

Variation in reproduction and  
condition of northern tuatara  
(*Sphenodon punctatus punctatus*)  
in the presence and absence of kiore

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# Variation in reproduction and condition of northern tuatara (*Sphenodon punctatus punctatus*) in the presence and absence of kiore

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## ABSTRACT

Aspects of reproduction and condition in northern tuatara (*Sphenodon punctatus punctatus*) were examined in the presence and absence of an introduced rat, the kiore (*Rattus exulans*), between 1996 and 1998. Female tuatara from five northern islands showed significant differences in gravidity rate, clutch size and body size. However, none of the variation in egg production was associated with the presence of rats. Gravidity rate was negatively correlated with latitude, and clutch size varied directly with female body size. Body size may be associated with island size and/or tuatara density. Independent of body size, northern tuatara had relatively small clutches compared with tuatara on Stephens Island.

The presence of kiore was associated with lower body condition in female tuatara. Tuatara on Lady Alice Island (kiore-removed) tended to be greater in mass for their snout-vent length (SVL) relative to other island categories, which may be the result of a temporary surge in food availability following eradication of kiore. Field metabolic rate of non-gravid females was higher on Lady Alice (3 years after kiore removal) than on Coppermine Island (3 months after kiore removal). The hormonal response to short-term stress in male and female tuatara on Coppermine (kiore-inhabited at the time) was higher than on Green Island (kiore-free). These associations need further investigation to determine whether presence of kiore is the causal factor.

Size-class distributions were consistent with previous surveys indicating an under-representation of juvenile and subadult tuatara on kiore-inhabited islands. A density estimate for Coppermine (12–26 tuatara/ha) was very similar to another rodent-inhabited island and an order of magnitude lower than density estimates for rat-free islands, indirectly supporting an effect of kiore on recruitment.

Keywords: tuatara, *Sphenodon*, kiore, *Rattus exulans*, gravidity rate, clutch size, field metabolic rate, stress response, juvenile recruitment, reproduction.

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# 1. Introduction

Tuatara are sphenodontian reptiles of Gondwanan origin confined to New Zealand's offshore islands. Subfossil remains and historic records indicate that tuatara became extinct on the mainland (North and South Islands) by about the time of European arrival c. 200 years ago. Additionally, some populations on offshore islands have become extinct within the last 150 years (Cree & Butler 1993).

The influence of the Pacific or Polynesian rat (*Rattus exulans*) on surviving island populations of northern tuatara (*Sphenodon punctatus punctatus*) has long been of interest to New Zealand herpetologists and conservation managers. Pacific rats, known locally as kiore, were brought to New Zealand in early Polynesian times. They eventually become established on many offshore islands during pre-European or early European times (Brook 1999; Holdaway 1999).

Crook (1973) was the first to suggest that kiore might be harmful to tuatara. In a survey of 23 islands with tuatara present (six of these with kiore) he noted that encounter rates (the frequencies with which tuatara were sighted) were lower on the six islands where tuatara co-existed with kiore than on 16 out of 17 islands without kiore. He also presented evidence suggesting that population size-class distributions for tuatara differed between islands with and without kiore. Tuatara populations on islands with kiore had a greater proportion of large animals than on kiore-free islands. On the kiore-inhabited islands, no tuatara were less than 180 mm snout-vent length (SVL) (i.e. all were approximately adult-sized). These observations suggested that kiore impaired the recruitment of juvenile tuatara. Tuatara were also absent from seven kiore-inhabited islands where one would otherwise expect them to be present (relictual populations of tuatara have since been found on two of these, Mauitaha and Stanley). Crook (1973) concluded that the failure to find a single kiore-inhabited island which also supported a clearly self-maintaining population of tuatara strongly suggested that the presence of kiore could cause the extinction of tuatara.

These observations and interpretations have been supported by several subsequent studies (for review, see Cree & Butler 1993). By the early-mid 1990s, the simultaneous co-existence of kiore and northern tuatara had been confirmed on nine offshore islands. Recruitment failure (total absence of juvenile tuatara) was evident on six of these kiore-inhabited islands during a survey in 1989 (Cree et al. 1995), although separate surveys have caught a few subadult-sized tuatara over the past twenty years Newman 1980; Cree & Butler 1993). Tuatara were judged to be on the verge of extinction on four of these islands (Whitaker 1978, 1993; Whitaker & Daugherty 1991; Cree et al. 1995; R. Pierce, pers. comm.). In addition, it has been suggested that populations of tuatara that co-exist with kiore may have significantly lower clutch sizes (number of shelled eggs per gravid female; Newman et al. 1994) and low levels of reproductive activity (Cree et al. 1995) compared with populations on islands that lack kiore. Recent palaeoecological studies have also implicated

kiore in the pre-European extinction of tuatara on the North and South Islands (Worthy & Holdaway 1995; Worthy 1997).

Despite wide acceptance that kiore have detrimental effects on tuatara (e.g. Atkinson & Moller 1990, but see also Craig 1986), evidence for these negative impacts is entirely circumstantial, and the mechanism by which kiore may inhibit or prevent recruitment in tuatara is unknown. There are two ways that the hypothesis of detrimental interaction can be tested. Ideally, interactions between kiore and tuatara would be tested on islands sufficient in number to provide adequate replication for statistical purposes. These islands would be randomly allocated to two treatments, “kiore present” and “kiore not present”, and would need to be identical in all factors thought to be potentially relevant to tuatara, including latitude (climatic effects), size, biotic composition, and history of modification. The status of the tuatara populations would then be followed over a biologically relevant time-frame (tuatara live at least 60–70 years, Dawbin 1982). Such an experiment is not possible, because of wide geographic spread of the islands occupied by tuatara, diverse histories of modifications, variation in island size, differences in biotic composition, differences in the range of habitats present, concern for other island species, and cost.

A second approach is to manipulate kiore populations such that the extent and effects of their interactions with tuatara can be measured at a single location in the form of a large-scale experiment (Raffaelli & Moller 2000). This second approach was used in recent studies of lizard populations on offshore islands. As with tuatara, there was circumstantial evidence suggesting that some endemic lizards are harmed by the presence of kiore (Whitaker 1973; McCallum 1986). The development of techniques to eradicate rats from offshore islands has allowed tests of the response of resident and translocated lizards to rat eradication (Townes 1994, 1996). The sequential eradication of kiore from several northern islands likewise provided an opportunity to compare tuatara reproduction and population parameters among islands which were still inhabited by kiore, had recently been inhabited by kiore and were naturally free of kiore (and all other introduced rodents).

In this study, we explore a variety of different parameters of reproductive output and other potential indicators of individual and population ‘health’ of tuatara among islands of differing kiore status. This enables us to examine possible mechanisms for variations in reproductive output, to assess whether the relationship between kiore and tuatara is detrimental, and to make management recommendations to improve the survival prospects of tuatara.

## 2. Aims

We had three aims (Figure 1). The first was to test the hypothesis that kiore have negative effects on the reproductive output of female tuatara. The second was to test the hypotheses that aspects of physical and physiological condition of male and female tuatara were altered in the presence of kiore. The third was

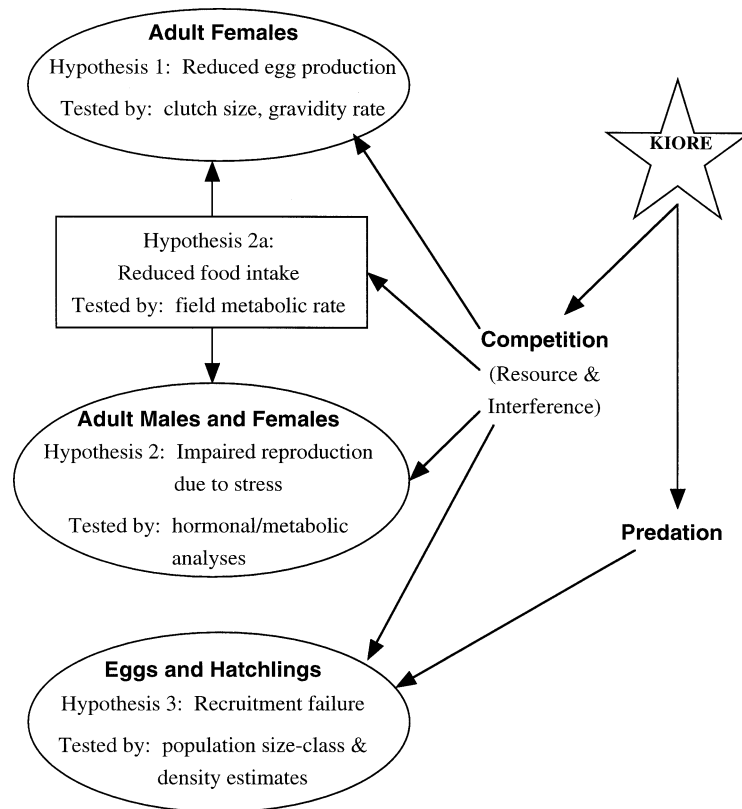


Figure 1. A summary of hypotheses examined in the present study.

to test the hypothesis that there is reduced recruitment of tuatara in the presence of kiore.

The first hypothesis was proposed by Newman et al. (1994), who observed that female tuatara on Lady Alice Island (inhabited by kiore at the time) had a lower mean clutch size than females on rat-free Stephens Island, despite having a larger mean body size. Generally in reptiles, clutch size is positively correlated with female body size (Dunham et al. 1988). Although females of some species may increase their gravidity rate (percentages of adult females carrying shelled eggs) to compensate for producing smaller clutches, i.e. they produce fewer eggs more often, no significant difference was observed in mean gravidity rates between Lady Alice and Stephens females (Newman et al. 1994). Newman et al. (1994) therefore proposed the following hypothesis to account for the clutch size anomaly on Lady Alice: clutch size was being limited by reduced food resources due to competition with kiore. Subsequently, kiore have been demonstrated to compete with tuatara for food resources (Ussher 1999), but there have been no studies on whether or how this may affect reproduction of female tuatara. An alternative hypothesis is that any variation in clutch size of tuatara is independent of kiore and is, instead, either genetically fixed or influenced by ambient effects such as local climate.

To test the hypothesis that kiore influence clutch size, we compared variation in aspects of egg production (clutch size and gravidity rate) among female tuatara from several northern islands, including islands influenced by the current or past presence of kiore. Thus, we aimed to determine whether the presence of kiore was associated with reduced egg production, over and above other potential sources of variation among islands.



In addition to presence/absence of kiore, variables considered were island size, island latitude, and tuatara density. Our study included Lady Alice, the same population of tuatara sampled by Newman et al. (1994). We were thus able to compare our egg production data on Lady Alice (after eradication of kiore in 1994) with those obtained in the 1980s before kiore were eradicated (Newman et al. 1994), to assess whether there was evidence for a change in egg production on Lady Alice following the removal of kiore.

The second aim of the research programme was to examine variation in physical and physiological condition among tuatara populations. Differences in such aspects might shed light on possible mechanisms for variation in egg production among islands, if such variation was found.

First, three aspects of physical condition were examined. The first, an index of body condition (mass relative to snout-vent length), was compared for both males and females among all islands where sufficient samples were obtained. Such indices of body condition may need to reach a certain minimum level before reptiles can reproduce (Macartney & Gregory 1988), and females with higher condition may produce more/bigger offspring (Ford & Seigel 1994). Secondly, we examined the incidence of eye abnormalities. Tuatara are mainly visual hunters (Wojtusiak 1973; Meyer-Rochow 1988); any loss or impairment of vision (e.g. Castanet et al. 1988) may reduce the ability to feed, and therefore have implications for breeding behaviour and success. Finally, we examined the incidence of tail loss among tuatara populations. Tuatara, like many lizards, can regenerate their tail following loss (caudal autotomy) due to predation or injury; but this represents an energy loss that in lizards may reduce growth and breeding success (Martin & Salvador 1997; Niewiarowski et al. 1997; Wilson & Booth 1998).

We also examined two aspects of physiological 'condition'. The first involved a comparison of field metabolic rate (FMR) between two islands that differed in the time since kiore were removed. The rate at which animals are able to assimilate and metabolise energy is likely to affect rates of reproduction, and the rate of energy intake and amount of time spent foraging are in turn affected by food availability. We examined food intake indirectly by measuring FMR (Secor & Nagy 1994; Christian et al. 1996; Henen et al. 1998). This provides information on the energy expended by free-living individuals over periods of days to weeks and, in combination with data on changes in body mass over the same time, can enable estimates of food consumption to be made. The technique also provides information on water turnover.

The second aspect of physiological condition was to compare the hormonal response to capture and short-term confinement between tuatara from a kiore-free and a kiore-inhabited island. Tuatara, like other reptiles, produce and secrete increased amounts of corticosterone from the adrenal gland in response to novel or threatening situations (Tyrrell & Cree 1998). This adrenal hormone travels in the bloodstream to other parts of the body, where it contributes to the body's stress response. A short-term increase in corticosterone is presumed to be adaptive, in that it increases the concentration of glucose in the bloodstream to provide immediate energy to the brain and locomotory system, and suppresses reproductive behaviour and sex hormone levels so that energy can be channelled into strategies that enhance short-term personal survival instead (Guillette et al. 1995).

However, a prolonged increase in corticosterone (chronic stress) may have serious consequences in reptiles, including reduced growth in juveniles (Elsey et al. 1990a), reduced reproduction in adults (Elsey et al. 1990b) and reduced immunity (Aguirre et al. 1995). Recent evidence for reptiles and birds indicates that the elevation in plasma corticosterone in response to capture may be greater or more prolonged in animals that are in poorer condition, e.g. diseased (Aguirre et al. 1995), parasitised (Dunlap & Schall 1995) or food-restricted (Heath & Dufty 1998; Kitaysky et al. 1999). We hypothesised that tuatara on the kiore-inhabited island would have a higher and/or more sustained elevation in plasma corticosterone concentrations in response to capture than tuatara on a rat-free island.

The final hypothesis (reduced recruitment in the presence of kiore; Crook 1973; Whitaker 1978; Cree et al 1995) was tested by comparing population size-class structure among all islands. In addition, an estimate of density was obtained for one kiore-inhabited island where low numbers, identifiable individuals and a high rate of recapture allowed a mark-recapture model to be used (Coppermine). This was compared with published data for density on several other islands, kiore-removed and kiore-free.

## 3. Methods

### 3.1 STUDY SITES

Searches for northern tuatara were made on six uninhabited island reserves along the north-east coast of the North Island of New Zealand (Figure 2). Only two islands with kiore and tuatara (Coppermine & Hen) could be sampled, as at the start of this study (1996), the only other tuatara-kiore islands (Little Barrier and Mauitaha) had insufficient tuatara to sample (Whitaker 1993; R. Pierce, pers. comm.). The six islands visited were Aorangi (Poor Knights Group), Lady Alice, Coppermine and Hen (Hen and Chickens Group), Green (Mercury Group) and Ruamahua-iti (Aldermen Group). The islands varied in size, in latitude and in history of introduced mammals (Table 1). Data collection varied among islands (Table 2), as cost and time limitations prevented all islands being visited in all years for all studies.

### 3.2 CAPTURE METHODS

All tuatara were caught by hand, with most animals caught at night during a period from 30 minutes to 3.5 hours after dusk. All animals were weighed to the nearest 5 g with a Pesola® spring balance, and snout-vent length (SVL) was measured. Female tuatara  $\geq 170$  mm SVL and males  $\geq 180$  mm SVL were classified as adults, based upon previous data from Stephens (Cree et al. 1992; Newman et al. 1994). Hormonal measurements support these estimates for size at maturity for some of the populations of northern tuatara sampled here

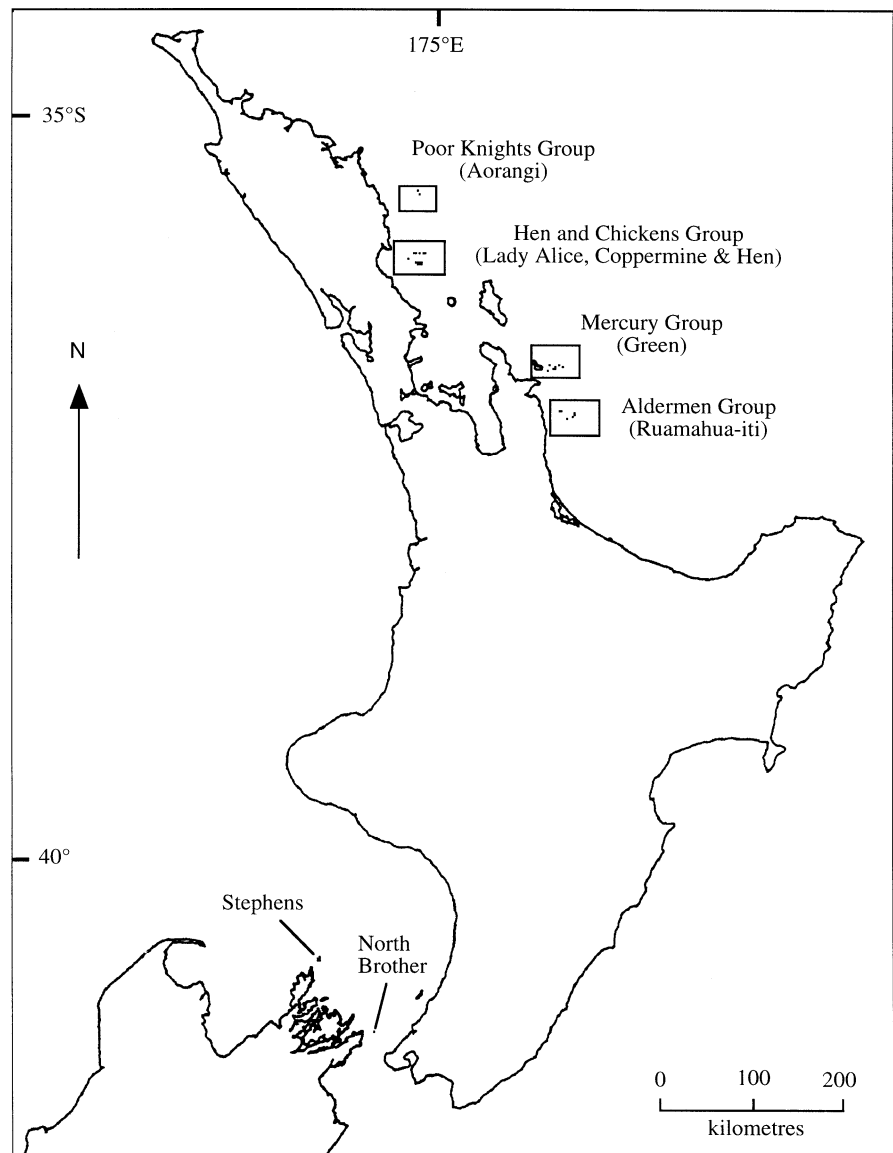


Figure 2. Map of the North Island and upper South Island of New Zealand, showing all of the northern islands sampled, plus Stephens and North Brother Islands.

(Cree et al. 1995). However, the likelihood that there was variation in size at maturity among islands is addressed further below (see Discussion).

All tuatara were examined for evidence of previous capture. Some recaptures could be identified with certainty because the animals had already been toe-clipped by previous workers (Whitaker, Newman, Cree, Daugherty). Other recaptures were inferred from body dimensions (SVL, vent-tail length, tail regeneration length), scars or other distinguishing marks, and location; adult tuatara are highly sedentary (Newman 1987). All data for identifiable tuatara were entered into a computer database (records not presented in this report, but available from the senior author).

No tuatara was toe-clipped or otherwise permanently marked during this study, because of objection by local iwi. All tuatara were released, without apparent harm, at their point of capture. Each animal was individually marked on the flank using a non-toxic pen to prevent recapture during the same field trip. In a few cases, this temporary marking stayed on between field trips, but it was eventually lost during moulting.

TABLE 1. ISLANDS SAMPLED DURING THIS STUDY.

ISLAND	LATITUDE	AREA (ha)	COMMENTS
Aorangi	35° 28' S	110	Occupied by Maori prior to 1823, perhaps for many generations. <sup>1</sup> Introduced pigs became feral, eradicated in 1936. <sup>2</sup> Forest regeneration has since occurred. Kiore-free.
Lady Alice (Motumuka or Mauimua)	35° 54' S	155	Lady Alice and others in this group (Coppermine & Hen) occupied by Maori in pre-European times, <sup>3</sup> now clad in regenerating forest. <sup>4</sup> Cattle present between 1890 and 1924. <sup>5</sup> Kiore established perhaps as recently as early 1800s, <sup>6</sup> but were eradicated by aerially spread poison bait in 1994.
Coppermine (Huarewa or Maupae)	35° 54' S	79.5	No history of European mammals. Arrival of kiore unknown, but date presumably similar to Lady Alice. Attempt to eradicate kiore in 1992 using ground-spread bait was unsuccessful, kiore numbers quickly recovered. <sup>7</sup> Kiore successfully eradicated by aerially spread poison bait in 1997.
Hen (Taranga)	35° 57' S	500	No introduced European mammals. Kiore are present.
Green	36° 39' S	2.3	Little evidence of human modification. No history of introduced mammals
Ruamahua-iti	36° 58' S	25	Islands in this group once intermittently occupied by Maori. <sup>8</sup> Forest regeneration evident. <sup>9</sup> No history of introduced mammals.

Note: Island areas are from Taylor (1989).

References: <sup>1</sup> Fraser (1925); <sup>2</sup> Veitch & Bell (1990); <sup>3</sup> Prickett (1984); <sup>4</sup> Cameron (1984); <sup>5</sup> McCallum et al. (1984); <sup>6</sup> Brook (1999); <sup>7</sup> R. Pierce, pers. comm.; <sup>8</sup> Moore (1973); <sup>9</sup> Court et al. (1973).

TABLE 2. YEARS<sup>1</sup> AND RESEARCH TOPICS FOR WHICH TUATARA ON NORTHERN ISLANDS WERE SAMPLED IN THE PRESENT STUDY.

RESEARCH TOPIC	ISLAND					
	Aorangi	Lady Alice	Coppermine	Hen <sup>2</sup>	Green	Ruamahua-iti
Aspects of egg production			1996		1996	
		1997	1997		1997	1997
	1998	1998	1998		1998	
Physical indices of condition			1996		1996	
		1997	1997	1997	1997	1997
	1998	1998	1998		1998	
Physiological indices of condition						
		1997	1997			
Field metabolic rate						
Hormonal stress response					1997	
Population size-class structure		1997	1997	1997	1997	1997
	1998					
Population density			1996			
			1997			
			1998			

<sup>1</sup> All sampling in spring (September-December) except for hormonal stress response (February-March).

<sup>2</sup> Insufficient samples (n = 2 males and 1 female) were obtained on Hen Island to include in most studies.

### 3.3 ASPECTS OF EGG PRODUCTION

Data on aspects of egg production were determined for female tuatara caught in spring (September–November, 1996–98), when shelled eggs are present in the oviducts (Newman et al. 1994). Clutch size and gravidity rate were determined for females that could confidently be assessed as adult ( $\geq 170$  mm SVL), using a radiographic technique similar to that used previously for tuatara (Newman & Watson 1985; Cree et al. 1991a; Newman et al. 1994). We tested and rejected ultrasonography as an alternative method to detect and count eggs in female tuatara. Radiography is widely used in egg-laying reptiles for veterinary and research purposes (e.g. Frye 1981) and is performed when the embryo is minute, well in advance of organ differentiation. No harmful effects have been reported from widespread use in female turtles (Gibbons & Greene 1979) or tuatara (Thompson et al. 1998).

Gravidity rates were calculated for each island in each study year (Table 2). Data for two islands (Lady Alice and Green), the only islands on which enough different females were captured in different years, revealed no year-to-year variation in independent estimates of gravidity rate ( $P > 0.05$ ). Therefore, data (excluding recaptures) were pooled across years to obtain an overall estimate for each island, based on the largest possible sample size. Gravidity rates were compared among islands using a G-test, and examined for rank correlation with other variables (island size, presence/absence of kiore, and density) using Spearman's rank correlation test, and with latitude using regression analysis.

Density was ranked using the rough estimates in the Tuatara Recovery Plan (Cree & Butler 1993) as well as encounter rates on our field trips, in the following ascending order: Coppermine, Aorangi, Lady Alice, Ruamahua-iti, Green. Coppermine had rats removed in July 1997, but was classed as a kiore-inhabited island for all years (1996–98), as we assumed that gravidity and clutch size in spring of 1997 and 1998 had been determined prior to the time of rat removal. On Stephens, vitellogenesis (accumulation of egg yolk) begins nearly two years or more in advance of nesting (Cree et al. 1992), ovulation is between March and April (6–7 months before nesting), and egg shells are radio-opaque by July (Cree et al. 1991a). Females that were known or inferred to have been recaptured across years provided information on the frequency of egg production on some islands. Some females were X-rayed twice on Lady Alice during late spring 1997 (November–December), to obtain information on the time of nesting. Evidence of nesting activity was also searched for. Searches were made during the day for potential nesting areas and signs of digging, and at night for females digging or nest-guarding.

Mean clutch size was calculated for each year for each island. Islands on which sufficient independent samples were obtained across years, at similar mean body sizes, revealed no evidence of variation in mean clutch size across years ( $P > 0.05$ ). Therefore, data were pooled across years to obtain a mean estimate for each island, based on the largest possible sample size. Mean clutch sizes and mean body sizes (SVL) were compared among islands using one-way analysis of variance (ANOVA) where variances were homogeneous, and Kruskal-Wallis tests when variances were heterogeneous. As clutch size varies significantly with body size in tuatara (Newman et al. 1994), and significant variation in body

size among islands was observed, clutch sizes were compared among islands using analysis of covariance (ANCOVA). Body size (snout-vent length, SVL) was used as the covariate, and islands were grouped according to rat status.

### 3.4 PHYSICAL AND PHYSIOLOGICAL CONDITION

#### 3.4.1 Physical condition

The relationship between ln body mass (corrected for tail loss; Newman et al. 1994) to body length (SVL) was used as an index of body condition and compared between islands (grouped according to rat status) separately for males and non-gravid females in spring using ANCOVA. Gravid females were excluded because egg mass would alter the relationship between body mass and SVL. The incidences of eye abnormalities (including cataracts, eyeballs missing or sunken with eyelids shut) and tail loss were compared among islands for each sex of adult tuatara using G-tests. All data were pooled across years and excluded definite and probable recaptures.

#### 3.4.2 Field metabolic rate (FMR)

We compared FMRs of non-gravid female tuatara on two islands, Coppermine (3–5 months after kiore removal) and Lady Alice (4 years after kiore removal). The study was limited to these samples by the effort required for capture and recapture, and by the cost of the analyses. In view of the increase in large invertebrates such as weta (which figure highly in tuatara diet; Ussher 1999) observed on nearby Whatupuke Island following rat removal in 1993 (Ussher 1995), we hypothesised that FMR of tuatara would be higher on Lady Alice than on Coppermine.

Female tuatara were caught by hand during spring 1997 (Coppermine: 22–31 October; Lady Alice: 4–12 November) and body temperatures were recorded at capture. The females were marked using non-toxic ink on the flank, X-rayed, and non-gravid females were selected for study ( $n = 15$  on Coppermine;  $n = 11$  on Lady Alice). An initial blood sample (0.7 mL) was taken from the caudal vein to determine background isotope levels. Where possible, a urine sample was also collected for comparison with blood. Doubly labelled water (0.2 mL) was then injected intraperitoneally. The water contained a 2:1 mixture of >95 atom %  $^{18}\text{O}$  and >99 atom %  $^2\text{H}$ . The stable isotope deuterium was used as the hydrogen isotope in this study (e.g. van Marken Lichtenbelt et al. 1993; rather than tritium,  $^3\text{H}$ ) to avoid local concerns relating to radioactivity. The animals were held in cloth bags for 24 hours to allow for isotope equilibration. A second blood sample (0.7 mL) was then taken and the animals were weighed before being released at their home burrow or capture site. Air temperatures during the initial field trip to each island, and during the final trip to recapture the animals (see below), were recorded at a tuatara burrow. One temperature probe was placed in shade at the burrow entrance (5 cm above the ground) and one was placed 20 cm inside the burrow. Temperatures were recorded hourly using dataloggers (Stowaway@XTI, Onset, Pocasset, Massachusetts).

Approximately 4–7 weeks after the initial field trip, attempts were made to recapture the study animals. Ten were recaptured on Coppermine during 15–18

December (47.8–51.1 d after injection of isotope) and eight on Lady Alice during 5–14 December (27.8–32.6 d after injection of isotope). The recaptured animals were reweighed, blood-sampled (0.7 mL), and released at their capture sites. The blood and urine samples were flame-sealed in heparinised capillary tubes (75 µL) and initially kept cool, then refrigerated. Later the blood samples were distilled (Wood et al. 1975), and the resulting water was analysed for  $^2\text{H}$  and  $^{18}\text{O}$  by isotope ratio mass spectrometry in the laboratory of Keith Newgrain, CSIRO Wildlife and Ecology, Australia. Rates of  $\text{CO}_2$  production and water loss were calculated from changes in isotope concentrations in body water over the release period (Lifson & McClintock 1966; Nagy 1980; Nagy & Costa 1980) and FMRs were calculated (Nagy 1980; equation [2]). Statistical comparisons of means were made using Student's *t* tests.

### 3.4.3 Hormonal stress response

Comparison was restricted to one kiore-inhabited island (Coppermine) and one kiore-free island (Green) because of the intensity of effort and the cost of the sampling involved, but both sexes were sampled. The study was carried out during late summer 1997 (Coppermine: 11–19 February; Green: 25 February–2 March). Free-roaming adults were captured by hand during the period from 30 minutes to 3.5 hours after dusk (1900–2230 hours NZST). Sample sizes were 17–20 individuals for each sex. Blood samples (1 mL) were taken from the base of the tail using a sterile needle and syringe within the first 10 minutes after capture (usually <5 min). Half of the blood went into heparinised vials for this study, and half into EDTA vials for a separate study of plasma lipids (Blair 2000). The animals were then placed in cloth bags and transported to the field camp. In most cases, additional blood samples (0.5 mL) were collected at 3 and 18 hours post-capture. Animals were released, without observed harm, at their capture site within 24 hours after capture.

Blood samples were briefly held on ice, then centrifuged. The plasma was stored in liquid nitrogen and later analysed using extraction and tritiated radioimmunoassay techniques for corticosterone (Tyrrell & Cree 1998). Samples were also analysed for testosterone and progesterone (Coddington & Cree 1995), and glucose (Sigma Diagnostics [Trinder] kit, Procedure No. 315); these data are to be presented elsewhere.

Differences in plasma concentrations of corticosterone over time (0, 3, and 18 h) were analysed using a two-way repeat-measures ANOVA (island and sex as fixed factors, and time as the repeated measure). Hormone data were log-transformed to obtain homogeneity of variance.

## 3.5 POPULATION SIZE-CLASS STRUCTURE

It was not possible on Green and Lady Alice to positively identify all tuatara in order to exclude recaptures from analyses. Population size-class structures were therefore compared between islands sampled in October–December in a single year (1997 for Lady Alice, Coppermine, Green and Ruamahua-iti, and 1998 for Aorangi). Data were divided into size classes, 50–99 mm SVL, 100–149 mm SVL and every 10 mm SVL thereafter. As the sample sizes are low when subdivided in this way, only a qualitative analysis was made.

### 3.6 DENSITY ESTIMATE ON COPPERMINE ISLAND

By combining our data for Coppermine during 1996–98 with a previous survey in 1989 (Cree et al. 1995, and unpubl. data), it was possible to use mark-recapture modelling to estimate the population size at the eastern end of the island (Figure 3). It was not possible to do this for the western end, as the number of visits to this end of the island was limited by unsuitable weather for crossing the steep gut that divides the island. Tuatara are unlikely to pass this gut. The total area of the eastern end (23.2 ha) was estimated from a map of the island using a digital scanner (SigmaScan, Jandel Scientific). The area providing suitable habitat for tuatara was estimated as 7.4 ha. The actual search area (2 ha) was estimated by multiplying the track length (Figure 3) by a 20 m swath.

Capture history data for the search area at the eastern end were analyzed with assistance from Dr R. Barker (Department of Mathematics and Statistics, University of Otago) using a Cormack-Jolly-Seber model (Lebreton et al. 1992) incorporating sex-effects using program MARK (White & Burnham 1999). Model selection was carried out using Akaike's Information Criterion (Burnham & Anderson 1998). The best-fitting model had inter-trip survival probabilities constant through time with no difference between male and female tuatara, but time-specific capture probabilities that varied in parallel for the two sexes. In the 18/5/96 sample, not all of the search area was sampled and tuatara subsequently found in the area excluded in this sample were given a capture probability of 0 for the 18/5/96 sample.

Abundances for the search area were estimated separately for males and females using the Jolly-Seber model and the overall estimate for each period was obtained by summing the male and female estimates. Trend estimates were obtained using the model of Pradel 1996 in program MARK (White & Burnham 1999), with survival and capture probabilities modelled using the best fitting model from the above analysis. Overall abundance on the eastern end of the island was extrapolated from the search area to the area of suitable habitat. Density was also estimated on this basis.

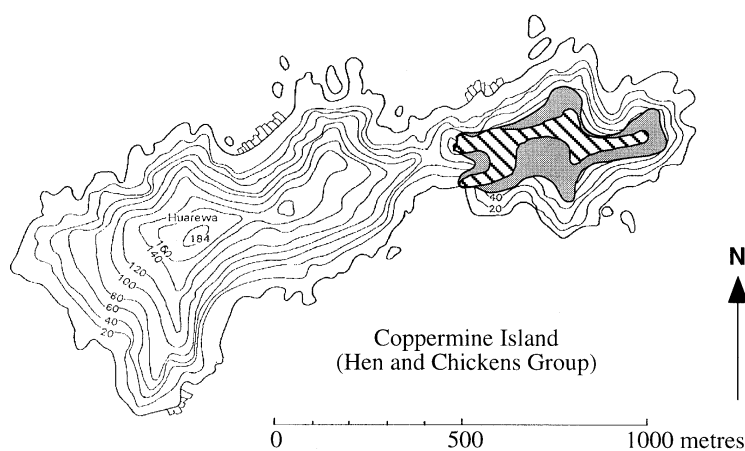


Figure 3. Map of Coppermine Island showing search area used for calculating tuatara abundance at eastern end of island (search area - diagonal shading; area of potential tuatara habitat - shaded grey).



### 3.7 STATISTICAL ANALYSIS

Unless otherwise stated, results are presented as mean  $\pm$  SE. Probability values of  $<0.05$  were accepted as indicating statistical significance. Statistical tests were performed using Datadesk (Macintosh version, Odesta Corporation, Illinois) and Minitab (Macintosh version, State College, Pennsylvania).

## 4. Results

### 4.1 ASPECTS OF EGG PRODUCTION

#### 4.1.1 **Gravidity rate**

G-tests were performed on clutch frequency data from all females X-rayed on five islands, and pooled across years after removing all recaptured females. It was not possible to include Hen in any of the egg production analyses, as only one female was caught over an 11-day field trip in spring 1997, and equipment damage prevented it from being X-rayed.

A significant difference in gravidity rate was observed among the remaining five islands ( $\chi^2 = 9.5$ ,  $df = 4$ ,  $P < 0.05$ ; Figure 4a). Gravidity rate was negatively correlated with latitude ( $\chi^2 = 0.809$ ,  $df = 4$ ,  $P = 0.024$ ), but was not rank correlated with island size, kiore status (rat-free, rat-removed and rat-inhabited) or density estimate. Gravidity information for 14 recaptured females (nine on Coppermine and five on Lady Alice) that were gravid in one year showed that none were gravid the next. However, two on Coppermine were gravid in the third year.

#### 4.1.2 **Clutch size and body size**

Clutch sizes in individual tuatara ranged from 4 to 13 eggs. Mean clutch sizes varied significantly among islands ( $H = 10.44$ ,  $df = 4$ ,  $P = 0.034$ ), ranging from  $8.15 \pm 0.68$  eggs on Aorangi to  $5.89 \pm 0.20$  eggs on Ruamahua-iti (Figure 4b). There was also a significant difference in mean body size of gravid females among islands ( $F_{[4,65]} = 27.18$ ,  $P < 0.001$ , Figure 4c), with females on Aorangi being the largest ( $222 \pm 4$  mm SVL) and Ruamahua-iti the smallest ( $179 \pm 3$  mm SVL). When all islands were grouped, clutch size showed a positive, significant correlation with female SVL ( $P < 0.05$ ). However, when the effect of variation in female SVL was taken into account as a covariate, there was no significant difference in clutch sizes between islands of differing rat status ( $F_{[2,68]} = 0.15$ ,  $P = 0.858$ , Figure 5). In other words, the difference in clutch size among islands (Figure 4b) is explained by the difference in body size (Figure 4c).

#### 4.1.3 **Time of nesting**

X-rays taken during a field trip to Lady Alice in early December 1997 showed that four previously gravid tuatara (X-rayed during 4-8 November, 1997) had laid their eggs in the interim. Another previously gravid female (X-rayed with

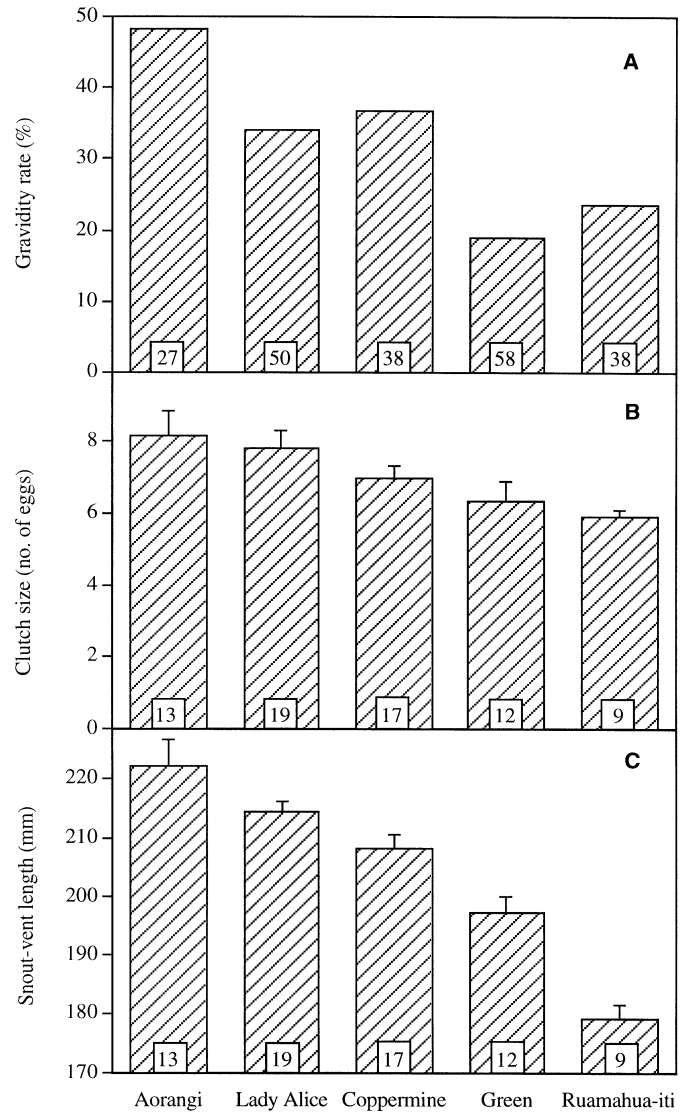


Figure 4. Comparison of gravidity rate (top), clutch size (middle, mean  $\pm$  SE) and body size (bottom, mean SVL  $\pm$  SE) of gravid female tuatara among five islands. Data pooled among years for each island (excludes recaptures). Sample sizes are given at the base of each bar.

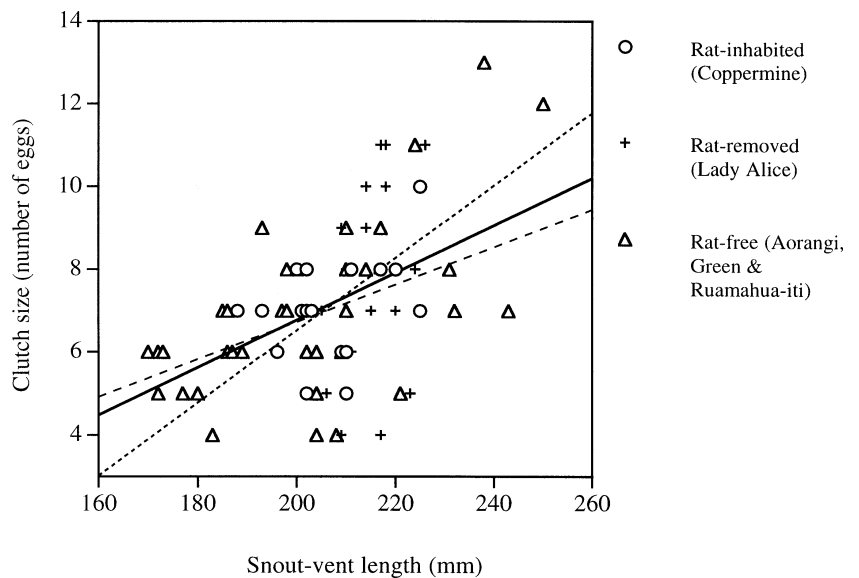


Figure 5. Relationship between female snout-vent length and clutch size among northern islands with rats present (Coppermine, dashed line), rat-removed (Lady Alice, dotted line), and rat-free (Aorangi, Green and Ruamahua-iti, solid line), during spring 1996-98.

five eggs on 10 November, 1997) was observed nesting during 7–13 December on Lady Alice. No other evidence of nesting activity was found on any island, despite extensive searching.

## 4.2 PHYSICAL AND PHYSIOLOGICAL CONDITION

### 4.2.1 Physical condition

As noted above, there were significant differences in body sizes (SVLs) of adult females between islands; this also applied to males ( $F_{[4,208]} = 50.30$ ,  $P < 0.001$ ; Figure 6). Therefore, analysis of body condition with respect to kiore status used a subset of the total data to encompass a similar size range for each category of islands (males 201–266 mm SVL, females 184–234 mm SVL). Body condition showed significant differences among both males ( $F_{[2,223]} = 8.76$ ,  $P < 0.001$ ) and females ( $F_{[2,147]} = 13.16$ ,  $P < 0.001$ ), with respect to kiore status (Figure 7). Males and non-gravid females on Lady Alice (rat-removed) tended to be greater in mass for their SVL relative to other island categories. Females on Coppermine (rat-inhabited) had low condition relative to rat-removed and rat-free islands.

The incidence of eye abnormality differed significantly between islands in female tuatara ( $\chi^2 = 14.86$ ,  $df = 4$ ,  $P < 0.005$ , Figure 8a), but not in males ( $\chi^2 = 3.45$ ,  $df = 4$ ,  $P > 0.05$ ). The incidence of tail loss differed significantly between islands in both sexes (males,  $\chi^2 = 12.06$ ,  $df = 4$ ,  $P < 0.05$ ; females,  $\chi^2 = 10.48$ ,  $df = 4$ ,  $P < 0.05$ , Figure 8b). When islands were compared according to kiore status, there was a significant difference in the incidence of eye abnormality for both sexes (males,  $\chi^2 = 384.55$ ,  $df = 2$ ,  $P < 0.001$ ; females,  $\chi^2 = 11.267$ ,  $df = 2$ ,  $P < 0.005$ ), with rates being highest on the rat-removed island (10.6% of males and 19.1% of females on Lady Alice).

Comparing rates of past tail loss between islands according to kiore status, there was a significant difference observed in males ( $\chi^2 = 11.78$ ,  $df = 2$ ,  $P < 0.005$ ), but not in females ( $\chi^2 = 3.29$ ,  $df = 2$ ,  $P > 0.05$ ). The rate of tail loss in males was higher (94%) on the rat-inhabited island (Coppermine) than on average for rat-free islands (75%).

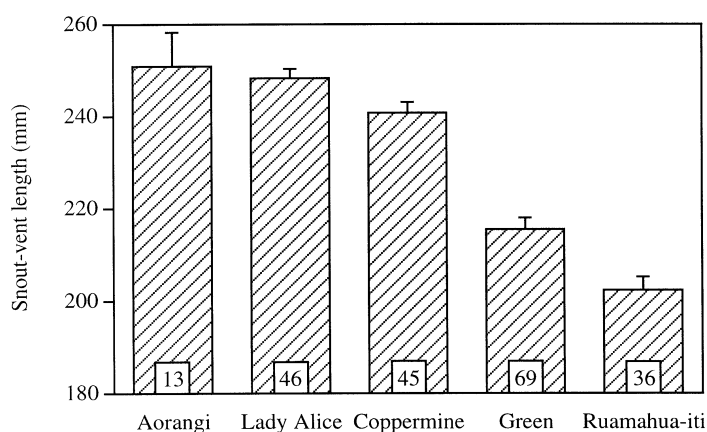


Figure 6. Comparison of body size (mean SVL  $\pm$  SE) of male northern tuatara on five islands, pooled for spring 1996–98 (excluding recaptures). Sample sizes given at base of columns.

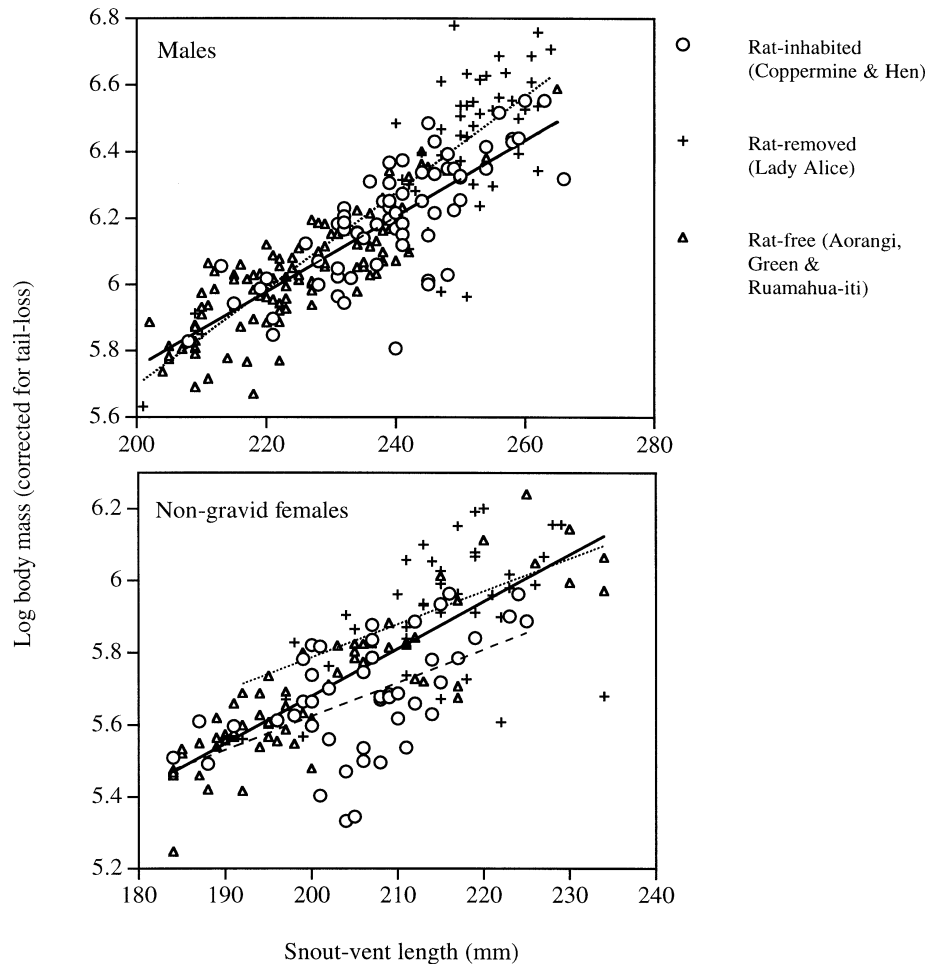


Figure 7. Body condition in comparably sized male (range: 201–266 mm SVL) and non-gravid female (184–234 mm SVL) tuatara among rat-inhabited (Coppermine & Hen, dashed line), rat-removed (Lady Alice, dotted line) and rat-free islands (Aorangi, Green and Ruamahua-iti, solid line), pooled for October–December, 1996–98. Note: range of X and Y-axes differs between graphs, and the regression line for males on rat-free islands overlies that for males on rat-inhabited islands.

#### 4.2.2 Field metabolic rate (FMR)

Ten of the 15 non-gravid females (67%) were recaptured on Coppermine, and eight out of 11 (73%) on Lady Alice (Table 3). The number of days elapsing between recaptures was unavoidably longer on Coppermine (starting earlier and finishing later in spring) because of the time taken to find and recapture animals and the impossibility of being on both islands at the same time. The slightly later start on Lady Alice explains the slightly warmer (by 1.3°C) mean body temperatures of tuatara at first capture than on Coppermine ( $t = 4.804$ ,  $df = 7$ ,  $P < 0.01$ ; Table 3). Datalogger recordings of temperatures inside a tuatara burrow and at the burrow entrance during field trips also indicated that tuatara on Coppermine would have experienced a slightly greater range but similar mean temperatures to those on Lady Alice. For example, on Coppermine, mean air temperatures recorded hourly at the burrow entrance were  $14.0 \pm 1.7^\circ\text{C}$  on the initial field trip and  $17.9 \pm 1.6^\circ\text{C}$  on the final field trip, whereas on Lady Alice they were  $14.7 \pm 2.4^\circ\text{C}$  and  $16.6 \pm 2.6^\circ\text{C}$  respectively (mean temperatures within the burrow fell within these values). Little rain fell during the field trips. Overall, weather conditions were typical of spring in other years.

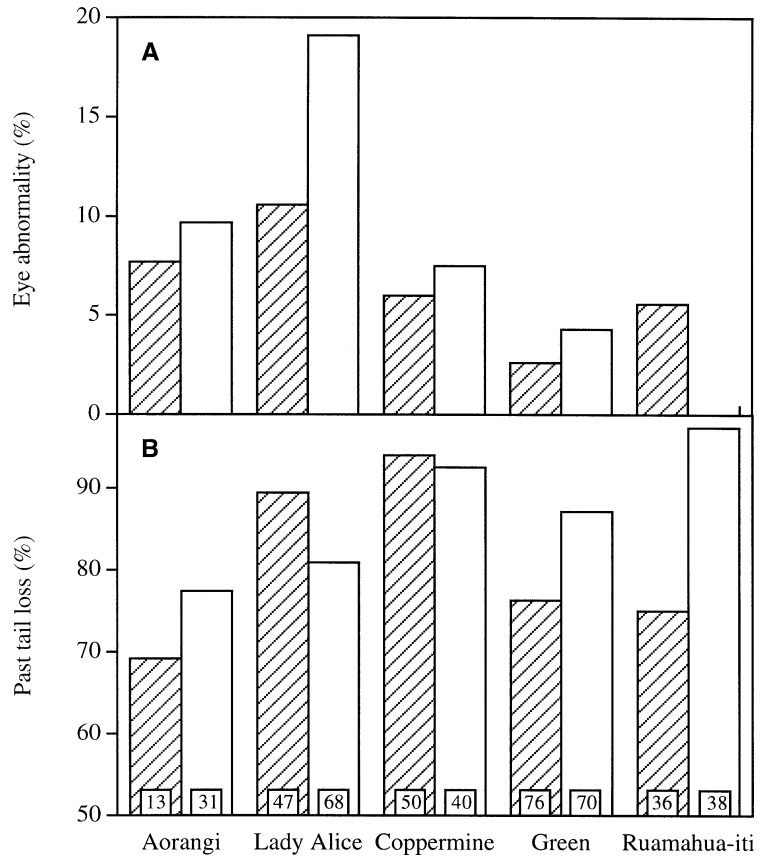


Figure 8. Frequency of eye abnormality (A), and evidence of past tail loss (B) in male (hatched bars) and female (open bars) northern tuatara among five islands. Data pooled for 1996-98 and excludes recaptures. Sample sizes shown at base of columns.

At the start of the study, the sampled tuatara were significantly longer and heavier on Lady Alice than on Coppermine ( $t \geq 2.66$ ,  $P \leq 0.02$ ; Table 3). Tuatara on Lady Alice also showed a greater change in body mass over the course of the study (calculated as a daily average, i.e.  $\% d^{-1}$ ) than on Coppermine ( $t = 3.954$ ;  $P < 0.01$ ). All of the females on Lady Alice gained mass, whereas those on Coppermine stayed close to their initial mass.

Only four females provided sufficient urine at initial, equilibrium and final sampling periods to analyse for isotopes. Therefore, all data presented are based on blood values. The FMR for one female on Lady Alice appeared spurious (at  $0.005 \text{ mL CO}_2 \text{ g}^{-1} \text{ h}^{-1}$ , it was substantially lower than for other tuatara, and considered biologically unlikely); it was excluded from calculation of the mean FMR. Among the remaining tuatara, FMR values ranged from  $0.022 \text{ mL}$  to  $0.069 \text{ mL CO}_2 \text{ g}^{-1} \text{ h}^{-1}$ , and the mean value (Table 4) was significantly higher on Lady Alice than on Coppermine ( $t = 2.89$ ,  $df = 15$ ,  $P < 0.05$ ). No significant

TABLE 3. BODY TEMPERATURE, SIZE AND CHANGE IN BODY MASS FOR NON-GRAVID FEMALE TUATARA IN THE FMR STUDY.

ISLAND	NO. OF DAYS	INITIAL BODY TEMP. ( $^{\circ}\text{C}$ )	SVL (mm)	INITIAL BODY MASS (g)	FINAL BODY MASS (g)	CHANGE IN BODY MASS ( $\%d^{-1}$ )
Coppermine n = 10	$49.84 \pm 0.99$	$12.7 \pm 0.2$	$205 \pm 1$	$271.0 \pm 11.9$	$272.8 \pm 12.4$	$0.01 \pm 0.03$
Lady Alice n = 8	$30.94 \pm 2.65$	$14.9 \pm 0.4$	$214 \pm 3$	$358.4 \pm 19.6$	$378.3 \pm 21.2$	$0.18 \pm 0.03$

TABLE 4. FIELD METABOLIC RATE (FMR) AND RATES OF WATER INFLUX AND EFFLUX FOR NON-GRAVID FEMALE TUATARA IN SPRING 1997.

ISLAND	SAMPLE SIZE	FMR (mL CO <sub>2</sub> g <sup>-1</sup> h <sup>-1</sup> )	WATER INFLUX (mL kg <sup>-1</sup> d <sup>-1</sup> )	WATER EFFLUX (mL kg <sup>-1</sup> d <sup>-1</sup> )
Coppermine	10	0.036 ± 0.003	20.8 ± 2.1	20.7 ± 2.1
Lady Alice	8 (7 for FMR)	0.049 ± 0.004	22.6 ± 4.6	21.3 ± 4.4

differences were observed between islands in mean rates of water influx or efflux ( $P > 0.05$ ; Table 4).

#### 4.2.3 Hormonal stress response

Both sexes of tuatara had low plasma concentrations of corticosterone at capture on both islands (mean ± SE ≤ 2.36 ± 0.58 ng/mL; Figure 9). Both populations showed a significant increase in corticosterone concentrations over time, but the response over time showed a highly significant difference between the two islands ( $F_{(2,136)} = 44.54$ ,  $P < 0.001$ ). Coppermine tuatara of both sexes had higher plasma concentrations of corticosterone in response to capture (3 and 18 h) than Green tuatara. Females showed larger responses than males ( $F_{(1,136)} = 16.30$ ,  $P = 0.0001$ ).

Other data (not presented) revealed differences between islands, and sometimes between sexes, in the response over time for other indicators of the stress response. Glucose concentrations showed a greater increase on Coppermine than on Green ( $P < 0.001$ ), and a greater increase in females than males ( $P =$

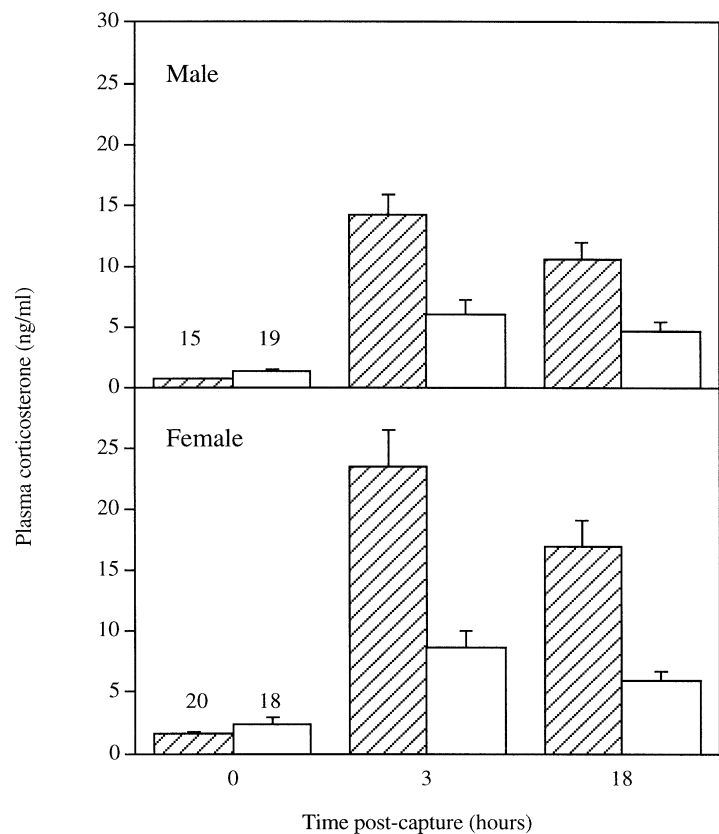


Figure 9. Plasma corticosterone concentrations (mean ± SE) in response to short-term stress (3 and 18 hours) in male and female northern tuatara on Coppermine (hatched bars) and Green Islands (open bars). Sample sizes given at capture apply to all sampling times.

0.0009). Testosterone concentrations, which predictably were much higher at capture in males than females, showed a significant difference between the sexes in the change over time ( $P < 0.001$ ). Although the change over time in testosterone did not differ between islands ( $P = 0.38$ ), there was a significant island by sex interaction ( $P < 0.004$ ). Overall, testosterone concentrations declined to a greater extent in males than in females, and the decline in males was greater on Coppermine than on Green.

### 4.3 POPULATION SIZE-CLASS STRUCTURE

Tuatara appeared to grow to different sizes on different islands. The proportion of large adult tuatara tended to be higher on the more northerly and larger islands (Figure 10), and maximum adult size for both males and females showed the same trend (i.e. highest on Aorangi and lowest on Ruamahua-iti). The three

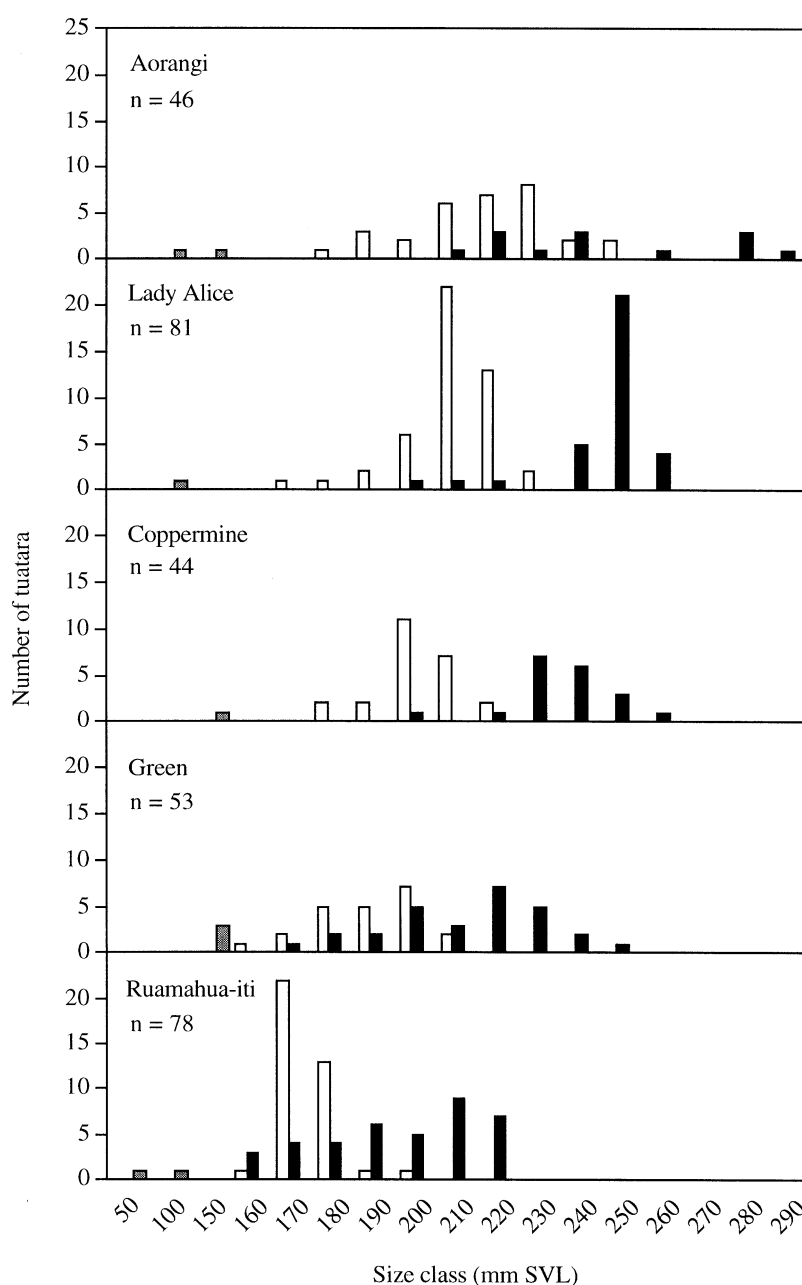


Figure 10. Number of tuatara (males, dark; females, white; unsexed juveniles, grey) per size class (every 10 mm, except for 50–99 and 100–149 mm SVL) on five northern islands, sampled in spring 1998 (Aorangi), and 1997 (Lady Alice, Coppermine, Green, and Ruamahua-iti).

tuatara captured on Hen were also large adults (two males of 252 and 255 mm SVL, one female of 222 mm SVL). The distributions of the samples tended to be bimodal, with adult males growing to larger sizes than adult females.

Although juvenile and small adult-sized tuatara were not numerous on any of the islands, there appeared to be an underrepresentation of small tuatara on Coppermine and Lady Alice in particular, with only one animal less than 170 mm SVL caught on each island. Other evidence is consistent with reduced recruitment on rat-affected versus rat-free islands. Compared with Aorangi and Green, the distribution curves for adults on Lady Alice, and to a lesser extent Coppermine, are skewed toward relatively large individuals within each sex. Also, Coppermine and Green, which were sampled across more years than other islands, show differences in sizes of tuatara captured when the data across all years (1996-98) are pooled. In total, only two tuatara <170 mm SVL (juveniles and probable subadults) were seen during seven field trips to Coppermine (out of 214 total captures, including recaptures). On Green, 15 tuatara <170 mm SVL were seen during five field trips (out of 252 total captures, including recaptures).

The distribution curve for tuatara on Ruamahua-iti was skewed toward smaller rather than larger adults. A smaller range of female body sizes was seen on Ruamahua-iti (only two size-classes contained more than one female) compared to the other islands (five to seven size-classes containing more than one female). This constraint was not seen in males on Ruamahua-iti, although the maximum male body size on this island was at least three size-classes smaller than any other island.

#### 4.4 DENSITY ESTIMATE ON COPPERMINE ISLAND

Overall, the analysis of tuatara abundance in the search area on the eastern end of Coppermine provided no evidence of time or sex differences in inter-trip survival. However, there was strong evidence of capture probability varying with time, and weaker evidence that capture probabilities differed between the sexes. Averaging across the best three models using Akaike weights (Burnham & Anderson 1998) gave an estimate of inter-trip survival of  $\phi = 0.938 \pm 0.019$ . Estimated capture probabilities for female tuatara ranged between  $0.477 \pm 0.065$  and  $0.860 \pm 0.092$ . Male capture probabilities were lower, ranging between  $0.321 \pm 0.099$  and  $0.761 \pm 0.126$ .

Jolly-Seber abundance estimates indicated an increase in the tuatara population within the search area between the March 1989 and the October 1996 samples, followed by a slight decrease (Figure 11). A similar conclusion was obtained from the analysis based on the model of Pradel (1996) where a model with one proportional population change parameter before, and a second one after, the October 1996 samples indicated an increasing population up to the October 1996 sample ( $\gamma = 1.091 \pm 0.022$ ) and a decreasing population following this sample ( $\gamma = 0.938 \pm 0.021$ ). However, when the sole February estimate ( $47 \pm 4$  tuatara) is excluded, all other estimates of total population size within the search area (made in May, September, October, or December) were similar, ranging from 23 to 42 tuatara. Marked animals clearly survived the poison drop, which occurred in July 1997.



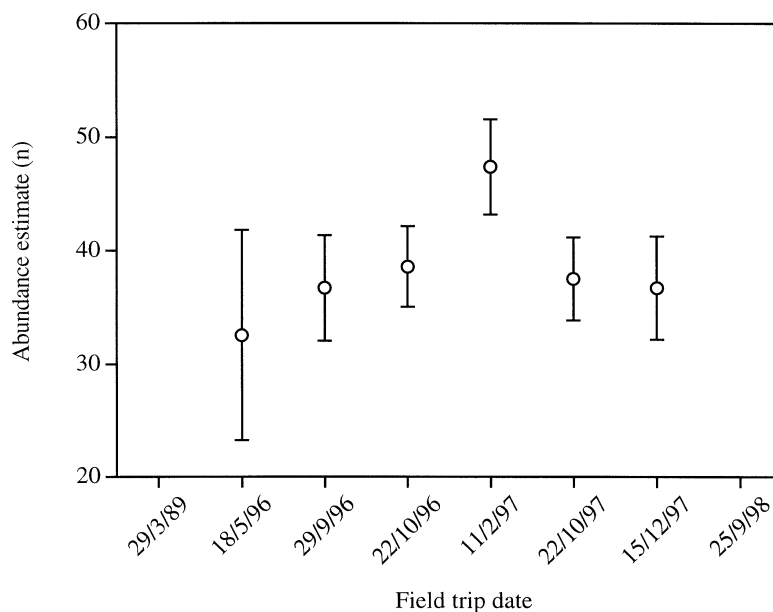


Figure 11. Abundance estimates of the population from the Jolly-Seber model fitted separately to female and male mark-recapture data collected along the path transect at the eastern end of Coppermine Island.

Overall, the number of tuatara estimated for the search area ranged from 23 to 52 animals (12–26 tuatara/ha). When extrapolated to the estimated area of suitable habitat, the abundance of tuatara for the entire eastern end of the island is estimated as 86–194 tuatara. If similar proportions of suitable tuatara habitat apply to the western end of the island, the estimated population on Coppermine ranges from 256 to 582 tuatara.

## 5. Discussion

### 5.1 ASPECTS OF EGG PRODUCTION

#### 5.1.1 Gravidity rate

Significant variation in gravidity rate among tuatara from five northern islands was found when data collected over 1–3 years were pooled. However, this variation was not attributable to the presence of kiore, as the gravidity rate of 36.8% on Coppermine (kiore-inhabited) was intermediate between that on kiore-free islands. Furthermore, the gravidity rate on Lady Alice during 1997–98, 3–4 years after kiore removal (34.0%), was within the range observed when kiore were present in the 1980s (22.2–45.5%; Newman et al. 1994).

Instead, gravidity rate among the five northern islands was negatively correlated with latitude. It was highest (48.2%) on the most northerly island (Aorangi) and lowest (19.0–23.7%) on the two most southerly islands (Green and Ruamahua-iti). Confirmation of this trend for northern tuatara (and elimination of possible trends with island size and/or female snout-vent length) would require additional sampling, including more southerly islands. Comparison with data for islands in Cook Strait obtained in other years are equivocal as to whether there is such a trend throughout the range of tuatara. On Stephens Island (*S. punctatus*), gravidity rates across six years ranged from 8.2 to 29.6% (Newman et al. 1994).

and on North Brother Island (*S. guntheri*), gravidity rate (inferred from egg-laying in response to oxytocin injection) was 19.5% in 1989 (Cree et al. 1991b). Most of these values are within the range observed here for at least some northern tuatara. However, a stronger comparison would compare data using the same techniques from the same years, with large sample sizes for strong statistical power.

Assumptions made in comparisons of gravidity rates among islands are that animals are correctly sexed, that size of maturity is not underestimated, that egg-shelling is sufficiently advanced to be detectable radiographically in all females that have ovulated, that nesting has not begun, and that gravid and non-gravid females are not clumped in ways (e.g. in location or behaviour) that would influence their capture rate (Cree et al. 1991a). Sex of adult tuatara can be judged with fairly high accuracy (Cree et al. 1991a), and was judged by the same person in all field trips; therefore, any likelihood of sex misidentification was probably low and equal for all islands. Differences in female body size among islands indicate that females on Green and Ruamahua-iti are likely to have been mature at <170 mm SVL. If so, our sampling would probably have led to an overestimation (rather than underestimation) of gravidity rate on these islands, as egg production increases with female SVL (Dunham et al. 1988).

X-rays of all tuatara clutches showed calcification consistent with advanced stages of egg-shelling. We completed data collection for estimates of gravidity rates by early November in all but one case. Sampling on Green in 1997 was delayed until 18–24 November by equipment problems, but the proportion and number of gravid females was comparable to that in 1996 and 1998, when sampling was completed by 4 November. Furthermore, the only definitive evidence of nesting was observed on Lady Alice during 7–13 December 1997 (other females are known to have laid sometime between early November and early December). Therefore, estimates of gravidity rates for northern tuatara made prior to mid-November are probably reliable, though further information on the time of nesting on different islands (and the possibility that this could vary among years) should be sought. The possibility that weather conditions differentially affect the emergence of gravid and non-gravid females also deserves consideration. The apparently high gravidity rate on Aorangi may have been due to a two-year gravidity cycle, but it could also have arisen if the less-than-optimal weather conditions (11.0–13.7°C for the first six nights) favoured greater emergence of gravid than non-gravid females relative to other islands.

### 5.1.2 Clutch size and body size

Clutch size, our second measure of egg production, varied significantly among tuatara from five northern islands. However, island populations differed significantly in snout-vent length, and once the effect of this variation was removed, no significant differences in SVL-adjusted clutch size were observed among islands. Further, SVL-adjusted clutch size did not vary significantly among five northern islands of differing kiore status during 1996–98, and the relationship on Lady Alice was similar to that in the 1980s when kiore were present (Newman et al. 1994). We thus found that the past or current presence of kiore has no influence on the relationship between clutch size and female SVL in northern tuatara (cf. Newman et al. 1994). Instead, northern tuatara appear to have low SVL-adjusted clutch sizes compared with tuatara on

Stephens, independent of the presence of kiore, and therefore, the difference appears to be one between northern islands in general and Stephens tuatara. This result was consistent with increases in clutch size with latitude observed in other reptiles, such as turtles (Iverson & Smith 1993; Lindeman 1997). However, turtles have a greater incidence of multiple clutching at lower latitudes (Cagle 1954), thus offsetting lower clutch sizes. A negative correlation between gravidity rate and latitude in northern tuatara suggests that inter-clutch intervals are shorter among the northern islands at lower latitudes. Further analysis of possible trade-offs in reproduction of northern tuatara, including an examination of the relationship between egg size and clutch size, is in progress in collaboration with D.G. Newman, and will be submitted elsewhere.

The limited data available for tuatara on North Brother Island (*S. guntheri*) suggest that variation in clutch size is as likely to be due to variation in island size as it is to be associated with the genetic difference (thought to be at subspecific level) between northern and Cook Strait tuatara. The single year of data available for egg production (in response to oxytocin injection) on North Brother suggests that tuatara there have characteristics closer to those of northern tuatara than to those on Stephens. Gravidity rate, mean clutch size and female SVL (19.5%,  $6.5 \pm 0.6$  eggs and  $192 \pm 2$  mm,  $n = 8$ ) observed on North Brother (Cree et al. 1991b) were most similar to those seen on Green (19.0%,  $6.3 \pm 0.6$  eggs and  $197 \pm 3$  mm SVL). This is of interest as these are the two smallest islands on which reproduction of female tuatara has been assessed (4 and 2 ha respectively). Nonetheless, Stephens and Lady Alice are of equivalent size, yet their tuatara have different clutch and body sizes.

Variation in snout-vent length among tuatara populations has previously been noted, although the causal factors are uncertain (Tracy 1997). Among the five northern islands studied here, the variation in body size (snout-vent length) of tuatara was associated with latitude, rather than population density. However, the power of the rank correlations used was very low and, as noted above, the relationship with latitude clearly does not hold throughout the entire geographic range of tuatara. Furthermore, island size varied in a similar pattern to latitude among northern islands, with larger islands to the north and smaller in the south. In order to examine whether tuatara body size is more strongly associated with island size rather than latitude (i.e. climatic difference), a larger sample size is needed. However, comparison of historical survey data among islands within groups such as the Mercury and Aldermen Islands (i.e. size variation among islands controlled for latitude) could be obscured by effects of density, as populations on small islands tend to be at higher density.

Monitoring future translocations of tuatara could be the key to separating and testing possible effects of island size and density on body size. Long-term monitoring of tuatara translocated from islands such as Green and Ruamahua-iti (small tuatara, high density) to Korapuki and other islands at equivalent latitudes presumed or known to have been tuatara-inhabited (e.g. Middle Chain) would allow us to test the relative effects of these influences. For example, adult tuatara could be moved from a small island/high density (Green or Ruamahua-iti) to:

- 1) a small island/low density (Korapuki, 17.5 ha; or Middle Chain, 23 ha); or,
- 2) a large island/low density (Tiritiri Matangi, 197 ha).

If density was the main determining factor, both populations of translocated tuatara would produce offspring reaching a larger mean SVL than the original population. If island size was the main determining factor, there would be a difference in SVL between the two translocated populations, with tuatara on the larger island growing to a larger SVL.

Testing these hypotheses would require monitoring of SVL in the translocated and original populations over generations, as body length can change in the offspring produced on the island, but not necessarily in the translocated adults which may have reached the end of their growth phase. Thus, changes in mean adult SVL could take decades to emerge.

### **5.1.3 Time of nesting**

Northern tuatara on at least one island (Lady Alice) appeared not to nest until late November-December. This was later than expected. Tuatara on Cook Strait islands (Stephens, Brothers) nest during October-December, with a peak in November (Dawbin 1982; Cree et al. 1991b). It had been predicted that tuatara on the warmer, northern islands would lay earlier (Newman & Watson 1985; Newman et al. 1994). Our inability to locate other nests on northern islands (in part because nesting was later than expected) meant that we were unable to compare nesting success between islands as initially planned. A similar or even later time of nesting than on Lady Alice has been observed in the tuatara enclosure on Little Barrier Island (late December-early January; Chris Smuts-Kennedy, pers. comm.). These observations have implications for the time that egg-laying is induced in captive populations of northern tuatara (i.e. Stanley and Cuvier Island tuatara at Auckland and Hamilton zoos), as eggs induced too early may have incomplete shelling and not have developed sufficiently to survive outside the female. Some clutches from induced captive females have indeed had this problem and a high mortality rate as a result (M. Bell, pers. comm.). Although the exact cause of the lack of calcium deposition in the egg shells is unknown, delaying the time that egg-laying of northern female tuatara is induced in captivity may help.

## **5.2 PHYSICAL AND PHYSIOLOGICAL CONDITION**

### **5.2.1 Physical condition**

The physical and physiological comparisons were carried out primarily to explore evidence for possible mechanisms of suppressed egg production for female tuatara on certain islands. However, as the results showed that the presence of kiore was not associated with reduced clutch size or gravidity rate of female tuatara, the basis for predicting differences in physical condition or physiological functioning of tuatara among islands differing in rat status has diminished, though not disappeared (see below).

Differences observed in body condition indices among islands, grouped according to kiore-status, indicated that male and non-gravid female tuatara on Lady Alice had a greater SVL-adjusted body mass than on either Coppermine or rat-free islands. These results were consistent with the hypothesis that tuatara would benefit from increased food supplies (i.e. increase their body condition

index) following the removal of kiore. We predict that the apparent increase in condition index following rat removal on Lady Alice will be temporary, disappearing over time as tuatara become more abundant and the relative increase in food disappears. This prediction is based on the lack of difference in body condition index between males on Coppermine (rat-inhabited) and the rat-free islands, although this similarity could also be due in part to a sample represented largely by males of smaller SVL on the rat-free islands (Figure 7). If maximum adult body length is being restricted by food intake on Green and Ruamahua-iti, then body mass of tuatara on these islands is also likely to be smaller than optimum. Any restrictions on food availability or intake may affect quality and hatchability of tuatara eggs, and may lead to decreased gravidity rate if females take longer to accumulate energy stores between clutches.

The translocation experiments described previously could be used to test the hypothesis that tuatara translocated from populations with small adult SVLs (e.g. Green & Ruamahua-iti) would increase in condition index (mass adjusted for SVL), after transfer to an island with higher food availability (due to lower density/larger island size). Utilising individuals toe-clipped in 1989 (Cree et al. 1995) would provide a pre-translocation growth history of more than ten years, with comparison to toe-clipped animals in the parent population providing a control. A study of tuatara translocated from North Brother to Titi Island in the Cook Strait has already demonstrated that adult tuatara can increase in body condition in response to lower density/increased food supply (Nelson & Daugherty 1997).

The individuals with lowest body condition (Figure 7) were often those which appeared to be aged, or to have blindness in one or both eyes (Tyrrell, pers. obs.). The highest incidence of eye abnormality (19.1%) was seen in females on Lady Alice. Castanet et al. (1988) hypothesised that a higher rate of eye damage observed on Lady Alice than on Stephens may have been due to fights with the large seabird species present on Lady Alice. The presence of kiore has been linked with the disappearance of small burrow-dwelling seabird species (Imber 1975). Tuatara sampled on Lady Alice tend to be concentrated in Grave Bay and may have been more likely to share burrows with large flesh-footed shearwaters than smaller seabirds such as diving petrels which predominate on Green and Ruamahua-iti (Skegg 1963). Very few seabirds were present on Coppermine in our search area (Figure 2), although birds may have been more numerous historically. Tuatara on Aorangi, with the second highest incidence of eye damage, were seen co-habiting with Buller's shearwaters, another large seabird. Any measure of indices of eye abnormality or past tail loss is going to be age-dependent to a degree, as older animals have had more time in which to be afflicted. The greater proportion of eye abnormality in tuatara on the three northernmost islands may also therefore be due to a greater proportion of larger/older animals in the population. This is also consistent with low turnover rates of adult tuatara compared with islands with dense populations and where the tuatara are smaller.

### **5.2.2 Field metabolic rate (FMR)**

Our study is the first to provide data on field metabolic rates (FMR) in northern tuatara. FMRs in female northern tuatara are the lowest reported for active reptiles (Christian & Green 1994; Secor & Nagy 1994; Christian et al. 1998), and

probably reflect the lower normal activity temperatures of tuatara compared to other reptiles. Although studies of FMR (using doubly-labelled water containing tritium) have been made for tuatara on Stephens (Green 1989), detailed methods and results have yet to be published and are not available for comparison. The present study demonstrates the feasibility of the technique (in terms of injection dosages, times between injection and recapture, etc.). It also shows that blood sampling is necessary for adequate sample sizes, as tuatara cannot be relied on to provide urine samples when required.

The results obtained here indicate a significant difference in FMR of non-gravid female tuatara between Coppermine and Lady Alice in spring 1997. This difference was measured in the absence of differences in water influx and efflux. In conjunction with greater increase in mass of tuatara observed on Lady Alice relative to Coppermine, the difference is consistent with an increase in food consumption for tuatara following an extended period since rat removal. However, further studies across a range of islands over various time frames following rat removal would be needed to determine whether this association is consistent. We cannot eliminate the possibility that the difference in FMR between the two islands was due to differences in time over which FMR was measured. However, this is an unlikely explanation, because FMR was adjusted for time, and while tuatara on Coppermine would have experienced a slightly greater range of temperatures than those on Lady Alice, mean temperatures on both islands were very similar. Ideally, future comparisons among islands should be conducted over the same time frame, and studies be made under controlled conditions to show the effect of food supply on FMR. The FMR technique could also be considered for the larger species of lizards on offshore islands. While the FMR technique can tell us a lot about the functioning of individual animals, it is labour-intensive, involves expensive laboratory analyses, and may not be as applicable to very small species of reptiles, which may be difficult to recapture. Radiotransmitters, used to relocate individuals for most FMR studies overseas, might alter FMR of small reptiles, as wearing transmitters could represent a significant energy cost.

### **5.2.3 Hormonal stress response**

The only previous studies to examine handling-induced changes in plasma hormone concentrations in wild tuatara have been carried out on Stephens. In one study, males and females held in cloth bags for 3 hours in January had a significant elevation in plasma corticosterone compared with free-roaming controls (Tyrrell & Cree 1998). Another study in November showed that males held in cloth bags had significant declines in plasma testosterone concentration by 12 and 24 hours (but not 3 hours) after capture (Cree et al. 1990). The present study on northern tuatara confirms and extends these results. The increase in corticosterone in northern tuatara was maintained at least until 18 hours after capture, and was associated with an increase in plasma glucose concentration and a tendency in males toward reduced plasma testosterone concentration.

More interestingly, the present study shows that the magnitude of the response can vary between islands. Tuatara on Coppermine had much higher concentrations of corticosterone at 3 hours and 18 hours after capture (mean values

10.6–23.5 ng/mL) than on Green (mean values 4.8–8.7 ng/mL). The mean levels on Coppermine were also high relative to those seen on Stephens at 3 hours after capture (11 ng/mL in both males and females; Tyrrell & Cree 1998). The greater increase in corticosterone on Coppermine compared with Green is consistent with the greater increase in plasma glucose levels and the greater decline in male testosterone levels. Collectively, these results indicate that the Coppermine animals were mounting a greater 'stress response' to capture and confinement than were the Green animals. This is consistent with our prediction that the response would be greater in tuatara living in the presence of kiore.

Stress responses that are reflected by sustained elevations in plasma corticosterone, and declines in plasma testosterone in males, have implications for reproduction, behaviour, growth and immunity (Guillette et al. 1995). As an example of the possible ecological effects from sustained elevations in corticosterone, male lizards (*Uta stansburiana*) treated with implants of corticosterone in the field had reduced home ranges (DeNardo & Licht 1993). Such a change in behaviour could have flow-on effects on, for example, food consumption and mating success.

A possible indication that food consumption differed between islands was that male and female tuatara on Green both had significantly higher levels of glucose at capture than Coppermine tuatara (data to be presented elsewhere). In addition, a concurrent study, which used half of the blood collected at capture in this study, found that plasma levels of long-chain n-3 polyunsaturated fatty acids, triacylglycerol, and cholesterol were all higher in tuatara on Green than on Coppermine (Blair 2000). Such differences implied dietary differences between the two islands, with tuatara on Green hypothesised to consume more insect larvae (high triacylglycerol and cholesterol source), seabirds (rich source of eicosapentaenoic acid and docosahexaenoic acid), and perhaps crabs than on Coppermine.

The possibility that tuatara in the presence of kiore are chronically stressed should in theory be tested across a greater number of islands. In practice this is not feasible. Free-roaming tuatara still exist in the presence of kiore on Hen, Maitaha, and Little Barrier Islands, but the numbers are so low that a study like the one conducted here would be impossible. Another approach would be to see whether the difference observed here between Coppermine and Green disappears now that kiore have been removed from Coppermine. It may be necessary to wait several years before repeating the experiment and to have two teams collecting samples at the same time. Although we sampled the two islands as quickly as possible, and weather conditions remained similar, the sampling was sequential and we cannot eliminate the possibility that the difference was the result of seasonal changes. Yet another approach would be to see whether the same association exists in New Zealand lizards. Comparison among a range of kiore-free and kiore-inhabited islands might still be possible for species such as the large nocturnal Duvaucel's gecko *Hoplodactylus duvaucelii*.

### 5.3 POPULATION SIZE-CLASS STRUCTURE

Considerable variation was observed in the size-class structure among the five populations for which we obtained samples of >44 animals. Some of this variation reflects natural variation in SVL of tuatara, as previously discussed (i.e. tuatara are naturally small on Ruamahua-iti in particular). However, some of the remaining variation is consistent with previous suggestions of recruitment failure in the presence of kiore (Crook 1973; Cree et al. 1995). In particular, there was a near-absence of tuatara <170 mm SVL on Coppermine during 1996–98. Due to the wide variation in size-classes between islands, it may be best to use each island as its own control (changes in proportion of small tuatara over time). A review of unpublished data also indicates that field trips in late summer (February–March) have tended to catch more juveniles than those in spring (October–November). A previous field trip to Aorangi in March 1989 found that 34% of the animals caught (9/26 tuatara) were <200 mm SVL and three were <170 mm SVL (Cree et al. 1995). These proportions are higher than observed here in spring, and suggest that season should be controlled for in inter-year comparisons.

The apparent absence of juvenile tuatara in the presence of kiore has been attributed by some researchers to behavioural change and inappropriate search techniques (Craig 1986). Our sampling methodology concentrated mainly on catching tuatara on the surface at night, and while we did not actively seek juvenile tuatara, which tend to be more diurnal and cryptic, hiding underneath logs and in vegetation cover (Dawbin 1982), we did expect to catch subadult-sized animals (150–170 mm SVL) if they were present. Subadults are nocturnal in habit, occupying similar habitat to adult tuatara. We therefore conclude that the lack of small tuatara observed in intensive sampling of Coppermine was a real reflection of demographic bias to adults.

We hypothesise that if the presence of kiore was responsible for the low rate or absence of recruitment of tuatara on Coppermine, then the number of juveniles and subadults should increase in the future and represent a greater proportion of total captures in subsequent field trips. This appears to be happening already on Lady Alice, with 6 juveniles out of a total of 13 tuatara caught during a field trip in March 1999 (R. Parrish, pers. comm.). Our study showed that female tuatara are producing eggs on Coppermine in similar numbers per clutch, and at similar rates, compared to females on rat-free islands. While we cannot comment on the quality and hatching survival rates of eggs due to the failure to locate nests, it is highly likely that kiore would prey upon both eggs and small juveniles.

Locating nests of tuatara is extremely difficult. As we were unable to find nests on islands other than Lady Alice (in part due to the later than expected time of nesting), we were unable to compare nesting success in the presence and absence of kiore. The very small populations left on islands that still have kiore (Hen, Little Barrier and Mauitaha), and the low percentage of females that will be carrying eggs in any year mean that the most probable method of obtaining information on potential predation of eggs or interference of kiore during the nesting of tuatara is to monitor artificial nests of either tuatara eggs (induced) or similar-sized birds' eggs. A pilot experiment carried out in May 1996 on Coppermine (C. Tyrrell unpubl. data) showed that kiore will readily dig up and



consume hard-boiled quail eggs half-buried in tuatara-style nests. Infra-red video monitoring of artificial tuatara nests on a kiore-inhabited island such as Hen could be carried out to test whether predation by kiore occurs.

The capture rate of tuatara on Hen (three tuatara in 11 nights in 1997) was extremely low for such a large island (500 ha), but consistent with previous surveys (unpubl. internal reports, Department of Conservation: principal investigator, year: I. McFadden 1984; A. Cree 1989; R. Parrish 1994). The collector Andreas Reischek and his well-trained dog failed to find any tuatara in the southern and western areas of Hen in December 1880 (Reischek 1881), but found several adult tuatara in the north-eastern area during a subsequent trip (Reischek 1885). Until the time of our study, no more than 29 tuatara had ever been caught on Hen at any one time, and all tuatara caught and measured were large adults >200 mm SVL. In March 1984, two small tuatara were seen, but not caught, plus two clutches of eggs were found (one clutch had nine dried eggs and one eggshell, and the other clutch was viable and reburied; I. McFadden, pers. comm.). All three animals caught in 1997 had been toe-clipped in 1989, as were ten of the 24 caught in 1994. A field trip to Hen in April 2000 caught 40 tuatara (three previously toe-clipped; R. Parrish, pers. comm.). All were adult, and apart from the smallest animal (186 mm SVL), ranged in size from 205 to 268 mm SVL (R. Parrish, pers. comm.). There has been no evidence for tuatara recruitment on Hen in at least the past seventeen years. Although Hen has some value in the short-term as a kiore-inhabited control for islands on which kiore have been eradicated (Cree et al. 1995), there is a high risk that tuatara will eventually become extinct on Hen without intervention to ensure successful breeding.

#### 5.4 DENSITY ESTIMATE ON COPPERMINE ISLAND

Recent criticisms of mark-recapture estimates of tuatara density include inappropriate use of mathematical models, and poor data collection techniques in which excessive handling may influence the likelihood of short-term recapture (Cassey & Ussher 1999). Cassey & Ussher (1999) also considered that comparisons between studies may be invalidated by variables such as environment, individuals, observers and studies, so they recommended line transect methods as having the most potential for monitoring tuatara populations. However, regardless of survey method, a proportion of tuatara are likely to be in burrows at night, and therefore not visible on the surface and available for sampling. Estimates of density from line transects (Cassey & Ussher 1999) are just as likely to be influenced by recent prior sampling for other studies (e.g. Ussher 1999) or by movement of researchers along paths through the area prior to sampling. On Coppermine, and most northern tuatara islands, vegetation obscures direct sight of the majority of tuatara, especially at night during surveying, and most animals are heard moving and need to be approached in order to bring them into view. Line transect methods, while potentially useful in open terrain to gather data on relative or absolute abundance, fail to provide essential information such as the sex, body size (SVL) and mass of individual tuatara which provides the demographic data vital to assessing the conservation status of a population.

Our mark-recapture method used between-trip estimates based on permanently marked or identifiable individuals, thereby avoiding possible effects of short-term recapture and any other handling. Our population estimate for Coppermine (256–582 tuatara) was in line with a previous coarse estimate of abundance (low hundreds) based on capture frequency (Cree & Butler 1993). In addition, the upper limits of abundance estimates in the search area were very similar for May, October and December surveys (41–42 individuals). While the model suggested that tuatara appear to be disappearing from the population at a rate of 6% a year, this may have been in part due to a number of tuatara which were captured in February 1997 only (possible increase in emergence associated with warm weather and/or mating). These results suggest that it will be important to control for season in future comparisons of density between islands or over time.

Density estimates for Coppermine (12–26 tuatara/ha) were very similar to Lady Alice (13.6–17.7 tuatara/ha in 1996, post kiore-eradication; Cassey & Ussher 1999). These figures are much smaller than for the population of tuatara that co-existed with house mice on Whenuakura (99 tuatara/ha, prior to the arrival of Norway rats; Newman 1986). They are also a magnitude smaller than density estimates for rat-free islands such as Ruamahua-iti (220–335 tuatara/ha; G. Ussher pers. comm.) and Stephens (1420 tuatara/ha in Keepers Bush; Newman 1987), and indirectly support an effect of disturbance such as predation by kiore and/or habitat destruction on recruitment. Extremely low densities of tuatara have also been noted on other islands on which kiore were present (Cuvier, Little Barrier, Mauitaha, Red Mercury and Stanley; Crook 1973; Whitaker 1978, 1993; Whitaker & Daugherty 1991; Cree et al. 1995; R. Pierce, pers. comm.).

## 6. Conclusions

Our study has shown that there is no significant difference in clutch size (adjusted for female SVL) or gravidity rate among populations of northern tuatara in relation to the presence or absence of kiore. Therefore, we rejected our hypothesis that kiore influence the clutch size of tuatara. Gravidity rate and clutch size differ between populations, but comparisons among islands are complicated by differences in tuatara body size. The maximum size of tuatara (and hence, clutch size) appears to be limited on some islands independently of the presence of kiore. Body size is correlated with latitude and may be also influenced by island size and/or population density. Independently of body size, northern tuatara have relatively small clutches compared with Stephens tuatara.

Some differences in physical and physiological condition among tuatara populations are consistent with kiore having a detrimental effect upon tuatara. The presence of kiore is associated with lower body condition of adult tuatara. Females on Coppermine have the lowest condition relative to rat-removed and rat-free islands. Tuatara on Lady Alice tend to be greater in mass for their SVL relative to other island categories, which may be the result of a temporary surge

in food availability following the eradication of kiore. Tuatara on some rat-free islands appear to be limited in maximum body size and their body condition may also be constrained. The incidence of eye abnormalities differs significantly between islands in female tuatara but not in males, but is highest in both sexes on Lady Alice. The rate of past tail loss differs significantly between islands, but is not consistently related to kiore status. The presence of large seabirds and the age structure of tuatara populations may explain some of the patterns seen. FMR in non-gravid females was lower on Coppermine three months after rat removal than on Lady Alice three years after rat removal. The hormonal stress response was greater on Coppermine in presence of kiore than on Green in absence of kiore. These differences may be related to the presence of kiore, but further work is needed if the relationship is to be confirmed.

The density estimate for the east end of kiore-inhabited Coppermine (12–26 tuatara/ha) is much lower than previously reported for any rat-free population of tuatara and is consistent with estimates of very low density of tuatara on islands where kiore were present. The low rate of recruitment observed historically in tuatara populations that coexist with kiore is not due to lack of egg production. Female tuatara on Coppermine produce similar-sized clutches to other tuatara populations, and at similar rates of egg production. Our data therefore support the hypothesis that there is reduced recruitment of tuatara in the presence of kiore. We predict that predation by kiore on eggs and small tuatara is the major mechanism of impact upon tuatara recruitment. Physical and physiological data also raise the possibility that quality and hatchability of tuatara eggs might be negatively affected by the presence of kiore.

## 7. Recommendations for management and future research

1. More research is needed to understand the relative effects of island size, latitude and tuatara density on variation in tuatara body size (SVL). We recommend that hypotheses about variation in SVL be tested in conjunction with planned translocations of wild tuatara to new islands. This will require the appropriate selection of tuatara for translocation, as well as long-term monitoring after release.
2. Evidence obtained on Lady Alice suggests that adult tuatara show an increase in body condition (greater mass for length) within a few years of kiore removal. We recommend that the hypothesis of a short-term improvement in body condition following removal of kiore be tested by monitoring tuatara on Lady Alice and Coppermine over the next few years. Ideally, body mass and SVL should be measured yearly for the next five years to test whether the condition of Coppermine tuatara initially increases and that of Lady Alice tuatara levels off or decreases. Inclusion of another island on which kiore status is

unchanged would help eliminate the possibility of variation among years in ways unrelated to kiore status.

3. Variation in eye abnormality and tail loss was noted among island populations, but it was not consistently related to kiore status. We recommend further research to investigate the possible influence of large seabirds on tuatara (e.g. eye damage). An initial approach would be to compare indices of eye abnormalities among tuatara from different areas on Lady Alice which have different compositions of seabird species present.
4. Some tuatara in this study had been permanently marked (toe-clipped) in previous studies. The recapture of these animals provided valuable information on reproductive frequency and density, and they could also be used to provide information on growth, longevity and reproductive history. No further toe-clipping was carried out in this study because of iwi objection. A new, culturally acceptable method(s) of permanent identification, suitable for tuatara of all sizes, is an important research and management need. This will ensure that potentially valuable information on many aspects of tuatara biology is not lost.
5. We found only three adult tuatara on Hen, despite the large size of the island and the availability of suitable habitat. This result is consistent with previous surveys indicating very low density and negligible recruitment, but may have been exacerbated by unfavourable weather for tuatara emergence. We recommend a comprehensive survey of Hen in favourable weather (preferably in late summer), to see whether any juvenile or subadult-sized tuatara can be located, to obtain formal estimates of density and to determine whether the population is greater than the  $\leq 80$  adults (43 males and 37 females) that have been caught within the past 17 years.
6. Once sufficient survey information has been gathered on Hen, it should be assessed to decide on short-term and/or medium-term actions to avert extinction. Short-term actions could include a return in mid-November to collect eggs via induction for head-starting, or preferably, the collection of gravid females for holding in captivity either on Hen or the mainland, so that they can lay eggs in rodent-free enclosures according to their own time scale. If headstarting is used, we recommend research to determine the minimum size of tuatara vulnerable to kiore predation. However, eventual eradication of kiore from Hen is recommended as the most cost-effective solution to help ensure that a viable population of wild tuatara remains on this island ecosystem in the long term.
7. If further information on the extent of predation by kiore on tuatara eggs is sought, we recommend the burial of eggs (tuatara or similar-sized birds' eggs) in tuatara-style nests in spring on a kiore-inhabited island such as Hen and monitoring either via infra-red recorder or by checking daily.
8. The hormonal and FMR studies were limited, as they were comparisons between pairs of islands. There was not sufficient time, nor were there sufficient funds or wild tuatara on kiore-inhabited islands at the time of the study to include additional islands. We recommend a study of FMR in captive tuatara to help confirm the influence of food and water supply on metabolism. The low inter-animal variation in our FMR study, compared with other metabolic measures, meant that reliable results could be obtained using a small sample size. We also recommend a repeat of the hormonal study on Coppermine and Green

in 5 years to check whether the removal of kiore has altered stress responses. We predict that Coppermine tuatara would have a reduced response, while Green tuatara would stay the same over time.

9. Density estimates for Coppermine (this study) and Lady Alice (Cassey & Ussher 1999) indicate that tuatara on these previously kiore-inhabited islands are present at much lower densities than tuatara on rat-free islands. We recommend long-term monitoring (collection of population size-class data and density) on Coppermine and Lady Alice to detect whether changes occur following kiore removal. The long-term nature of tuatara reproduction, growth and recruitment means that monitoring should probably take place once every two to five years post-eradication rather than yearly, and over at least the next 10-20 years, in order to detect changes in population composition and density due to recruitment.

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