rare, accounting for less than 2% of all time budgets. I therefore present the results for the three most common activities: foraging, resting and body maintenance. Analysis using the predictor variables was only preformed on foraging activities, as described above. The level of significance for all tests is $\alpha = 0.05$.

5.2 Results

5.2.1 Seasonal variation in time allocation

Foraging was the dominant activity, occupying more than 75% of time budgets throughout the year (Fig. 5.1). Time allocated to foraging showed pronounced seasonal variation ($F_{2, 196} = 29.65$, P < 0.001), with robins spending the largest proportion of time budgets foraging in the pre-breeding period. followed by the breeding season and then the post-breeding period (Table 5.1, Fig. 5.1). During the breeding season the time males spent foraging did not vary significantly between the different stages of breeding, (Fig. 5.2; $F_{4, 67} = 2.32$, P = 0.065).



Figure 5.1. Proportion $(\pm 1 SE)$ of time budget female (**n**) and male (**n**) robins spent foraging, resting and undertaking body maintenance activities during (a) pre-breeding 2004, (b) males only during the breeding season of 2004-2005 and (c) post-breeding 2003-2005. Numbers in columns show sample sizes.

Table 5.1. Difference of least square means (DLSM) between pre-breeding, breeding (male only) and post-breeding in the proportion of time robins allocated to foraging (arcsine transformed). Individual robins are included as a random effect in the analyses. Bonferroni adjustment was applied to pair wise comparisons.

	Estimate	SE	t
Pre-breeding & Breeding	0.126	0.042	3.01**
Pre-breeding & Post-breeding	0.280	0.039	7.20***
Breeding & Post-breeding	0.154	0.032	4.86***

P < 0.01, *P < 0.001



Figure 5.2. Proportion $(\pm 1 SE)$ of time budget males spent foraging during the 2004-2005 breeding season while they had no nest or fledglings (MF), while female is nest building and incubating, and while feeding nestlings or juveniles. Numbers in columns show the number of time budgets conducted during the different breeding activities.

Other than foraging, resting and body maintenance behaviours were the only other activities that made up a substantial proportion of time budgets (Fig. 5.1). The most apparent seasonal pattern for these activities was seen during post-breeding observations when robins (males and females) spent the least amount of time foraging. The time normally assigned to foraging was utilized for resting (9.6% \pm 1.8%) and body maintenance (5.8% \pm 1.4%) activities (Fig. 5.1c). This was a larger proportion of time budgets than during the pre-breeding period, when resting and body maintenance activities only accounted for 1.8% \pm 1.2% and 1.6% \pm 1.0% respectively (Fig. 5.1a, c).

It was also slightly longer than the breeding season resting time $(3.6\% \pm 1.1\%)$ and body maintenance time $(3.9\% \pm 1.3\%;$ Fig. 5.1b, c).

Similar to foraging time, robins (males and females) displayed seasonal changes in foraging attack rate ($F_{2, 196} = 14.89$, P < 0.001). However, unlike foraging, attack rates were not significantly different between pre-breeding and the breeding season, with both periods recording higher attack rates than post-breeding (Fig. 5.3a; *DLSM* pre- & breeding = 0.002, *SE* = 0.030, P > 0.100). Foraging attack rate between the different stages of breeding was not significant (Fig. 5.3b; $F_{4, 67} = 1.58$, P = 0.190).



Figure 5.3. (a) Foraging attack rates ($\pm 1 SE$) for female (\blacksquare) and male (\Box) robins during pre-breeding 2004, the 2004-2005 breeding season and post-breeding 2003-2005 period and (b) Foraging attack rates ($\pm 1 SE$) for males during the 2004-2005 breeding season while he has no nest or fledglings (MF), while female is nest building and incubating, and while feeding nestlings and juveniles. Foraging attack rate is defined as the number of attacks on invertebrates per minute spent foraging.

5.2.2 Sex-related differences in time allocation

Time budgets during pre-breeding were similar for males and females (Fig. 5.1a; *foraging* $F_{1, 47} = 2.24$, P = 0.141; *resting* F = 0.89, P = 0.350; *body maintenance* F = 1.56, P = 0.218). However, during post-breeding females spent more time foraging (Fig. 5.1c; $F_{1, 48} = 4.84$, P = 0.035) and less time resting (F = 4.74, P = 0.034) than males. Males and females spent similar amounts of time in body maintenance activities (F = 0.70, P = 0.408).

Foraging attack rates differed between sexes during the pre-breeding observations ($F_{1, 47}$ = 4.48, P = 0.039) with females exhibiting lower attack rates than males (Fig. 5.2a). Females also tended to have slightly lower foraging attack rates during post-breeding but this was not significant (Fig. 5.2a; $F_{1, 48}$ = 2.65, P = 0.110).

The number of foraging attacks per time budget observation was used to calculate the average number of invertebrates consumed within one minute and one day during the three observation periods (Table 5.2). Although the highest foraging attack rates were not observed in the breeding season, combined with longer days and a relatively high foraging attack rate, males achieved the highest number of daily attacks during this period. The longer foraging time of females during post-breeding results in similar overall foraging attack rates for both sexes, while the higher foraging attack rate of males pre-breeding results in higher daily attack rates than females.

Table 5.2. The average foraging attack rate calculated from each observation period (total time budget) for the pre-breeding, breeding season and post-breeding periods for male and female robins. Daily foraging attack rates were calculated assuming an average of 10 h of daylight during pre-breeding, 12.45 h in the breeding season and 12.5 h during post-breeding using the average sunrise and sunset times for each period.

	Pre-breeding		Breeding	Post-bi	Post-breeding	
	Male	Female	Male	Male	Female	
Attack/min ⁻¹	1.29 ± 0.08	1.06 ± 0.12	1.10 ± 0.04	0.80 ± 0.04	0.75 ± 0.04	
Attack/day ⁻¹	774	636	841	600	562	

5.2.3 Pre-breeding period

Temperature had no significant effect on the proportion of time spent foraging or foraging attack rates during the pre-breeding period (Table 5.3). The mean temperature during these observation sessions was 6.2° C (*SE* = 0.296, *range* = 0-10°C). Time of day also had no effect on foraging behaviour. Food availability only had a significant effect on male foraging attack rates, with reduced attack rates on high biomass territories (Table 5.3).

5.0 Foraging behaviour

Table 5.3. Effect of sex, temperature (°C), time of day (h^{-1}) , and invertebrate biomass (g) of foraging time and foraging attack rates on North Island robins during the 2004 pre-breeding period. Effects of these factors on foraging time and foraging attack rate are analysed using general linear mixed modelling, results are for univariate models. Sexes are separated in the foraging attack analyses because of the significant effect of sex.

	Pre-breeding (n = 49)			I	Male (n = 30)			Female (n = 19)		
Foraging time	Estimate	SE	1	Estimate	SE	t	Estimate	SE	Т	
Sex [male]	0.075	0.051	1.50							
Temperature	-0.017	0.012	-1.40							
Time	0.023	0.017	1.31							
Biomass	-0.078	0.062	-1.26							
Foraging attack rate	(min ⁻¹)									
Sex [male]	-0.121	0.057	-2.12*							
Temperature	0.016	0.014	1.14	-0.009	0.016	-0.62	0.038	0.023	1.69	
Time	0.025	0.020	1.23	0.029	0.019	1.52	-0.006	0.044	-0.13	
Biomass	-0.165	0.109	-1.51	-0.268	0.105	-2.55*	-0.046	0.209	-0.22	

*P < 0.05

5.2.4 Breeding season

Temperature (*mean* = 12.9° C, *SE* = 0.306, *range* $5-22^{\circ}$ C) had significant effects on foraging during the breeding season, with males spending less time foraging and having lower attack rates as temperature increased. Time of day and invertebrate biomass had no significant effect (Table 5.4).

Table 5.4. Effect of temperature (°C), time of day (h⁻¹), and invertebrate biomass (g) of foraging time and foraging attack rates on male North Island robins during the 2004-2005 breeding season. Effects of these factors on foraging time and foraging attack rate were analysed using general linear mixed modelling, results are for univariate models. The individual male is included as a random effect in the analyses.

	Breeding $(n = 104)$				
Foraging time	Estimate	SE	t		
Temperature	-0.019	0.007	-2.65***		
Time	-0.022	0.012	-1.80		
Biomass	-0.104	0.107	-0.98		
Foraging attack rate (min ⁻¹)					
Temperature	-0.024	0.001	-4.73***		
Time	-0.003	0.009	-0.30		
Biomass	-0.127	0.075	-1.68		

***P < 0.001

5.2.5 Post-breeding period

Temperature (*mean* = 14.9°C, *SE* = 0.178, *range* 9-20°C) also had a negative effect on foraging time during the post-breeding time budgets (Table 5.5). When separate analyses were carried out for sexes, we see this effect was only significant for males. Food availability and time of day did not affect foraging time when both sexes were included (Table 5.5). However, when the post-breeding observations were separated for sexes, I found that males on territories with high invertebrate biomass spent more time foraging (Table 5.5). Because male foraging activity was negatively affected by temperature during post-breeding the model {temperature biomass} was run, resulting in no effect of either variable (*temperature estimate* = -0.023, *SE* = 0.015, *P* = 0.137; *biomass estimate* = 0.249, *SE* = 0.199, *P* = 0.223). The trend for female robins and biomass was negative, with females foraging slightly less on high biomass territories Temperature was not included in the analysis as it only had a significant effect on males.

(Table 5.5). Temperature, time of day and invertebrate biomass did not significantly affect foraging attack rate (Table 5.5).

5.0 Foraging behaviour

Table 5.5. Effect of sex, temperature (°C), time of day (h^{-1}), and invertebrate biomass (g) of foraging time and foraging attack rates on North Island robins during the post-breeding period (2003-2005). Effects of these factors on foraging time and foraging attack rate are analysed using general linear mixed modelling, individual robins are included as random effects, results are for univariate models. Sexes are separated in the foraging time analyses because of the significant effect of {sex}.

	Post-breeding (n = 140)		Male (n = 81)			Female $(n = 59)$			
Foraging time	Estimate	SE	Т	Estimate	SE	ť	Estimate	SE	t
Sex [male]	0.098	0.045	2.18*						
Temperature	-0.022	0.011	-2.14*	-0.036	0.013	-2.68*	< 0.001	0.016	0.01
Time	-0.006	0.012	-0.52	0.005	0.017	0.31	-0.020	0.017	-1.16
Biomass	0.144	0.141	1.02	0.391	0.180	2.17*	-0.224	0.207	-1.08
Foraging attack rate (min ⁻¹)									
Sex [male]	-0.046	0.028	-1.63						
Temperature	-0.011	0.007	-1.71						
Time	0.011	0.008	1.36						
Biomass	0.014	0.088	0.16						

*P<0.05

5.0 Foraging behaviour

5.3 Discussion

Robins exhibited marked seasonal changes in behavioural activities across the three observation periods, altering their time budgets according to their annual cycle and environmental conditions. It appears that pre-breeding was the most difficult period for individuals to obtain sufficient food for essential energy requirements. The shorter days during pre-breeding compared to post-breeding greatly reduced the mean daily foraging time by approximately 20%, while mean temperatures of 6.2°C meant high thermoregulatory costs for individuals. It is hardly surprising that robins responded by increasing their proportion of time spent foraging to 94%, similar to other small passerines during winter (Powlesland, 1981; Moreno et al., 1988; Enoksson, 1990). Individuals can also respond to energy limitation by minimizing their energy expenditure, often observed as an increase in less expensive foraging techniques or an increase in resting time (Hickey and Titman, 1983; Lundberg, 1985; Haylock and Lill, 1988; Lill, 1991). However, it appears that both male and female robins during the pre-breeding period are primarily energy-maximizers, virtually foraging constantly during all available time.

During the pre-breeding period, robins not only increased their foraging time but also had higher foraging attack rates. This significant increase was surprising considering the low invertebrate biomass collected during this period (300% less than post-breeding and 170% less than the breeding season). This increased attack rate parallels results for the brown thornbill (*Acanthiza pusilla*) in temperate wet forest in south-eastern Australia (Haylock and Lill, 1988) and the rifleman (*Acanthisitta chloris*) inhabiting lowland forest on the South Island, New Zealand (Lill, 1991). Reductions in interspecific and intraspecific competition for food resources were possible explanations in these studies. Robins hold territories all-year round, and while I did not record the numbers of potential competitors at the study sites, most species were present all-year round. More likely robins foraging behaviour helps locate inactive prey during colder temperatures through the use of foot-trembling and wing-flicking to stimulate prey movement. Reduced prey mobility during these colder temperatures would allow robins to capture prey more easily. Whether these prey are of similar size and contain the same energy

content as other months would be interesting to measure, as it possible that prey items are on average smaller during this period.

Males exhibit a slightly higher foraging attack rate than females during the pre-breeding period, resulting in a higher overall capture rate. This is surprising as males are hypothesized to minimize their foraging time. By definition, time-minimizers should forage just long enough to satisfy their basic energy requirements, as extra energy gain does not increase their reproductive success (Hixon, 1982; Hixon and Carpenter, 1988). Extra time can be invested in non-foraging activities such as inactive periods, extra breeding opportunities, mate guarding or territorial defence (Schoener, 1971; Lundberg, 1985; Askenmo et al., 1992). This result could be explained by the robins' mating system, which is socially and genetically monogamous with pair bonds generally maintained until the death of one of the pair (Ardern et al., 1997; Armstrong et al., 2000; Powlesland et al., 2000). Of three detailed studies of the North Island robin, polygyny was only observed once (Powlesland et al., 2000) while sequential polyandry (Davies, 1991, females switching males during the breeding season leaving previous male to raise juveniles) was observed twice in each of the three studies (this study pairs n = 100, Armstrong et al., 2000 n = 103; Powlesland et al., 2000 n = 53). It is surprising that sequential polyandry was not more common within this study as single males were extremely common in all forest fragments, adjacent to occupied territories. Such strong monogamy may explain the apparent high-energy intake by males during the prebreeding period. Males with partners during this period can be confident about their mating success and future parenthood, thus they can afford to maximize their condition.

High energy demands during the breeding season result in high rates of foraging among avian species (e.g. Hickey and Titman, 1983; Lundberg, 1985). Energy expenditure during the breeding season is thought to be substantially higher for females as they invest more in gamete formation, often forming eggs only when enough food is available (Perrins, 1970; Perrins, 1996). Males on the other hand invest very little in gamete formation and should show time-minimizing behaviour even within the breeding season. Males in this study showed no time-minimizing behaviour, with little variation in foraging behaviour between different breeding stages. This is probably due to the large amount of energy they invest in reproduction. From early September males begin courtship feeding, supplying the female with the extra food required for egg formation (Krebs, 1970). They then supply her with food throughout incubation (incubation feeding), and subsequently feed the offspring. This extrapolates into over six months of males obtaining food not only for their own maintenance but that of their females and offspring. Therefore, it is hardly surprising that males sustain high foraging attack rates and maintain similar daily overall attack rates, as those observed pre-breeding, using the longer daylight hours during the breeding season for foraging.

While it is difficult to quantify the different energy requirements for both sexes during the pre-breeding and breeding periods, we might expect that during moult (postbreeding), energy requirements for both sexes would be similar. Interestingly, it was during these post-breeding observation periods that I observed females foraging significantly more than males. However, when I extrapolate foraging attack rate and foraging time for both sexes we see overall foraging attack rates were almost identical and lower than during other periods. It appears that robins are time-minimizing during this period, with time devoted to resting and body maintenances activities increasing. While it has been argued that moult is energetically expensive (e.g. Lindström et al., 1993), a detailed study on dippers (*Cinclus cinclus*) found no evidence to suggest moult elevated basal metabolic rates or daily energy expenditure (Brown and Bryant, 1996). It seems that moult may not be costly for robins either, as we would expect robins to be able to maintain high foraging attack because food availability was highest during this period and conditions were mild.

The reduced foraging attack rate for females during post-breeding observations may be related to territory quality. During post-breeding, male robins can be found on their normal breeding territories whereas females appear to be aggressively displaced and acquire a small section of the previous breeding territory. Invertebrate sampling between these non-breeding territories of males and females may reveal a difference in food availability. However, this does not explain the reduced foraging attack rate for females pre-breeding when they forage along side their males. And there is no reason to suggest that females would forage less efficiently than males.

The only consistent pattern in regards to ambient temperature and foraging behaviour was recorded during the breeding season. Males reduced their foraging time and foraging attack rate with increasing temperatures. This probably reflects the decrease in

80

thermoregulatory costs and an increase in invertebrate activity during warmer conditions (Bryant and Tatner, 1988). The lack of an effect of temperature during the pre-laying period probably reflects the limited range of temperatures recorded. However, on a broader time-scale, the highest foraging rates occurred when temperatures were low (pre-breeding), whereas milder temperatures saw a reduction in foraging time (post- and breeding). The inconsistent relationship between foraging behaviour and invertebrate biomass may also be related to the problem of time-scale. On a broad time-scale, we see low foraging rates during times of high food availability (post-breeding) and high rates during low food availability (pre-breeding). Each individual time budget only sampled a small portion of the day. Attempting to correlate this behaviour with a cumulative-total trapping method (six-week period) may not have reflected food availability accurately over a smaller portion of the day (Hutto, 1990). A sampling method such as leaf-litter extractions using Burlese funnels (Southwood, 1994) directly after time budgets cease may be a more appropriate technique in further research.

Data from the comparison of male and female robins across their annual cycles reveals that the label of 'time-minimizer' for males and 'energy-maximizer' for females is not as appropriate in a strictly monogamous species. Both sexes apparently show time minimizing tactics during post-breeding observations while undertaking their annual moult, apparently the least energy-demanding period sampled. During pre-breeding, when robins virtually foraged constantly, the label of energy-maximizer is obviously appropriate, and similar for males during the breeding season. Robins show different foraging behaviour depending on the phase of their annual cycle under investigation and different seasonal conditions.



6.0 An inexpensive method for identifying passerine nest predators

Nest predation is often the main/primary cause of reproductive failure in bird species (Ricklefs, 1969). Although nest predation plays a crucial role in reproductive output, the event is rarely witnessed. Subsequently, the numerous ornithological studies that examine nest survival often lack any conclusive evidence or quantitative information regarding the identity of important nest predators within their research systems. This is partly due to the rarity of directly observing such events, as well as the inaccuracy involved when studies try to infer predator identification from signs left at the nest site (Storaas, 1988; Major, 1991; Brown et al., 1998; Lariviére, 1999; Williams and Wood, 2002; Staller et al., 2005) or from artificial nest studies (Zanette, 2002; Mezquida et al., 2004).

The variability in individual predator behaviour at nest sites causes the use of sign left at nests to be an extremely unreliable method of predator identification. Moors (1983a) inferred that "clean" signs left at nests in New Zealand were the result of stoat or weasel (*Mustela* sp.) predation and "messy" signs were the result of rats (*Rattus* sp.) or mice (*Mus musculus*). Camera footage set up at New Zealand robin (*Petroica australis*) and tomtit (*P. macrocephala*) nests revealed that these classification schemes were misleading. Not only was the overlap between rat scavenging and predation impossible to distinguish, but nest sign was also sometimes caused by parent birds removing egg and nestling remains after predation (Brown et

82

al., 1998). Even when researchers only attempt to classify nest predators into classes (e.g., avian, mammalian, snake) incorrect classification can be extremely high. Williams and Wood (2002) attempted to identify the class of nest predator from sign left at nests before observing video footage of the predation event. They found that the class of nest predator was misidentified in 57% of cases.

Motion-sensitive cameras and video cameras offer an extremely good method for identifying nest predators of eggs and nestlings (Picman, 1987; Major, 1991; Brown et al., 1998; Thompson et al., 1999; Zegers et al., 2000; Williams and Wood, 2002; Thompson and Burhans, 2003). In many studies it is often unfeasible to use cameras, the primary disadvantage is their high cost and thus the small number of predation events that can be recorded. Williams and Wood (2002) spent US\$45,000 for only nine video cameras and Thompson et al. (1999) US\$24.000 for six video cameras. although cheaper options are available (see Major and Gowing, 1994; King et al., 2001b). Cameras are also very labour intensive, with long set-up times, as well as requiring frequent battery and tape changes. further reducing sample sizes. Considering the frequent criticism of sample sizes used in studies of behavioural and evolutionary ecology (e.g., Moller and Jennions, 2002), it is essential that researchers respond with alternative methods, decreasing the cost and labour of intensive field methods and increasing available sample sizes. I suggest that nest predation studies with small budgets or limited time would greatly benefit from a cheaper alternative to using cameras, and a more reliable method than attempting to identify signs left by predators at nests.

Although impressionable eggs are often used in artificial nest studies to identify nest predators (e.g., Major, 1991; Rangen et al., 2000; Pärt and Wretenberg, 2002; Berry and Lill, 2003), I was only able to find two studies where they have been used for this purpose in active bird nests. One study involved an anseriform, the dusky Canada goose (*Branta canadensis occidentalis*) where domestic goose eggs were blown and filled with paraffin and petrolatum and placed in active nests (Anthony et al., 2004). The second study identified magpies (*Pica pica*) as nest predators at blackbird nests using plasticine eggs in active nests (Groom, 1993). Artificial eggs constructed of plastic and plaster of Paris are also frequently used in experiments testing species acceptance (or ejection rates) of brood parasite eggs (Rothstein, 1975; Kemal and

Rothstein, 1988; Davies and Brooke, 1989; Higuchi, 1989; Moksnes et al., 1991; Ortega et al., 1994; Briskie, 2003). Importantly, hatching success and clutch size were not affected by addition of artificial cowbird eggs in a study by Ortega et al. (1994), but they advised that different species may respond to the addition of artificial eggs differently. Considering the widespread use of artificial eggs, and the potentially high acceptance rate by many species it is surprising they have not been utilized in active nests more often. This method requires further investigation.

Here I describe a pilot study using artificial clay eggs in active European blackbird (*Turdus merula*), song thrush (*Turdus philomelos*), greenfinch (*Carduelis chloris*), goldfinch (*C. carduelis*) and chaffinch (*Fringilla coelebs*) nests in farmland and orchard habitat in New Zealand. I aimed to assess the birds' acceptance of artificial eggs and to assess whether imprints in the artificial eggs could be used to identify nest predators.

6.1 Methods

6.1.1 Study species and area

The response of European passerines to the addition of artificial eggs and subsequent predator identification was tested from September to January 2002-2005. The main study took place in the Benneydale region (175°22′E, 38°32′S) of central North Island, New Zealand. An additional site near Hamilton (175°19′E, 37°47′S) was utilized during 2004-2005 primarily for greenfinch, goldfinch and chaffinch nests. These nests were easily located in blueberry (*Vaccinium sp.*) orchards where these species were regarded as agricultural pests. The Benneydale study site is situated in an agricultural region, on the sheep and cattle farming Trusts of Te Hape, Tiroa and Wharakeri. Blackbird and song thrush nests were found in native podocarp-broadleaf fragments and exotic trees and shrubs while undertaking another project (Cassey et al., 2005). I systematically searched for nests in this habitat, often flushing the female from the nest or near the nest site.

6.1.2 Clay egg construction

Artificial eggs were made to mimic real eggs by moulding them from white, blue, and brown modelling clay to the size and shape appropriate for each species. All eggs

were coated three times with wood varnish (matt). This resulted in a soft centre, allowing predators to leave imprints, while the harder outer-surface allowed the female to sit on the egg without leaving imprints. Each egg took about five minutes to make, and applying the three coats of varnish took three to five days including drying time. These drying times could not be reduced as the clay cracked if it was dried too quickly.

6.1.3 Artificial clay egg attachment

In the first trial, the egg was placed in a song thrush nest with no attachment mechanism. After this nest was preyed on, I could not relocate the clay egg, which had been removed along with all the natural eggs. Eggs were then made with a short piece of black elastic protruding from the bottom, and this was tied to a short piece (~ 5 mm) of fine timber doweling that was moulded into the egg. The elastic was long enough that it could be threaded through the bottom of the nest, using a very thin piece of wire with a 'hook' on one end to push through the nesting material. The elastic was then tied to the nearest branch below the nest and the artificial egg was placed in the nest (Figure 6.1a, b). This attachment method prevented the complete removal of the artificial egg by predators. Excess elastic was pulled through to prevent either the incubating female or the nestlings from becoming entangled. Some excess elastic was necessary as it allowed females (and predators; Figure 6.1c) who rejected the artificial egg to eject it over the side of the nest.





Nests were normally only 1-2 m above the ground, making accessibility straightforward. One artificial egg was placed in each nest found during the laying

and incubation period. Because nests were found at different stages of development artificial eggs were added during the laying period (12/57), early incubation (27/57, days1-6 incubating, eggs were candled), late incubation (8/57, days 7-12 incubating) and 10 were during unknown stages of development. The ideal was to add the artificial egg early in the nesting period, allowing me to assess the female's behaviour towards the foreign egg for longer and increasing the chance of witnessing a predation event. In 39/57 cases one egg was removed from the clutch for use in another study at the same time the artificial egg removal is not necessary, as the experimental removal of one host egg has no effect on the rejection rates of model eggs (Davies and Brooke, 1989).

Most artificial egg rejections occur during the first three days (Davies and Brooke, 1989), therefore once an artificial egg had been added to a clutch I re-visited the nest 3-5 days later to confirm whether the female had accepted or rejected the egg. The artificial egg was considered rejected if after this period the female had removed the egg over the nest rim and the nest was still active (i.e. female seen flying off nest or eggs were warm). However, each time this behaviour was observed I replaced the artificial egg once more if the incubating female had not damaged it. If the female accepted the egg on the second occasion this was termed "partial acceptance". Nests were considered deserted if eggs were cold. After the artificial egg had been accepted I typically visited the nest every 3-6 days, until it either successfully fledged or was depredated. A control group of song thrush and blackbird nests, the two most common species were also monitored as above, the only difference being the lack of an artificial egg in each nest. This group allowed a comparison between the nesting success and desertion rates of experimental nests compared to controls. I calculated overall nest survival following the methods outlined in Shaffer (2004).

6.1.4 Predator identification

Predators were identified by positioning the skull (tooth and beak) of potential nest predators obtained from museum specimens to the imprints left on the experimental artificial eggs. Mammalian predators were easily identified to genus, as there were only five potential predator genera in the system, *Rattus*, *Mus*, *Trichosurus* (brush-tailed possum). *Mustela* and *Felis*, and these differ markedly in size and dentition.

The three main predatory bird species observed regularly at the study sites were the Australian magpie (*Gymnorhina tibicen*), Australasian harrier (*Circus approximans*) and Morepork (*Ninox novaeseelandiae*). All three species have characteristic beak shape and size, leaving distinctive imprints in the artificial clay eggs.

6.2 Results

6.2.1 Artificial clay egg acceptance

During the study 57 nests received an artificial egg, in 43 cases (75%) the female accepted the artificial egg and incubated is as one of her own (Table 6.1). In one case, the female continued to incubate the artificial egg for three days after her own eggs were preyed on, until the artificial egg was also preyed on. In 6 cases (10.5% of the 57 nests), the nest had been preyed on when next checked after adding the artificial egg, hence it was impossible to assess whether the artificial egg had been accepted (Table 6.1).

Of the 8 remaining nests (14%), the female rejected the artificial egg either by ejection or desertion (Table 6.1). Three females (one blackbird, one chaffinch, one goldfinch) ejected the artificial egg by hanging it over the nest rim, and one greenfinch apparently pulled the artificial egg apart. In four cases the female continued to incubate her clutch after removing the artificial egg. Four nests (one blackbird, three song thrush) were found deserted when next checked after the addition of the artificial egg (Table 6.1). However, it is unclear how many of these desertions were caused by the artificial egg for 5-10 days and that in the control group 5/28 song thrushes and 1/6 blackbird deserted nests. Desertion caused by the removal of one of the females own eggs seems unlikely, females who experienced partial predation during incubation never deserted their clutch during this study (pers. com). In three other cases (5.3%), all involving song thrushes, the female initially rejected the artificial egg by removing it over the edge, but subsequently accepted the egg when I replaced it back in the nest (Table 6.1).

87

Table 6.1. The individual response of five European passerine species after the addition of an artificial clay egg to their own clutch. Rejection includes removal of egg from nest (ejection) or abandonment of the nest immediately after receiving artificial egg (desertion).

			Rejected	Mode of rejection	
Species	Acceptance rate	Unknown	Total	Desertion	Ejection
Song thrush	30*/36	3	3	3	
Blackbird	5/8	1	2	1	1
Greenfinch	5/6		1		1 §
Goldfinch	3/5	1	1		1
Chaffinch	0/2	1	1		1
TOTAL	43/57	6	8	4	4

§ Only the elastic attached to the small piece of doweling remained in the nest, no clay.

* Three partial acceptance females, whereby the female initially ejected the artificial egg but subsequently accepted it after it was replaced.

6.2.2 Predator identification

Thirty predation events took place at nests containing artificial eggs. I was able to identify the type of predator in 19 cases (Table 6.2), while no imprints were recorded in the other 11 cases resulting in no identification. Nine of the eggs were imprinted by *Rattus* sp., and probably by *R. rattus* based on the distribution of rat species in New Zealand (King et al., 1996b; Innes, 2001). Where rats were identified as the predators, they generally left shell fragments in or on the nest rim, indicating eggs were eaten in the nest (Table 6.2). Most of the artificial eggs. Eight were identified as Australasian harriers and one as an Australian magpie (Table 6.2). The remaining egg was imprinted by an unknown bird species, the imprint was too faint to accurately identify. When large birds were identified as the predator shell fragments were rarely found in the nest and an attempt to remove the artificial egg from the nest was usually recorded (Table 6.2 & Fig. 6.1c).

Of the 30 predatory events, 25 nests failed during the incubation period. This high rate of predation during incubation is not surprising when the overall nest survival for a song thrush was only 12% for experimental nests and 11% (n = 28) for control

nests. Blackbird experimental nests had a higher success rate with 56% nest survival, and control nests 45% (n = 6). Females continued to incubate the artificial egg after their clutch hatched, making no attempt to remove the artificial egg along with the hatched shell fragments. Five nests subsequently failed during the nestling period, two after predation by *Rattus* sp. and the other three after predation by an unknown predator.

Table 6.2. Predator identification at the 30 active bird nests preyed on while containing artificial eggs. Numbers are given for nests where predator sign was left at the nest site and where partial predation occurred (one or more eggs from a clutch disappearing before complete predation).

Predator	17	Shell fragments	Clay egg out of nest	Partial predation
Rattus sp.	9	8	2	1
Harrier	8	1	7	2
Magpie	1	0	1	0
Unknown bird	1	0	1	0
No imprints	11	4	2	4

6.3 Discussion

The drive to incubate has meant that birds will accept and sit upon a variety of objects irrespective of whether or not they resemble eggs (Skutch, 1976). Fortunately, the willingness to accept egg-shaped objects has allowed researchers to use both artificial and telemetric eggs to study behavioural patterns during incubation such as parasitic egg acceptance, egg turning behaviour, and to monitor nest conditions. My study successfully demonstrated the use of an inexpensive method of predator identification in two European thrush species and three European finch species. The acceptance of the artificial egg by female blackbird and song thrush was high, with similar nest survival and desertion rates for experimental and control nests, indicating that predators were not attracted or repelled by the artificial eggs. For this method to be of practical use for researchers, study species clearly need to exhibit low desertion

rates towards the artificial egg. Species acceptance of model eggs will depend on their historical levels of parasitism and the incidence of intraspecific parasitism.

Blackbirds and song thrush have both shown high rejection rates toward model cuckoo (*Cuculus canorus*) eggs, 62-100% for blackbirds and 58-80% for song thrush, with egg ejection the preferred method of rejection (Davies and Brooke, 1989; Moksnes et al., 1991; Grim and Honza, 2001). However, Davies and Brooke (1989) also used model eggs painted to resemble blackbird and song thrush eggs and found significantly increased acceptance, with only 23% of blackbird and 14% of song thrushes ejecting the model egg. These values are very similar to those of this study, where 25% of blackbird and 8% of song thrush females rejecting artificial eggs. It is difficult to determine if desertion was associated directly to the artificial egg as control nests had similar desertion rates. Most other studies have found similar desertion rates to those recorded in this study with 6-22% for blackbirds (Osborne and Osborne, 1980; Moors, 1983b; Kentish et al., 1995; Hatchwell et al., 1996) and 18% for song thrush (Moors, 1983b).

A large number of previous studies have used clay eggs in artificial nests, but frequently report that the predation rates are different from those on natural nests (Davison and Bollinger, 2000; Pärt and Wretenberg, 2002; Zanette, 2002). This suggests that a different assemblage of nest predators prey on the different nest types, although without any direct predator identification from natural nests this remains largely speculative. Thompson and Burhans (2004) found similar predation rates for artificial and natural nests, but showed via video cameras that racoons (*Procyon lotor*) were the major nest predator at artificial nests while snakes were responsible for the predation at natural nests. The use of artificial eggs in active nests would be advantageous in such studies, which currently lack a cost-effective method for identifying predators at natural nests.

Nest predators that pose only a small threat to real nests can prey on contents of artificial nests at unnaturally high rates. Nest visitation by small mice, for example, can complicate artificial nest study results as it is unclear whether they are true nest predators (Buler and Hamilton, 2000), incidental scavengers facilitated by the lack of a parental bird defending the nest (Pärt and Wretenberg, 2002), or simply attracted by

90

the plasticine (Rangen et al., 2000). Similar biases exist for small birds scavenging undefended nests in artificial nest experiments (Zanette, 2002; Boulton and Clarke, 2003). This study eliminates these biases and one of the major criticisms for the use of artificial nests.

Like camera failures, the addition of an artificial egg to a nest does not guarantee that every predator will be identified, as 37% of predatory events recorded no imprints. The absence of any mustelid or felid imprints within this study may indicate that the artificial eggs do not deceive these predators, and it is possible that they represent the proportion of unidentified predators. A pilot study, either with cameras or in captivity, could reveal if these predators are likely to take artificial eggs. Outside New Zealand, there are two potential difficulties with using this methodology (i) predation by snakes and (ii) a much larger array of potential nest predators. Thompson and Burhans' (2004) study failed to detect snake predation at any artificial nests, although snakes accounted for 65% of predation at natural nests. It seems unlikely that snakes would attempt to eat an artificial egg, so species that suffer high predation due to snakes may also not be suitable candidates for this method. In areas with a larger number of potential nest predators, imprints may be difficult to identify (Major et al., 1994; Maier and DeGraaf, 2001) or several different predators may visit a nest between visits by researchers (Lariviére, 1999). Because New Zealand has only a limited number of potential predators, it makes predator identification from imprints relatively straightforward. Therefore I believe this method would be of explicit interest for New Zealand conservation managers. Interestingly, my study identified Australasian harriers as a major nest predator resulting in the failure of 27% of the study nests. How this result compares with predation on other New Zealand bird species, either native or exotic, is currently unknown.

In summary, I present data from a method for quantifying and identifying natural nest predators that had relatively low rates of nest abandonment and high rates of predator identification. Arguably, this is not a benign technique as it involves direct manipulation at active nests. However, there seems no reason why this method should not be investigated further. Similar techniques are routinely being used in cuckoo host-parasitism experiments, while studies do not hesitate to use nest cameras although they also have the potential to cause high nest desertion rates (34% in

91

Williams and Wood, 2002). With each artificial egg costing less than \$0.20 NZD, construction time of five minutes, and field set-up of one minute I believe this method could add valuable information for future studies of incubation and nest predation. Before using artificial eggs I recommend pilot studies with different host species to assess rates of acceptance, probability of identifying imprints and to test hatching success and predation rates between control and experimental nests. I am surprised considering the large number of cuckoo host-parasite studies currently being conducted, with artificial and mimetic eggs in natural nests, that imprint data are not being routinely used to identify natural nest predators. Ultimately, if this method is to be successfully used by researchers to quantify proportions of different nest predators it will benefit from a study similar to that of Williams and Wood (2002) using both artificial eggs and video cameras to confirm its efficiency.



7.0 Final discussion

Understanding the causes of broad-scale population declines is one of the key research concerns in conservation biology (see Armstrong, 2005). Habitat loss through agricultural clearance, forestry and urbanization leads to a reduction in suitable breeding, migratory and stopover habitats. These impacts are undeniable, but are there additional consequences for declining avian species persisting in fragmented landscapes? Evidence suggests that bird species breeding in small fragments generally experience reduced nest survival due to an influx of nest predators and brood parasites from the surrounding matrix, especially within agricultural landscapes (e.g., Brittingham and Temple, 1983; Wilcove, 1985; Robinson et al., 1995; Donovan et al., 1997; Stephens et al., 2003). Management of declining species in fragmented landscapes will only be successful if we are able to identify the underlying factors that cause these declines (Armstrong, 2005).

My study tested the importance of habitat quality on the reproductive success and behaviour of North Island robins. Although metapopulation dynamics were not directly addressed in my project, they were assessed simultaneously for future analysis (Y. Richard unpublished PhD thesis; Boulton, Richard and Armstrong in prep.). Of the two habitat variables I directly measured (food and predator abundance), only food availability showed a positive relationship with nest survival. Invertebrate biomass was not associated with fragment size, isolation or disturbance, but did vary substantially among individual robin territories. It is possible that robins

are able to locate areas of high food availability, similar to ovenbirds (*Seiurus aurocapillus*, Burke and Nol, 1998). Therefore, measuring biomass at the *territory* scale, we might not be able to obtain an accurate measure of a *whole* fragment's food availability. Support for this idea that robins can move to higher quality territories was provided by one (of the only three pairs), which survived the three-year study. Breeding in a 33 ha fragment with low robin densities (0-6 robins), they moved their territory each year after numerous unsuccessful nesting attempts, always to a territory with higher biomass. In their third year, on the highest biomass territory they successfully bred and were located breeding on this territory again in September 2005. Because I did not measure biomass on occupied and unoccupied sites within a fragment, it is possible that smaller and/or highly disturbed fragments are unable to support large numbers of robins because there are fewer areas of high food availability. If robins choose areas of higher biomass it may explain the lack of relationship between biomass, fragment size, isolation and disturbance.

The lack of a relationship between rat tracking rates and nest survival infers that attempting to integrate this simple parameter with metapopulation dynamics would be inappropriate at predicting population growth rates. Does this mean that predator abundance is not a key determinant of habitat quality for this robin population? This seems highly unlikely, as introduced mammalian predators are widely believed to play a major role in the reproductive success of New Zealand's avifauna (Clout et al., 1995; James and Clout, 1996; Powlesland et al., 1999; Innes et al., 2004). Unfortunately it appears that tracking tunnels are unable to offer a quick and reliable indicator of nest survival for three reasons. Firstly, tracking tunnels on a grid system may create contagion problems, where one rat tracks multiple tunnels. In addition, it appears that rats may be behaving differently in degraded fragments (grazed) due to the lack of ground cover (Chapter 2 & 3). Secondly, nest failure is not solely due to predation (higher nest survival on high biomass territories offers some evidence that nest failure is sometimes due to starvation). Thirdly, rats may not be the only nest predator within this system. No doubt rats are responsible for some nest failures as they have been identified as major predators of robin nests before (Brown, 1997; Brown et al., 1998). However, another key predator, the stoat (Mustela erminea) (Murphy and Dowding, 1994; King et al., 1996a; King et al., 1996b; Alterio and Moller, 1997; King et al., 2001a), was regularly seen in the forest fragments. While

7.0 Final discussion

tracking tunnels, in some situations, may offer a quick and easy method to obtain relative rat densities similar protocols with reliable estimates are not available for monitoring stoats. The average home range of a male stoat in a podocarp (Podocarpaceae) forest can be as large as 210 ± 28 ha, and females 89 ± 14 ha (Miller et al., 2001). Such large home ranges in a fragmented landscape, with small fragment sizes and short distances between fragments, means the use of tracking tunnels would be inappropriate, confirming only the presence or absence of stoats.

Attempting to understand the responses of rats and stoats to fragmentation, and the importance of each as nest predators, will be extremely challenging due to variability in fragment size (i.e. standard protocols for tracking tunnels/trap spacing would be different for each fragment) and the difficulty with studying these animals. In addition complex predator-prey relations appear to exist between stoats and rats, with stoats switching to bird prey after rat numbers are reduced through control programs (Murphy and Bradfield, 1992; Murphy et al., 1998). Radio tracking and/or mark-recapture of predators in such an environment could provide valuable information not only for fragmented landscapes but also on how these animals re-colonize areas after intensive eradication programs.

Predator identification is required to determine the relative importance of each nest predator. My pilot study using artificial clay eggs in active bird nests (Chapter 6) offers an alternative method from using predator sign left at nest sites and/or cameras for predator identification. Although I did not test the acceptance of artificial eggs by native bird species, a study investigating nine native species' acceptance of artificial (modelling clay) cuckoo eggs supports the idea that this method is worth further investigation in New Zealand (Briskie, 2003). Robin acceptance of artificial shining cuckoo (*Chrysococcyx lucidus*) eggs was low, with robins accepting only 3/8 artificial eggs (Briskie, 2003). However, robins accepted 4/4 artificial long-tailed cuckoo (*Eudynamys taitensis*) eggs. These eggs, unlike shining cuckoo egg was also high in the study, 15/16 and 7/8 respectively, inferring that these two species may also be useful for further studies with this method. Unfortunately, while it is relatively simple to place artificial eggs in accessible nests, robin nests in my study were frequently

95

10-15 m high, meaning trees would need to be climbed to place an artificial egg in each nest. Although climbing to nests is time consuming, benefits would be threefold if we were able to (1) identify a large number of nest predators, (2) determine whether nest failure was attributed to predation or starvation and (3) access to nest contents means valuable information such as clutch sizes, egg and nestling weights could also be collected and used to further investigate the possibility of food limitation and nestling starvation and/or clutch reduction.

As well as a positive relationship with invertebrate biomass and nest survival, nest watch data also indicated reduced food availability in this fragmented landscape (Chapter 4). Perhaps the best evidence came from my observed low female nest attentiveness compared to a population of P. australis where food was not limiting (Mackintosh and Briskie, 2005). Low nest attentiveness is associated with a longer incubation period (Lyon and Montgomerie, 1985), and supplementary feeding studies are often able to reduce the incubation period (Nilsson and Smith, 1988; Sanz, 1996). Therefore, we might expect a species to try to maximize its nest attentiveness, especially when the risk of nest predation is high. This is especially true if lengthening the incubation period can only increase the risk of nest predation. If food limitation is causing lower nest attentiveness, this does not explain the possible negative consequences, as I did not find reduced nest survival associated with reduced attentiveness? A detailed study of female nest attentiveness and its significance on the incubation period may reveal differences in incubation length. The 19-day incubation period of North Island robins is estimated from only four nests (Powlesland et al., 2000). Such small sample sizes highlight the lack of knowledge of basic breeding parameters for this species. Nevertheless the trend indicates that North Island robins have slightly longer incubation periods than the South Island robin (17.7 days, n = 30 Powlesland, 1983). However, if this is a genuine difference then it may provide an explanation for the lower nest attentiveness exhibited by North Island females compared with South Island females?

What is even more surprising than low nest attentiveness is the negative effect male incubation feeding has on nest attentiveness. This is contrary to the predictions that male feeding should help females attain high nest attentiveness (Lyon and Montgomerie, 1985; Lifjeld and Slagsvold, 1986; Halupka, 1994). In fact, males

decreased female nest attentiveness through incubation feeding, therefore it appears that male incubation feeding rates do not support the female nutrition hypothesis. Two alternative hypotheses may explain the adaptive role recognized in male incubation feeding; the maintenance of pair bonds (Lack, 1940; Andrew, 1961) and the assessment of male quality (Nisbet, 1973). The pair bonds within this system were generally maintained until the death of either the male or female (usually the female). In six cases females divorced their previous partners (males remained single), leaving them for neighbouring single males. Unfortunately because of such low rates of females swapping mates, we cannot directly test whether males with reduced feeding rates are divorced for better males. Nest watch data for two of these six females from their divorced males and their subsequent partners both show that new males had higher incubation feeding rates (1 to 4.5 hr^{-1} and 1 to 6 hr^{-1}). However, females have ample opportunity to divorce males, as single males are extremely common within this system even within the extremely large fragments. The fact that they are socially and genetically monogamous and that females divorced males even after successful nesting attempts is in conflict with these two hypotheses.

Given the lack of fit for a relation between male incubation feeding and nest attentiveness to existing hypotheses, I suggest that robins within all of the fragments may have been food limited. It has been previously shown that supplementary fed and handicapped males (removed tail feathers) decreased their rate of incubation feeding, indicating that incubation feeding is associated with a cost (Lifjeld and Slagsvold, 1986; Smith et al., 1989). Males on poor territories may try to compensate by increasing the rate of incubation feeding, whereas females on high quality territories are able to obtain enough food themselves. In the robin's case, it appears that the female still needs to forage every time her male feeds her. A supplementary feeding study could reveal whether a decrease in male incubation feeding is associated with an increase in female nest attentiveness.

7.0 Final discussion



Figure 7.1. a) Male incubation feeding rates relative to nest predation rate (% nests lost during incubation) for open-nesting and hole-nesting northern-hemisphere species in comparison to North Island robin feeding and predation rates and b) Nest attentiveness relative to the rate of male incubation feeding for the same open and hole-nesting species plus North Island robin for comparison. This graph is reproduced from Figures 1 & 2 in Martin and Ghalambor (1999).

Alternatively the lack of conformance may be caused by the unique life-history traits that have evolved in a system without mammalian nest predators (Holdaway, 1989). Certainly robins do not conform to the northern hemisphere species investigated by Martin and Ghalambor (1999). This is particularly noticeable with respect to male incubation feeding rates, nest attentiveness and predation (see Fig. 7.1). Martin (2002) illustrated that life-history evolution could be explained by adult and juvenile mortality. That is, species with low adult mortality exhibit reduced nest attentiveness and longer incubation periods. While robins may now experience higher mortality

98

(especially females on nests), past evolutionary history may account for their low nest attentiveness and long incubation period. This study accentuates some interesting comparative studies for the future. For example comparisons between robin populations with different predation levels, nest predators, predatory history and before and after intensive predator control programs may reveal some interesting insights into the role of incubation feeding. Robins on predator free islands such as Tiritiri Matangi, where they have had no experience with mammalian predators for over 10 years, offer a unique opportunity to examine the plasticity of a combination of these incubation behaviours.

When attempting to measure food supply it is important to simultaneously monitor behavioural or reproductive measures that are known to be correlated with variation in food abundance (Hutto, 1990). Such monitoring helps confirm that a given measure of food *abundance* reflects food *availability* to a foraging species. While nest survival and female on-bout duration during incubation were positively correlated with invertebrate biomass, similar results for time budget observations were only obtained across a longer time-scale. Robins spent long periods foraging pre-breeding when invertebrate biomass was low and reduced their foraging time during post-breeding when high biomass was recorded. However, on a territory-scale I did not observe a difference in the amount of time spent foraging in relation to biomass measurements. This result may reflect the cumulative-total trapping of invertebrates over a six-week period (long time-scale) compared to the short time budget observation periods. For addressing the effects of food availability on time budgets it may have been more appropriate to collect invertebrates directly after each time budget.

The major concern for the long-term survival of many of New Zealand's avifauna is the impact of introduced mammalian predators. This study is encouraging for robin populations occupying small forest fragments on mainland New Zealand in regards to predation. Nest survival rates reached a similar level to a predator-free island population (Tiritiri Matangi 37%) and higher than for a very large forest without predator control (Pureora Forest 25%). Concerns that species experience lower nest survival in small fragments were not supported in this study, with higher nest survival associated with smaller fragments. Whether this higher survival is caused by a
reduction in nest predators is unknown, as it appears tracking tunnels in small and highly modified areas may be inappropriate at accurately measuring rat density. Alternatively, stoats may have a much larger impact than rats or nestling starvation may be high, resulting in the lack of a significant relationship between tracking rates and nest survival. Unfortunately food limitation appears to be of concern in both the small and large fragments within this study, with nest survival positively correlated with invertebrate biomass, and females exhibited low nest attentiveness across all fragments. The lack of a negative effect of fragmentation and the unusual behaviour of male incubation feeding compared to northern-temperate species highlight the need to be cautious when assuming similar trends for southern hemisphere species.

These results form the first detailed study to assess the impact of fragmentation on the reproductive success of a New Zealand species, revealing a number of interesting questions in regards to food limitation. In addition, this study has also highlighted the unusual incubation behaviour of this species. I particularly recommend the following directions for future research:

- Supplementary feeding experiments in forest fragments to determine the true extent of food limitation on nest survival, nest attentiveness and male incubation feeding from supplementary fed and control pairs.
- (2) A detailed study of robin incubation behaviour (attentiveness, male incubation feeding, incubation length) between mainland populations (high predation) and Tiritiri Matangi (no contact with mammalian predators for over 10 years) to determine the plasticity of these behaviours to nest predation.
- (3) A detailed study on the feasibility of using artificial clay eggs in active nests of native bird species for predator identification in New Zealand.
- (4) Further studies on the effects of fragmentation within New Zealand, especially those that incorporate nest survival data and the response of nest predators.

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