A comparison of the effects of predation by Norway (*Rattus norvegicus*) and Polynesian rats (*R. exulans*) on the Saddleback (*Philesturnus carunculatus*)

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ABSTRACT

The Saddleback (*Philesturnus carunculatus*) is now confined to New Zealand offshore islands free of the introduced carnivorous mammals, i.e.rats, feral cats and mustelids, which are assumed to have exterminated the species on the mainland during the last century. The North Island Saddleback (*P. zc. rufusater*) coexists with the Polynesian rat (*Rattus exulans*), while the South Island Saddleback (*P. c. carunculatus*) thrives only on rat-free islands. An experimental transfer to Kapiti Island, where Norway (*R. norvegicus*) and Polynesian rats occur, provided an opportunity to test the hypothesis that North Island Saddlebacks could coexist with both rat species. I compared the survival of Saddlebacks on Kapiti Island with that on Cuvier and Little Barrier Islands where the only rodent is *R. exulans*. On Kapiti Island, Saddlebacks suffered high mortality, and despite high productivity, there was insufficient recruitment of young to balance losses of adults. Significantly more nests sited less than one metre above the ground were preyed on by rats on Kapiti Island than on Cuvier and Little Barrier Islands. Saddlebacks on Kapiti Island which roosted in high or secure cavities survived longer than those birds which roosted in low or vulnerable places. These observations are consistent with the ground-foraging and predatory behaviour of *R. norvegicus*. On Kapiti Island, 21 rat-killed birds were found at nests and roosts, whereas no rat-killed birds were found at nests and roosts on Cuvier and Little Barrier Islands, although the contents of some nests were preyed on by *R. exulans*. On Kapiti Island, *R. norvegicus* faeces were found with the remains of several dead birds, providing direct evidence that this rat was the predator. The poor survival and recruitment of Saddlebacks on Kapiti Island, coupled with observations of rat-killed birds and plundered nests near the ground, suggest that Saddlebacks are unable to coexist with both rat species, and that *R. norvegicus* is probably an important predator. The cavity nesting and roosting habits of the Saddleback make this species especially vulnerable to mammalian predators.

KEYWORDS: Saddleback, *Philesturnus carunculatus*, predation, *Rattus norvegicus*, *Rattus exulans*

INTRODUCTION

The Saddleback (*Philesturnus carunculatus*) was formerly widespread in New Zealand and following the arrival of the Maori, is assumed to have coexisted with the Polynesian rat (*Rattus exulans*). However, Saddlebacks declined quickly after European settlement, and introduced carnivorous mammals, particularly rats and feral cats (*Felis catus*) have been blamed for the decline (Turbott 1947, Oliver 1955). Saddlebacks persisted on the mainland until after 1860, and circumstantial evidence suggests possible coexistence with the mainly ground-foraging Norway rat (*R. norvegicus*), which probably reached New Zealand in the 1770s (Atkinson 1973, 1978, 1985). Extinction of the North Island Saddleback (*P. c. rufusater*) has been attributed to the more arboreal ship rat (*R. rattus*), which spread through the North Island after 1860. *P. c. rufusater* was already rare when mustelids were introduced in the 1880s (Atkinson 1973, King 1984, 1990). The simultaneous spread of *R. rattus* and mustelids in the South Island after 1890, obscures which predator was to blame for the decline of the South Island Saddleback (*P. c. carunculatus*) (Atkinson 1973). By 1900 only two Saddleback populations remained, *P. c. rufusater* on Hen Island (where *R. exulans* is the only rodent), and *P. c. carunculatus* on the then rodent-free Big South Cape Islands. An invasion of *R. rattus* exterminated the Big South Cape Islands population by the mid-1960s, and confimed that this rat was an important predator (Atkinson & Bell 1973, Bell 1978). Transfers of surviving birds in 1964 to nearby rodent-free islands saved this subspecies (Merton 1975). Transfers of *P. c. carunculatus* were also made to islands with *R. exulans*. These have either failed or have ailing populations (Roberts 1991, Lovegrove, in press), suggesting that birds derived from the Big South Cape Islands population may be unable to coexist with *R. exulans*. By contrast, most recent transfers of *P. c. rufusater* to northern islands with *R. exulans* have been successful (Lovegrove, in press). Events on the Big South Cape Islands gave added urgency to a series of island transfers to conserve Saddlebacks, resulting in new populations on nine northern and ten southern islands (Merton 1975, Nillson 1978, Roberts 1991, Lovegrove, in press).

Between 1981 and 1990, 366 North Island Saddlebacks were transferred to Kapiti Island (Lovegrove 1992). Apart from an unsuccessful introduction in 1925 (Wilkinson & Wilkinson 1952), when there was probably ignorance of the effects of predators, (Lovegrove, in press) this was the first time Saddlebacks had been intentionally reintroduced to a habitat with *R. norvegicus* present. Hitherto all successful releases had been to islands with *R. exulans* only (*P. c. rufusater*), or to rodent-free islands (*P. c. carunculatus*). The release on Kapiti Island provided a unique opportunity to test whether Saddlebacks could coexist with both *R. norvegicus* and *R. exulans*. Saddlebacks formerly occurred on Kapiti Island (Cowan 1907), presumably in the presence of *R. exulans*, which probably arrived with the Maori in pre-European times. Sometime last century Saddlebacks disappeared from Kapiti, but since the island was greatly modified by fire (Esler 1967, Fuller 1985), and feral cats and domestic livestock were also present (Wilkinson & Wilkinson 1952), the cause of this local extinction is not clear. Today, Kapiti Island lacks ship rats, mustelids and feral cats, leaving *R. exulans* and *R. norvegicus* as the only potentially harmful introduced mammals (Cowan 1992). Thus the range of predatory mammals present on Kapiti Island is similar to the 1770-1860 period when Saddlebacks were apparently widespread on the mainland (Potts 1882, Buller 1888), and it was a reasonable assumption that Saddleback translocations to Kapiti Island might be successful.

In this study I compared survival and breeding success of Saddlebacks on Kapiti Island, where *R. norvegicus* and *R. exulans* occur, with Cuvier and Little Barrier Islands where Saddlebacks coexist with *R. exulans*.

STUDY AREAS

Kapiti Island nature reserve (1965 ha.) lies at 40°52' S 174°55'E, 50 km north of Wellington. Although a large area of the forest was cleared for farming during the last century, this had mostly ceased by 1900 allowing the forest to regenerate (Esler 1967, Fuller 1985). *R. exulans*, *R. norvegicus* and feral cats were probably present by 1840. Possums (*Trichosurus vulpecula*) were introduced in 1893, but these were eradicated between 1980 and 1986 (Cowan 1992). Domestic livestock has been removed, and cats were eradicated by 1940 (Veitch & Bell 1990). The only remaining introduced mammals are *R. exulans* and *R. norvegicus* (Daniel 1969, Cowan 1992). Nine Saddlebacks were reintroduced to Kapiti Island in October 1925, but despite breeding for several years, they had died out by 1931 (Wilkinson & Wilkinson 1952). In November 1992, the Saddleback population on Kapiti Island numbered about 40, following the transfers of 366 birds between 1981 and 1990 (Lovegrove, in press).

Cuvier Island nature reserve (170 ha.) lies at 36°27' S 175°46'E, 80 km north-east of Auckland. *R. exulans* arrived with the Maori who also burned part of the forest (Beever *et al.* 1969). Between 1889 and 1982, Cuvier Island had a staffed lighthouse, and cats and goats (*Capra hircus*) were introduced. These were eradicated during the early 1960s (Blackburn 1967, Merton 1970), and farm livestock was removed in 1982 when the lighthouse was automated. At the time of this study the only remaining introduced mammal was *R. exulans*, but this rat was eradicated in 1993 (P. Thompson pers. comm.). Saddlebacks were reported on Cuvier Island in 1878 (Oliver 1955), but this population was probably exterminated by feral cats. Twenty-nine Saddlebacks were transferred to Cuvier Island from Hen Island in 1968 (Merton 1970, Jenkins 1978), and the population now numbers about 1000 (Lovegrove, in press).

Little Barrier Island nature reserve (3083 ha.) lies at 36°12'S 175°04'E, 60 km north of Auckland. *R. exulans* was introduced by the Maori, followed by cats some time after 1870. Domestic animals were also introduced, but these are now confined to a small area of farmland near the ranger's homestead (Hamilton 1961). The original Saddleback population was probably exterminated by cats last century (Turbott 1947). An unsuccessful attempt was made to reintroduce them (8 birds) in 1925 (Wilkinson & Wilkinson 1952), when feral cats were still present. Feral cats were eradicated between 1977 and 1980 (Veitch 1983, Veitch & Bell 1990). Between 1984 and 1988, 188 Saddlebacks were reintroduced in four transfers (Lovegrove, in press). They are now well established and the population probably numbers about 1500.

METHODS

This study is based on observations of banded populations on the three islands. Most birds were individually colour-banded. The few unbanded birds were easily identified by their strong site attachment and individual song patterns (Jenkins 1978). Saddlebacks are highly vocal and conspicuous, and even on the two large islands in this study (Kapiti and Little Barrier), it was possible to locate practically all of the birds. Finding the birds was easiest during the first few years after release, when total numbers were still low. The survival figures for Cuvier Island are derived from a sample of the population living in the central part of the island, which was surveyed annually between 1968 and 1985 (Jenkins *et al.*, unpubl.).

For the analyses of survival and mortality on Kapiti Island, I used data obtained between 1981 and 1985 (T.G. Lovegrove, unpubl.). Although survival was also monitored between 1987 and 1991, Saddlebacks had enhanced survival during those years as a result of a behaviour and habitat manipulation experiment (Lovegrove 1992). Survival data for Cuvier Island are derived from Jenkins *et al.* (unpubl.), who have summarised survival between 1968 and 1985. Data for Little Barrier Island were obtained between 1984 and 1987 (T.G. Lovegrove, unpubl.).

For the analyses of predation, productivity and recruitment I used all available data for all study years on Kapiti, Cuvier and Little Barrier Islands. I included data from the 1987-90 period for Kapiti Island because, despite management, rat predation still appeared to be the most important cause of mortality. I was unable to monitor all recruitment on Cuvier and Little Barrier Islands, so projections of recruitment are based on demographic data for the Cuvier Island population given by Jenkins *et al.* (unpubl.). Since the Little Barrier population was expanding, and probably subject to few density dependent effects, the Cuvier Island figure I used represents a minimum level of recruitment, because the Cuvier Island population was already at equilibrium by the late 1970s (T.G. Lovegrove, unpubl.). Recruitment on Kapiti Island was determined by surveying the population each spring. Since Saddlebacks are capable of breeding in their first year (T.G. Lovegrove, unpubl.), new recruits were regarded as all first-year birds which had survived the winter.

A considerable amount of time was spent searching for and monitoring roosts and nests. This was justified because this was where I expected to find evidence of predation. The Saddleback nests and roosts in cavities, and other studies have shown that cavity-using birds are vulnerable to mammalian predators (Alerstam & Hogstedt 1981, Elliott 1990). If a bird disappeared, its nest or roost, if known, was checked immediately. I found roosts by following birds in the evening, or by searching sites (hollow trees, overhanging banks) where birds were last seen before roosting, or where they appeared at dawn. I located nests by following nest-building, incubating or brooding females, or adults carrying food. Adults were secretive, and nests were well hidden in ground or tree cavities or in large epiphytes. I examined nest contents (with a torch and mirror if necessary) on the first visit to determine the stage of breeding, thereafter I kept nest visits to a minimum to reduce the chances of attracting rats (Bart 1977). Apart from one visit to band young at 10-17 days of age, I usually monitored nests from 5-10 m away. I located many nests after initiation, so I used the Mayfield method to calculate breeding success (Mayfield 1975, Johnson 1979, see also Pierce 1986).

I checked pairs with dependent young at intervals of one to four days and watched families roosting to locate roosts of fledglings. Young were assumed to have become independent if they were seen without their parents, or if they had survived at least 30 days after fledging. The 30-day dependence phase used in the calculations may give a slight over-estimate of numbers of young that became independent, but most dependent young that were lost disappeared earlier than this.

To differentiate high and low Saddleback nests and roosts, and to emphasise the differences in climbing frequency of *R. norvegicus* and *R. exulans* (Atkinson 1985), I chose a height criterion of 1m. This is probably an arbitary figure, because *R. norvegicus* can climb higher than this (Hill *et al.* 1983, Atkinson 1985), especially through hollow branches or thick vegetation (T.G. Lovegrove, unpubl.). However, the lack of evidence for any *R. norvegicus* predation at Saddleback roost boxes on Kapiti Island placed at or near this height (T.G. Lovegrove, unpubl.), suggested that 1m was an appropriate height criterion for this analysis.

In ascribing predation to rats, it is important that the predator responsible be identified correctly. In this study I relied only on the feeding sign left at nests or roosts to identify the predator responsible. All dead birds and nests that were preyed on were photographed *in situ*, checked carefully for possible predator signs, and then collected for later reference. Recent work shows that this method has limitations. Savidge & Seibert (1988), Major (1991), and Brown (1994) used remote photography to identify predators at nests, which allowed feeding sign to be matched with various predators. They found that many predators did not leave consistently similar signs. For example Major (1991) and Brown (1994) both found that in addition to eating the contents of nests *in situ*, and leaving the characteristic untidy sign described by Flack & Lloyd (1978), and Moors (1978, 1983), rats also frequently carried prey from nests leaving very little sign at all. Brown (1994) also found that parent birds returned to nests after predation had occurred and sometimes removed broken eggshells, altering the sign left after rat predation. In my study I had the advantage of working on islands where predator species were few. On Cuvier and Little Barrier Islands the only rodent is *R. exulans*. On Kapiti Island, where both *R. norvegicus* and *R. exulans* occur, it was not possible to identify which rat was responsible unless faeces were found at the scene. Where adult or juvenile birds were killed on Kapiti Island, and where faeces were absent, I assumed that the rat responsible was *R. norvegicus* because there was no evidence for *R. exulans* preying on Saddlebacks in previous studies on Cuvier Island (P.F. Jenkins pers comm., T.G. Lovegrove, unpubl.). However, this is based on the assumption that *R. exulans* on Kapiti Island have similar predatory habits and diet to those on Cuvier Island. A study of the diet and ecology of rats on Kapiti Island (Dick 1985), showed that the diet of *R. exulans* consisted mostly of invertebrates, with smaller proportions of vegetation and seed, while *R. norvegicus* had a more omnivorous diet which included birds.

I noted two types of predation sign at nests:

(1) Untidy, e.g. eggshells broken into small fragments and mixed through the stirred up nest lining, or the remains of young or adult birds mixed through or lying on top of the nest material. The remains of most birds killed at nests by rats showed all the signs of rat predation described by Flack & Lloyd (1978) and Moors (1978, 1983). Although some bodies were almost whole when found, most were well-chewed with all flesh and soft parts gone, and reduced to mandibles, gnawed pieces of major bones, fragments of cranium, pieces of skin, and feathers. The larger wing and tail feathers were often snipped off close to the bases. Most prey was consumed on the first night, but sometimes rats scavenged dead birds over several nights, although they did not eat badly decomposed corpses. In three of the nine cases where birds were killed by rats at nests, the remains of the dead birds were found on the ground below the nest site. Although possums were common on Kapiti Island when the study began in 1981, and were present in declining numbers until eradication in 1986 (Cowan 1992), I did not find any predation sign that appeared characteristic of this species (Brown *et al.* 1993, Brown 1994, and J. Innes, pers. comm.).

TABLE 1 – Mean annual mortality of mixed-age site-attached Saddlebacks from census to census on Kapiti, Cuvier and Little Barrier Islands. This table shows mortality of established site-attached birds only, and does not include mortality associated with the releases on the three islands. Each row shows the numbers in a mixed-age cohort identified in a given year, and the numbers resighted in the following year. Data from Kapiti Island are from 1982 to 1986 only. After 1987 birds which roosted in special rat-proof boxes were introduced, and roost box-using birds had enhanced survival (T.G. Lovegrove unpubl.). Data from Cuvier Island are from Jenkins *et al.* (unpubl.). Only two consecutive years (1985 and 1986) of survival data were available for the Little Barrier Island population.

Year	No. alive year 1	No. alive year 2	No. dead
Kapiti Island			
1982	20	7	13
1983	17	11	6
1984	14	6	8
1985	6	3	3
Total	57	27	30
Mean annual mortality: 52.6%			
Cuvier Island			
1969	13	12	1
1970	35	33	2
1971	75	65	10
1972	96	71	25
1973	104	85	19
1974	94	72	22
1975	102	97	5
1976	97	95	2
1977	141	124	17
1978	136	132	4
1979	170	149	21
1980	154	142	12
1981	155	136	19
1982	142	139	3
1983	163	127	36
Total	1677	1479	198
Mean annual mortality: 11.8%			
Little Barrier Island			
1985	20	17	3
1986	17	16	1
Total	37	33	4
Mean annual mortality: 10.8%			

(2) Clean, e.g. nest empty and relatively undisturbed, apart from a few feathers in the nest cup, or spots of blood on the nest or at the entrance hole. Sometimes nest material in the bottom of the nest cup was pulled up slightly where the young had possibly grasped it when lifted out by the predator. Moors (1983) ascribed this sort of sign to stoats (*Mustela erminea*), because they usually remove prey from nests. Stoats are absent from all of the islands in this study, and my observations suggested that some of the clean predations were due to Moreporks (*Ninox novaeseelandiae*), which also remove prey from nests (Brown 1994, J. Innes pers. comm.). However, some of the clean predations on Kapiti Island could also have been due to rats, which are known to remove prey from nests (Major 1991, Brown 1994). In view of the lack of other evidence, I noted these as possible Morepork

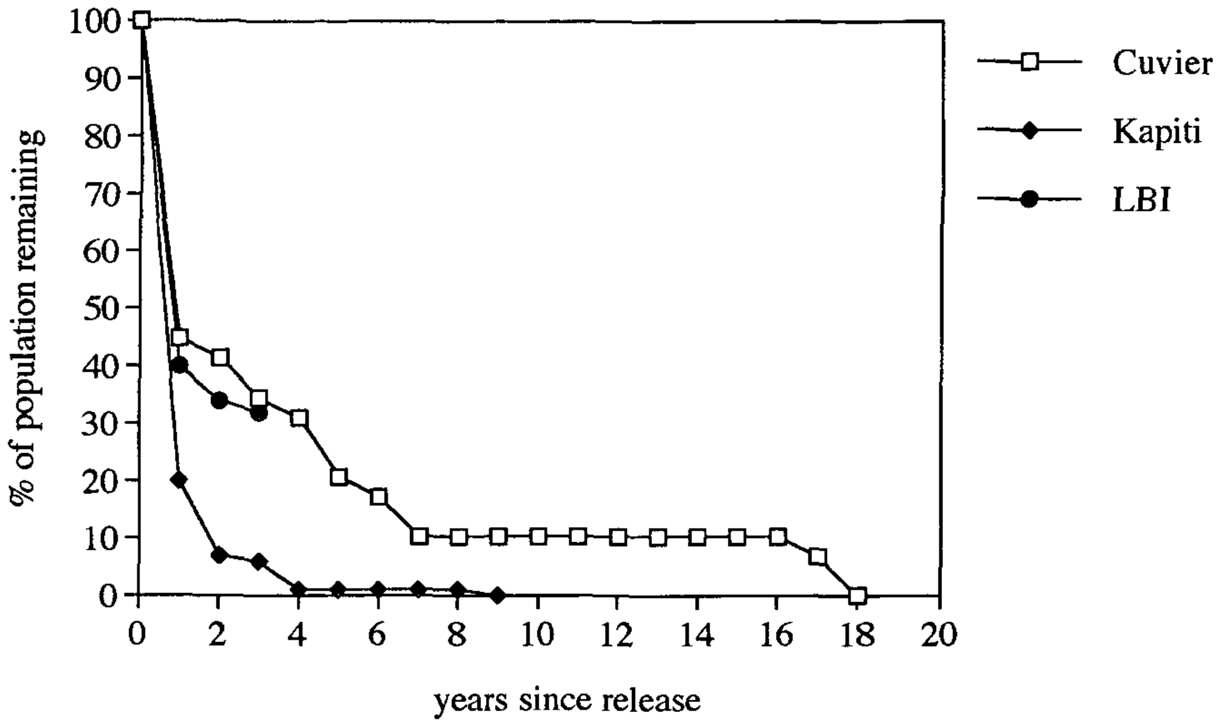

FIGURE 1 - Survivorship of translocated Saddlebacks on Kapiti (1981,N=100), Cuvier (1968, N=29 and Little Barrier (LBI) Islands (1984, N=50).

predation, possibly underestimating the number of nests preyed on by rats. At one nest on Kapiti Island where a rat preyed on a female and two large young, there were numerous feathers in the nest cup, and a trail of feathers led away along the ground for several metres towards a bank containing *R. norvegicus* burrows. Fourteen nests were preyed on by Moreporks. In 12 of these, the nest cups were completely clean, broken eggshells were found at the entrance to the nest cavity at one nest, and one female successfully escaped the attacker.

In this paper, brief reference is made to predators other than rats, to show that there are natural predators of Saddlebacks which cause some losses. All the other predators in this study were birds. On Kapiti Island they include Moreporks, Harriers (*Circus approximans*) and Weka (*Gallirallus australis*). On Cuvier and Little Barrier Islands there are Moreporks and Harriers but no Weka.

Since Cuvier and Little Barrier Islands have *R. exulans* only, data from these islands have been combined where appropriate, to increase sample sizes. Combining the data from these two islands is based on the assumption that the effects of *R. exulans* on Saddlebacks on both islands is similar. This assumption could be incorrect, moreover there could be factors other than *R. exulans* affecting the survival of Saddlebacks on the two islands.

TABLE 2 – Static* life tables for Saddlebacks on Kapiti, Cuvier and Little Barrier Islands. Figures for Kapiti Island have been compiled from four seasons between 1981 and 1985. Figures for Cuvier Island have been derived from the 1986-87 season (fledgling mortality) and from Jenkins *et al.* (unpubl.) (juvenile and adult mortality). Figures for Little Barrier Island have been derived from the 1984-85 season (fledgling mortality), and 1984-87 (adult mortality), and from Jenkins *et al.* (unpubl.) (i.e. using Cuvier Island juvenile mortality). The juvenile mortality figures shown for Little Barrier Island may be an overestimate, because unlike Cuvier Island, this was an expanding population, which probably lacked density-dependent effects. Age classes are as follows: 1 = Fledglings from fledging to independence (i.e. fledging to *c.* 30 days of age), 2 = Juveniles from independence to end of first year, 3 = All birds older than one year.

* Calculated on the basis of a cross section of the population at a specific time, in this case age classes (Krebs 1972).

Age class	Observed no. alive in each age group *x*	No. surviving at start of age interval *lx*	No. dying within age interval *dx*	Rate of mortality *qx*
Kapiti Island				
1	66	90	24	0.267
2	9	66	57	0.864
3	33	68	35	0.515
Cuvier Island				
1	53	64	11	0.172
2	35	60	25	0.416
3	1479	1677	198	0.118
Little Barrier Island				
1	17	20	3	0.150
2	35	60	25	0.416
3	33	37	4	0.108

RESULTS

Mortality of transferred birds during the first year

Mortality during the first year included the immediate post-release losses due to circumstances of the releases, (many releases featured high losses during the two-month territory formation and pair-bonding phase [Lovegrove in press]), as well as losses due to predation and other factors. Mortality of transferred birds in the first year after release was high on all three islands, but mortality on Kapiti Island was significantly higher than both Cuvier (χ^2_1=7.28, P <0.01) and Little Barrier Islands (χ^2_1=6.82, P <0.01) (Figure 1). On Kapiti Island 20% (N=100, 1981 release) of the transferred birds were still alive, compared with 48% (N=29, 1968 release) on Cuvier Island, and 40% (N=50, 1984 release) on Little Barrier Island. There was no significant difference between Cuvier and Little Barrier Islands in the survival of transferred birds (χ^2_1=0.67, P >0.5).

TABLE 3 – Productivity of Saddlebacks on Kapiti (1981-1990), Cuvier (1986-1987) and Little Barrier Islands (1984-1985).

Breeding characteristics	Kapiti Island	Cuvier Island	Little Barrier Island
No. nests known clutch	140	44	6
No. eggs	326	89	15
Mean clutch size ± S.D.	2.33 ± 0.6	2.02 ± 0.3	2.50 ± 0.6
No. breeding pairs	81	54	9
No. broods	146	54	13
No. broods pair^{-1}	1.80	1.00	1.44

Mean annual mortality of established birds

Mean annual mortality of established birds, (i.e. the territorial survivors after the initial two-month period of high post-release mortality [Lovegrove in press]) on Kapiti Island was 52.6% (N=57), which was significantly higher than Cuvier Island (11.8%, N=1677) (χ^2_1=80.45, P <0.001, and Litle Barrier Island (10.8%, N=37) (χ^2_1=16.99, P <0.001, (Table 1). There was no significant difference between Cuvier and Little Barier Islands in mean annual mortality of established birds (χ^2_1=0.09, P >0.5 (Table 1).

Life table analysis

A life table comparison between the Kapiti Island and the Cuvier and Little Barrier Island populations, showed higher mortality on Kapiti Island of fledglings, independent juveniles and adults (Table 2). The figures for Cuvier and Little Barrier Islands represented stable and expanding populations respectively, while the population on Kapiti Island was declining. On Kapiti Island mortality of juveniles was more than double the rate on Cuvier Island, and mortality of adults was six times higher.

Breeding success

Although Saddlebacks on Kapiti Island had similar clutch sizes and numbers of broods as Saddlebacks on Cuvier and Little Barrier Islands (Table 3), the overall breeding success on Kapiti Island was much lower (Table 4). Nests on Cuvier Island had the highest probability of fledging young (0.83 ± 0.003 [95% confidence limits]), while nests on Kapiti and Little Barrier Islands had probabilities of 0.60 ± 0.003 and 0.61 ± 0.012, respectively. The probability that fledglings would survive to independence on Kapiti Island (0.37 ± 0.002), was lower than Cuvier and Little Barrier Islands (0.82 ± 0.004 and 0.85 ± 0.006, respectively). Most fledgling mortality on Kapiti Island occurred during the first two weeks (Figure 2). Overall breeding success, i.e. probability of egg and nestling survival x fledgling survival (Mayfield 1975, Johnson 1979), was 0.22 ± 0.003 on Kapiti Island, compared with 0.68 ± 0.003 on Cuvier Island, and 0.52 ± 0.006 on Little Barrier Island.

TABLE 4 – Comparison of breeding success of Saddlebacks on Kapiti, Cuvier and Little Barrier Islands. Formulae given by Mayfield (1975) and Johnson (1979) were used to calculate values in this table.

Details	Kapiti Island	Cuvier Island	Little Barrier Island
Total nests[1]	156	41	13
Total nest days (N)	4216	1456	279
No. nests preyed on (P)	48	6	3
Probability of nest surviving to fledging (A)[2]	0.60 ± 0.003	0.83 ± 0.003	0.61 ± 0.012
Total fledglings	191	65	20
Total young lost (F)	89	11	3
Total fledgling days (N)	4029	1644	548
Probability of fledgling becoming independent (B)[3]	0.37 ± 0.002	0.82 ± 0.004	0.85 ± 0.006
Breeding success[4]	0.22 ± 0.003	0.68 ± 0.003	0.52 ± 0.006

1. This table excludes nests that were abandoned.
2. Since similar levels of predation were recorded for incubation and nestling phases these were combined. Duration of incubation and nestling periods, including egg laying, is approx. 45 days. $A = (1-P/N)^{45}$ (± 95% confidence limits).
3. 30 days was taken as sufficient time for young to become independent, but some, e.g. where no subsequent brood, were dependent longer than this. $B=(1-F/N)^{30}$ (± 95% confidence limits).
4. Probability of nest producing independent young = (A x B).

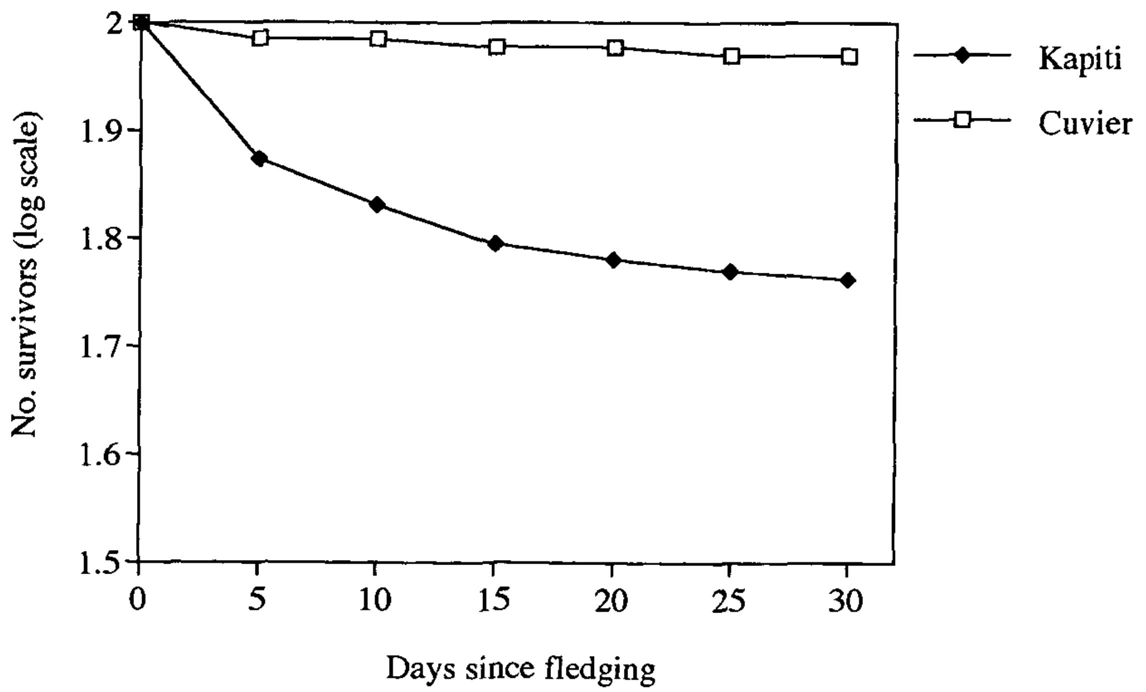

FIGURE 2 - Comparison of survivorship from fledging to independence of Saddleback young on Kapiti Island (N=202) and Cuvier and Little Barrier Islands (N=59).

TABLE 5 – Saddleback mortality and recruitment on Kapiti, Cuvier and Little Barrier Islands.

Year	Adult mortality	Juvenile mortality	[1] Recruitment rate required to maintain population	[2] No. fledglings recruited adult year $^{-1}$
Kapiti Island				
1981-1982	0.65	0.84	0.80	0.25
1982-1983	0.35	1.00	1.00	0.00
1983-1984	0.57	0.78	0.72	0.31
1984-1985	0.33	0.94	0.86	0.00
1987-1988	0.29	0.56	0.40	0.25
1988-1989	0.28	0.64	0.44	0.22
1989-1990	0.35	0.60	0.47	0.10
Cuvier Island [3]				
1986-1987	0.09	0.42	0.13	0.29
Little Barrier Island [4]				
1984-1985	0.15	0.42	0.20	0.65

1 Recruitment rate required to maintain population = adult mortality / (survival of young to reproductive age, s_0) - (loss of potential breeding adults before second year due to reduced survival, $s_0(s-s_1)$), where s_0 = 1, s = adult survival (i.e. 1 - adult mortality), and s_1 = juvenile survival (i.e. 1 - juvenile mortality) (Ricklefs 1973).
2. No. fledglings recruited adult year $^{-1}$ = (No. fledglings recruited at year 1 / No. pairs) / 2
3. Adult and juvenile mortality figures for Cuvier Island after Jenkins *et al.* (unpubl.). Figures for no. fledglings recruited adult year $^{-1}$ are from the 1986-1987 season.
4. Recruitment data for Little Barrier Island have been derived from juvenile mortality figures for Cuvier Island, given by Jenkins *et al.* (unpubl.). These figures may overestimate juvenile mortality on Little Barrier Island, because unlike Cuvier Island this was an expanding population, which probably lacked density-dependent effects.

TABLE 6 – Summary of rat predation at nests on Kapiti Island and on Cuvier and Little Barrier Islands. (Results from Cuvier and Little Barrier Islands are combined because of the small sample size of nests preyed on).

Status of nest	Kapiti I	Cuvier & Little Barrier Is
No. not preyed on	147	58
No. preyed on	23	8
Totals	170	66

Because of the high mortality of young, recruitment in the Kapiti Island population was insufficient to compensate for high adult mortality in all years of the study (Table 5). This contrasted with Cuvier and Little Barrier Islands where adult mortality was lower, and where recruitment exceeded the number needed to balance adult mortality (Table 5).

Predation

Both *R. exulans* and *R. norvegicus* prey on Saddleback nests. There was no significant difference in the numbers of nests preyed on by rats between Kapiti Island and Cuvier and Little Barrier Islands (χ^2_1=0.083, P >0.5) (Data from Cuvier and Little Barrier Islands were combined in this analysis because of the small

TABLE 7 – Summary of predation on adult and juvenile Saddlebacks at roosts and nests on Kapiti and Cuvier Islands. (A = adult, M = male, F = female, juv = juvenile). No predation was recorded on adult and juvenile Saddlebacks on Little Barrier Island.

Details	Age/sex	Kapiti Island		Cuvier Island
		No.	[1] No. birds yr^{-1}	No.
Preyed on by rat at nest	A/ M	1	0.14	0
	A/ F	9	1.29	0
Preyed on by rat at roost	A /M	4	0.57	0
	A/ F	3	0.43	0
	Juv	4	0.57	0
Preyed on by Morepork at nest [2]	A /F	1	0.14	0
Preyed on by Morepork at roost	A /F	1	0.14	0
Preyed on by Weka [3]	Juv	5	0.71	0
Preyed on by Harrier [4]	Juv	0	0.0	1

1. No. birds yr^{-1} = number of birds known to have been preyed on per year. Since there are seven seasons' data for Kapiti Island, this figure is given to allow direct comparison with the Cuvier and Little Barrier Island populations which were studied for one season only.
2. Although Moreporks occur on all three islands, they are rare on Cuvier Island.
3. Wekas only occur on Kapiti Island.
4. Harriers occur on all three islands.

TABLE 8 – Summary of other losses of Saddlebacks on Kapiti, Cuvier and Little Barrier Islands.

Details	Age/sex	Kapiti I		Cuvier I	Little Barrier I
		No.	[1] No. birds yr^{-1}		
Died on nest	A /F	0	0.0	1	0
Starved to death	Juv	0	0.0	7	0
Deformed (Collected)	Juv	0	0.0	1	0
Unknown losses	A /M	29	4.14	0	1
	A /F	25	3.57	0	1
	Juv	82	11.71	2	2

1. No. birds yr^{-1} = Number of birds known to have been preyed on per year. Since there are seven seasons' data for Kapiti, this figure is given to allow direct comparison with the Cuvier and Little Barrier populations, which were studied for one season only.

sample size) (Table 6). This suggests that nests on Kapiti Island and Cuvier and Little Barrier Islands have an equal chance of being preyed on by rats.

Nests appeared to be equally susceptible to rat predation at egg and nestling stages. On Kapiti Island 11 out of 191 nests were preyed on during incubation, and 12 out of 180 nests were preyed on during the nestling phase. On Cuvier and Little Barrier Islands *R. exulans* preyed on five out of 67 nests during incubation and three out of 62 nests during the nestling period.

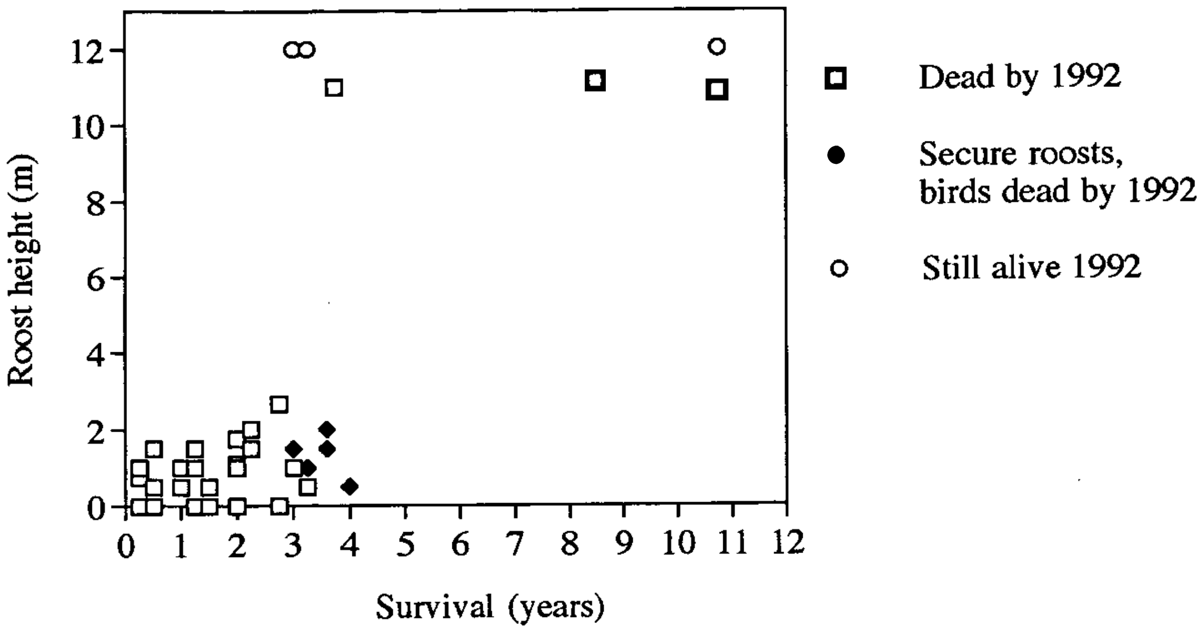

FIGURE 3 - Saddleback survival in relation to roost height on Kapiti Island (N=45).

The major inter-island difference between nest predations was that ten Saddlebacks (one male and nine females), were killed at nine of the 23 nests preyed on by rats on Kapiti Island (Table 7). By contrast no rat-killed birds were found at the eight nests preyed on by *R. exulans* on Cuvier and Little Barrier Islands. Of these two islands, the only bird found dead on a nest was on Cuvier Island, where an 11 year old female appeared to have died of natural causes (Table 8). On Kapiti Island faeces up to 15mm long, consistent with *R. norvegicus*, (Cunningham & Moors 1983), were found with the remains of two birds killed by rats at nests.

Another major difference between Kapiti Island and Cuvier and Little Barrier Islands was predation by rats on adult and juvenile Saddlebacks at roosts. On Kapiti Island, 11 birds were found killed and eaten by rats at 168 roosts which were monitored (Table 7). At 97 roosts on Cuvier and Little Barrier Islands I found no evidence that any bird was preyed on by rats. The remains of the 11 birds killed at roosts on Kapiti Island showed the characteristic untidy signs of rat predation. Seven of the dead birds were still inside the roost cavity, while the remaining four were on the ground just below their roosts. Faecal pellets measuring 14.5 and 22.9 mm in length (consistent with *R. norvegicus*), and containing some dark feather material, were found amongst the remains of one of the dead birds.

There was also a large number of losses of Saddlebacks for unknown reasons on Kapiti Island compared with Cuvier and Little Barrier Islands (Table 8). Since I monitored the outcome of 93% of nests (N=191) on Kapiti Island, I probably accounted for most of the losses of adults at nests. However, I did not find all roosts. The 168 roosts which were monitored on Kapiti Island represented only about 35% of total roosts. Thus the known losses at roosts as a result of predation by rats may be only a small proportion (about one third) of what actually occurred.

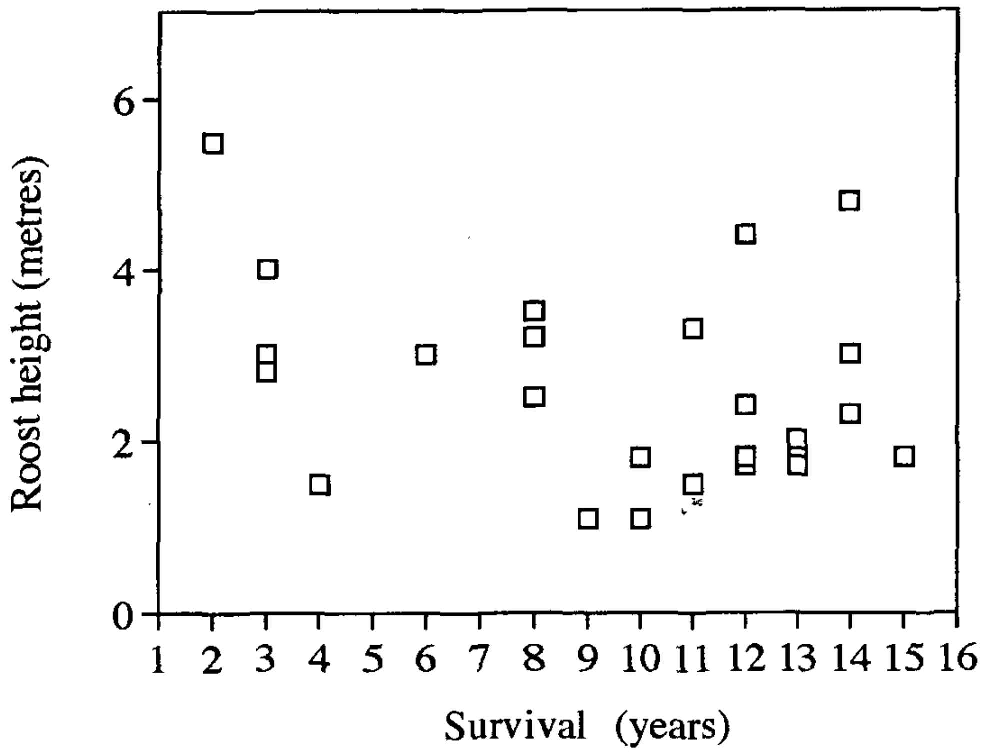

FIGURE 4 - Saddleback survival in relation to roost height on Cuvier Island (N=26).

Predators

Analyses of the heights of nests and roosts (Table 9) that were preyed on help to elucidate which rat was responsible for killing Saddlebacks on Kapiti Island, because the ground-foraging *R. norvegicus* is a less active climber than *R. exulans* (Atkinson 1978, 1985). There was no significant difference between Kapiti Island (13.6%, N=176) and Cuvier Island (7.4%, N=54) in the proportion of nests built on or within one metre of the ground (χ^2_1=1.5, P >0.1); however, significantly more nests (χ^2_1=7.9, P <0.01) were built within a metre of the ground on Little Barrier Island (45.5%, N=11) (Table 9). Despite the large proportion of nests (84.7%, N=176) on Kapiti Island sited above one metre, a disproportionate number (12 of 23 nests), was preyed on by rats on or within one metre of the ground (χ^2_1=17.51, P <0.001). By contrast, on Cuvier and Little Barrier Islands, nests on or within a metre of the ground were just as vulnerable to rats as those built above one metre (χ^2_1=0.69, P >0.25) (N=65) (Table 9). (Nest predation data from Cuvier and Little Barrier Islands were combined because of the small sample size).

Significantly more roosts on Kapiti Island (70.8%, N=168) were sited within one metre of the ground than on Cuvier Island (χ^2_1=77.04, P <0.0001, N=80), and Little Barrier Island (χ^2_1=11.95, P <0.001, N=17). This may reflect the lack of old trees and therefore tree cavities on Kapiti Island. As 70% of known roosts on Kapiti Island were sited within a metre of the ground, and 52% of the nests preyed on by rats were below one metre (Table 9), it is not surprising that all 11 birds found rat-killed at roosts on Kapiti Island were roosting on or within one metre of the ground.

TABLE 9 – Heights of Saddleback nests and roosts on Kapiti, Cuvier and Little Barrier Islands, showing heights where roost and nest predation by rats occurred. Column A shows numbers of nests/roosts at a particular height, column B shows numbers preyed on. For Kapiti Island, tabulated figures for predation at nests include cases where adults were killed by rats, and nests in which the contents only were preyed on.

Height (m)	Kapiti Island		Cuvier Island		Little Barrier Island	
	A	B	A	B	A	B
Nests						
>10	6	0	0	0	1	0
9-10	0	0	0	0	1	0
8-9	2	1	0	0	1	0
7-8	0	0	2	1	1	1
6-7	4	0	4	0	0	0
5-6	3	0	9	1	0	0
4-5	1	0	7	1	0	0
3-4	9	1	4	0	1	0
2-3	54	3	8	1	0	0
1-2	70	6	16	1	1	0
0-1	27	12	4	0	5	2
Totals	176	23	54	5	11	3
Roosts						
>10	7	0	0	0	0	0
9-10	0	0	0	0	0	0
8-9	0	0	1	0	0	0
7-8	0	0	0	0	0	0
6-7	3	0	4	0	1	0
5-6	0	0	3	0	2	0
4-5	0	0	7	0	0	0
3-4	8	0	13	0	2	0
2-3	9	0	17	0	3	0
1-2	22	0	26	0	4	0
0-1	119	11	9	0	5	0
Totals	168	11	80	0	17	0

Roosting and survival

Saddlebacks which either roosted higher than one metre, or used more secure roosts on Kapiti Island, had better survival than those which roosted below one metre, or used vulnerable sites (χ^2_1=15.16, P <0.0001, N=45). Of 13 birds which survived more than three years on Kapiti Island, only two roosted below one metre or used vulnerable roosts. In contrast, 25 of 32 birds which survived less than three years roosted below one metre, or used vulnerable roosts (Figure 3). The three birds which survived longest on Kapiti Island all had roosts above ten metres (Figure 3). Low, secure roosts were those sited below two metres under overhanging banks or bluffs, where the birds perched on roots which looped down into the gap beneath the overhangs. None of the birds found dead at roosts on Kapiti Island used this sort of roost. Instead, they perched directly on the ground, in rocky crevices, or beneath overhanging banks or in leaning hollow tree trunks. Although

I did not find any roosts on Cuvier Island below one metre, many of the long term survivors had low roosts (Figure 4), and many roosted in sites which would have been vulnerable if they were on Kapiti Island (e.g. large hollow tree trunks leaning out horizontally). All roosts on Cuvier Island would have been accessible to *R. exulans*. Two birds on Cuvier Island which roosted at 1.1 m lived for nine and ten years respectively. Long-term survival on Cuvier Island did not appear to be related to roost height as on Kapiti Island.

The poor survival of fledglings and juveniles on Kapiti Island (Table 2) may be related to their roosting behaviour. After they fledge it may take several days for young birds to find roosts. Even though adults show their young where to roost (T.G. Lovegrove unpubl.), since fledglings fly very poorly, they may be physically incapable of reaching a high or secure roost. All four dependent juveniles found killed by rats at roosts were roosting on the ground, and 81% of roosts used by fledglings and juveniles (N=105) were on or within one metre of the ground.

Morepork, Harrier and Weka predation

At least two female Saddlebacks may have been killed by Moreporks on Kapiti Island, one at a nest and one at a roost. Although I found no remains, I inferred that Moreporks were the most likely predators because they are known to carry prey away, and on subsequent days, Moreporks were seen at the places from which the two birds had just disappeared. Saddlebacks are most vulnerable to Morepork predation just before dusk when the last feeding visits are made to nests, or when they are about to roost. On Cuvier Island a Harrier preyed on a juvenile. All that remained was a pile of plucked feathers in an open place near a waterhole. I saw five fledglings being killed by Weka on Kapiti Island. The corpses were bruised as a result of being shaken, and in two the viscera were eaten. The signs differed from rat predation in that most of the flesh and muscles were still present, and the bones were not chewed. However, these bodies were recovered early, and Weka would probably have scavenged more of the remains later. Weka did not seem to be able to swallow Saddleback fledglings whole, as they do with Robin (*Petroica australis*) and Whitehead (*Mohoua albicilla*) fledglings, and mice (*Mus musculus*) (pers. obs.). Saddlebacks are most vulnerable to Weka in the first few days after fledging when they can barely fly. I found no evidence that any well-grown juvenile or adult Saddleback was preyed on by Weka on Kapiti Island.

Predator recognition

On Kapiti Island, I never saw any interactions between Saddlebacks and *R. norvegicus* by day. On Cuvier Island a female Saddleback threatened a *R. exulans* which approached her nest during the day. The bird advanced several times with lowered head and raised wings to within 20-30cm of the rat. This display was repeated until the rat had retreated several metres from the nest. During this interaction the bird did not call. Other displays, accompanied by very loud calling, were seen when Weka caught young fledglings on Kapiti Island. The parent birds fluttered on and near the ground a metre or two from the Weka, like dotterels (*Charadrius* sp.) giving distraction displays. They also shepherded surviving young higher in the branches. Whenever Saddlebacks with young saw a Weka approach, they moved quickly off the ground and usually gave loud alarm calls. Saddlebacks also clearly recognise Moreporks as potential predators, because they are often vocal participants in mixed species mobbing displays of Moreporks. If a Harrier approached Saddlebacks feeding in the canopy, they gave alarm notes, then dropped swiftly out of sight.

DISCUSSION

On Kapiti Island, where both *R. norvegicus* and *R. exulans* occur, the transferred North Island Saddlebacks had high mortality after release (Figure 1), followed by high mean annual mortality of established site-attached birds (Table 1). Despite a high breeding rate, breeding success was low, juvenile mortality was high, and too few young were recruited to compensate for high adult losses. In contrast, on Cuvier and Little Barrier Islands, where *R. exulans* is the only rat, the mortality of transferred birds was lower, there was lower mean annual mortality of established birds, survival of juveniles was higher, and sufficient young were recruited to balance adult losses (Tables 2, 3, 4 & 5 and Figure 2).

On Kapiti Island, significantly more nests placed on or within a metre of the ground were preyed on by rats. This contrasted with rat predation at nests on Cuvier and Little Barrier Islands, where high and low nests were equally vulnerable (Table 9). This difference is consistent with the known ground-foraging habits of *R. norvegicus*, and the ground and arboreal-foraging habits of *R. exulans* (Atkinson 1978, 1985).

Another factor, highly suggestive of the importance of *R. norvegicus* as predators of Saddlebacks on Kapiti Island, was the high mortality of birds using low roost sites. The birds which survived longest used either secure low roosts, or very high roosts, where they were less likely to be encountered by *R. norvegicus* (Figure 3). This contrasted with Cuvier Island where long-term survival did not appear to be related to roost height (Figure 4).

On Kapiti Island, 21 rat-killed birds were found dead at roosts and nests, and in three cases *R. norvegicus* faeces were found with the remains, directly implicating this rat species. In contrast, apart from nestlings, no rat-killed birds were found at any of the nests and roosts on Cuvier and Little Barrier Islands.

Of the 17 adult Saddlebacks found killed by rats on Kapiti Island, 12 were females (Table 7). Females were more vulnerable than males because they were at risk at both nests and roosts. The cumulative loss of breeding females from populations greatly reduces their chances of recovery. Elliott (1990), Beggs & Wilson (1991) and J. Innes (unpubl.) have respectively shown the vulnerability of mainland populations of Yellowhead (*Mohoua ochrocephala*), Kaka (*Nestor meridionalis*) and Kokako (*Callaeas cinerea*) when predation on breeding females is unsustainable.

Compared with Cuvier and Little Barrier Islands, there were more losses of Saddlebacks for unknown reasons on Kapiti Island. Many of these unknown losses were juveniles (Table 8). This study showed that 71% of all known roosts, and 81% of the roosts used by fledglings and juveniles on Kapiti Island were on or within 1m of the ground. In view of the known losses of Saddlebacks roosting on or within 1m of the ground, and the fact that I only found about a third of all roosts, many of the unknown losses on Kapiti Island could have been due to *R. norvegicus* predation at roosts that I did not find.

Further evidence for predation on Saddlebacks by *R. norvegicus* was provided indirectly between 1987 and 1991, when birds which had been conditioned to roost in safe artificial sites (roost boxes) were introduced to Kapiti Island, along with similar numbers of natural roost-using (control) birds. The roost boxes, attached between 1-2m above the ground to smooth, vertical tree trunks, provided roosts that were secure from *R. norvegicus* predation. At the end of the three-year experiment, 16 of 59 roost box-using birds and 4 of 63 natural roost-using birds were still alive. The roost box-using birds had significantly higher survival than the natural roost-using birds (χ^2_1=9.59, $P < 0.01$). The mortality rate of the adult roost box-using birds on Kapiti Island after 1987 was 0.137, compared with 0.513 for the birds using natural roosts (T.G. Lovegrove unpubl.). The mortality rate of the birds on Kapiti Island, which roosted in boxes, was nearer that of Saddlebacks on Cuvier Island (0.118, Table 2). The success of roost boxes in providing secure roosts prompts the question of how successful the Kapiti Island Saddleback translocations might have been had the forest been older, with more natural roost cavities inaccessible to *R. norvegicus*.

The work on Cuvier and Little Barrier Islands showed that *R. exulans* is an important nest predator, and during this study *R. exulans* preyed on a similar proportion of total nests as both *R. norvegicus* and *R. exulans* on Kapiti Island (Table 6). However, while damage to the contents of nests by the two rats appeared to be similar, no nesting adults were known to have been killed by *R. exulans*.

The lack of evidence of *R. exulans* predation on adult and juvenile Saddlebacks may relate to the size of the rat and its prey, (Imber 1978), or to the behaviour of *R. exulans*, which may not be as effective as other rats in attacking passerines (Atkinson 1978). This study suggests that *R. exulans* on Cuvier Island (mean weight 92g, S.D.= 28.4, range 20-138, N=213), rarely take healthy or active birds of Saddleback size (mean weight 73 g, S.D.=7.5, range 59-94, N=215), but smaller or helpless prey (e.g. nestlings up to 60g) may be vulnerable. Elsewhere, *R. exulans* have been known in exceptional circumstances to prey on nesting albatrosses (Kepler 1967), and Imber (1978) and Brooke (1995) have shown that *R. exulans* may prey on petrel chicks which exceed their weight. *R. exulans* may be able to kill petrel chicks because they are unable to flee or defend themselves, or because parents which could defend them are absent. Similar factors may apply, especially if the parent has been flushed at night, for Saddleback nestlings in a cavity which they are not old enough to escape.

The only predators of adult and juvenile Saddlebacks on islands with *R. exulans* were other birds (Harrier and Morepork). Along with Weka and New Zealand Falcon (*Falco novaeseelandiae*), these are likely to have been the most important Saddleback predators in pre-human New Zealand. Other now-extinct carnivorous and omnivorous birds (Holdaway 1989, Atkinson & Millener 1991) may have also preyed on adults, juveniles and the contents of nests. Saddlebacks clearly recognise avian predators, and respond to Moreporks, Harriers and Weka. The observation of a Saddleback on Cuvier Island apparently defending its nest against *R.*

exulans suggests that even such naive endemic species may learn to respond to introduced predators.

Because it readily uses ground cavities for roosting if tree holes are lacking, the Saddleback is especially vulnerable to ground predators. Roosts may be used for several months or even years, and excreta and moulted feathers at roosts may attract mammals hunting by scent. Secluded ground roost cavities probably provided adequate protection from indigenous avian predators such as Weka which hunt by sight, but they offered little protection against the suite of carnivorous mammals introduced after 1770. This is consistent with studies elsewhere, which show that cavity-using behaviour gives some protection from avian predators, but may be ineffective against predatory mammals (Alerstam & Hogstedt 1981, Elliott 1990). Because Saddlebacks use cavities for both nesting and roosting, they are doubly vulnerable to mammalian predators. Moreover Saddlebacks also spend much time at roosts. During winter on Kapiti Island, they roost as early as 15:30 and do not emerge until 08:00 the following day (T.G. Lovegrove unpubl.). The Stitchbird (*Notiomystis cincta*) also nests and roosts in cavities (Castro *et al.* 1994), and thus it is possibly no coincidence that both species were among the first extinctions on the mainland when the predatory mammals brought by Europeans reached New Zealand.

Some birds that are now rare or extinct may have coexisted with *R. exulans*, *R. norvegicus* and feral cats, all of which were present on the mainland by 1800 (King 1984, 1990). Atkinson (1973) has suggested that predation by *R. rattus* was an important factor in the declines of Stitchbird, Bellbird (*Anthornis melanura*), Robin, Piopio (*Turnagra capensis*) and Saddleback in the North Island after 1860. It was a reasonable assumption that Saddlebacks would survive when they were reintroduced to Kapiti Island in 1981. This island is a biological relic of the 1770-1860 period, in that it lacks *R. rattus,* feral cats and mustelids, and so has fewer predators than pre-1860 mainland New Zealand. However, this study has shown that *R. norvegicus,* possibly in concert with *R. exulans*, can extirpate Saddlebacks from islands. Since feral cats are also known predators, causing the extinction of Saddlebacks on Little Barrier and Cuvier Islands (Turbott 1947, Merton 1970), how then did they survive so long on the mainland after 1770?

The answer may lie in the behaviour and longevity of Saddlebacks. On Kapiti Island, a small proportion of the population roosted and sometimes nested high, and these birds escaped predation. If their offspring had similar habits, and the imprinting of young on roost and nest sites indicates this is possible (T.G. Lovegrove unpubl.), some could have persisted until the 1860s. Rather than coexisting with *R. exulans, R. norvegicus* and feral cats, Saddleback numbers were probably declining gradually after 1770. Data from translocations to Kapiti Island show that Saddlebacks may persist for some time with these predators. Nine birds were released in 1925, when feral cats were still present, and some survived and bred until 1931 (Wilkinson & Wilkinson 1952). Between 1981 and 1983, 244 birds were released. Three from these releases were still alive in 1990. It is perhaps not surprising that there would have been mainland survivors in the 1860s, if the data from Kapiti Island are extrapolated to a mainland population which may have numbered millions (Smith 1889, O'Callaghan 1980).

The results of this study suggest that given enough time, *R. exulans* and *R. norvegicus* alone could have eventually eliminated Saddlebacks from the mainland, while feral cats and the later-arriving *R. rattus* and mustelids preying on the tree-roosting and nesting survivors, merely hastened an inevitable decline. *R. norvegicus* may have also been important in the declines of other vulnerable ground and cavity-nesting species, which were already rare or local by the 1860s e.g. Shore Plover (*Thinornis novaeseelandiae*) (Oliver 1955), Laughing Owl (*Sceloglaux albifacies*) (Williams & Harrison 1972), Kakapo (*Strigops habroptilus*), Bush Wren (*Xenicus longipes*), and Huia (*Heteralocha acutirostris*) (Oliver 1955).

The presence of *R. norvegicus* means there is only very limited scope for further transfers of threatened species to Kapiti Island. Further releases of other endangered animals and the recovery of the small surviving Saddleback population will depend on removal of *R. exulans* and *R. norvegicus*. Plans are now afoot to eradicate all rats from Kapiti Island (R. Empson pers. comm.). In view of recent successes in rodent eradication on other islands (Towns *et al.* 1990, Taylor & Thomas 1993) this should be achievable with present techniques.

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