ELSEVIER

Biological Conservation 99 (2001) 3–16

BIOLOGICAL CONSERVATION

www.elsevier.com/locate/biocon

Raising the prospects for a forgotten fauna: a review of 10 years of conservation effort for New Zealand reptiles

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Abstract

The native terrestrial reptile fauna of New Zealand comprises the last representatives of the Sphenodontida — two species of tuatara (*Sphenodon*) — and about 60 species of lizards in four endemic genera: *Hoplodactylus* and *Naultinus* (Gekkonidae), *Cyclodina* and *Oligosoma* (Scincidae). The entire fauna is strictly protected by legislation, but both species of tuatara, one quarter of the geckos and half of the skinks are now regarded as requiring urgent conservation action. The most widespread problem appears to have been predation by introduced mammals. Tuatara and many resident species of lizards on islands now have prospects of expanding in range and abundance following successful campaigns to eradicate introduced predatory mammals, especially rodents. In addition, 12 species of lizards and both species of tuatara have been reintroduced to islands within their former range once predators were eradicated. Habitat destruction and introduced predators remain as particular problems to lizards in the mainland North and South Islands. Solutions to habitat loss and predation may come from targeted predator control and innovative new approaches to ecosystem management.

Keywords: Conservation; Restoration; Predation; Reptiles; Tuatara; *Sphenodon*; Geckos; *Hoplodactylus*; Skinks; *Cyclodina*; *Oligosoma*

1. Introduction

The New Zealand terrestrial reptile fauna is probably best known for the presence of tuatara (*Sphenodon* spp.) — representing the last of the Sphenodontida — an order of reptiles present 225–80 million years ago in Europe, Africa and North America (Daugherty et al., 1992 and references therein). Less well known, but equally significant, is the lizard fauna of at least 60 described and undescribed species of Gekkonidae and Scincidae (Daugherty et al., 1990a,1994). The fauna is represented by only four genera: *Hoplodactylus*, *Naultinus*, *Cyclodina*, and *Oligosoma*. Unlike most other New Zealand vertebrates, some genera have radiated widely. For example, skinks in *Oligosoma* and geckos in *Hoplodactylus* each comprise at least 22 species (Daugherty et al., 1994).

Like other New Zealand animals, the reptiles have suffered extinctions and severe range declines, but many reptiles are now undergoing a resurgence following aggressive and carefully directed conservation activities. Following a long period of passive conservation through legislated protection, significant advances over the last 10 years have enabled a shift from documentation of the extent of declines in various species and habitats (the inventory phase) to one of identifying and aggressively attacking causes of decline (the management phase).

The hazards of relying on preservation by legislation for conservation of tuatara were detailed by Daugherty et al. (1992), and one point warrants reiterating: despite absolute protection of tuatara and many species of lizards on island nature reserves and wildlife refuges, populations of rare reptiles continued to either disappear, become reduced to alarmingly low numbers, or show evidence of failed recruitment. A possible explanation for this phenomenon became evident through associations between reduced density and diversity of lizards, declining populations of tuatara and the spread of Pacific rats (*Rattus exulans*) to islands (Crook, 1973; Whitaker, 1973, 1978; McCallum, 1986). Unfortunately,

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0006-3207/01/$ - see front matter
PII: S0006-3207(00)00184-1

the removal of rodents from islands appeared an insurmountable hurdle (discussion in Dingwall et al., 1978), raising the prospect of gradual loss of the previously secure island faunas through the inevitable spread of introduced rats. The prospect became reality when Norway rats (*R. norvegicus*) reached 2 ha Whenuakura Island in about 1982 and the entire population of > 130 resident tuatara disappeared (Newman, 1987, 1988).

However, rats were not the only problem. New Zealand now has more species of introduced mammalian predators (11) than any other archipelago (Towns et al., 1997). Largely stemming from the effects of such organisms (Towns and Daugherty, 1994), recent assessments of conservation status listed both species of tuatara, 24% of geckos and half of the skinks either in the high categories for action (Category A and B of Molloy and Davis, 1994), or as threatened species by the IUCN (Baillie and Groombridge, 1996; Table 1).

The following review describes strategic advances that over the last 10 years have helped set priorities for the recovery of some of these rare species. We then outline two advances and one problem for conservation of this fauna. The advances are in the removal of threats and recovery of tuatara and lizards on islands, and the reintroduction of species to islands from which predators have been removed. The problem is posed by management of habitat refuges on the mainland North and South Islands, where threats may be controlled, but not necessarily resolved.

Table 1
New Zealand reptiles with high priority ratings (A or B) under Department of Conservation (DOC) assessments (Molloy and Davis, 1994) and/or ranked as threatened or near threatened by IUCN (Baillie and Groombridge, 1996)[a]

Species/taxon	DOC category	IUCN category	Recovery plan
Sphenodon guntheri	A	VU	Yes
S. p. punctatus (northern)	B		Yes
S. punctatus (southern)	B		Yes
Hoplodactylus sp. ("Dansey Pass")	B		No
H. kahutarae	B	LR	No
H. sp. ("Matapia Island")	B		No
H. sp. ("Mt Arthur")	B		No
H. nebulosus	B		No
H. rakiurae	B	LR	No
H. stephensi	B		No
Cyclodina alani	B	VU	Yes
C. macgregori	B	VU	Yes
C. whitakeri	B	VU	Yes
C. sp. ("Mokohinau")	A		Yes
Oligosoma fallai	C	LR	In draft
O. sp. ("Garston")	A		No
O. grande	A	VU	Yes
O. homalonotum	A	VU	Yes
O. infrapunctatum		LR	In draft
O. longipes	B		No
O. microlepis	A	VU	In draft
O. sp. ("Open Bay")	A		No
O. otagense	A	VU	Yes
O. striatum	A	VU	Yes
O. waimatense	B	VU	No
O. sp. ("West Coast")	B		No

[a] Relevant IUCN categories are VU (vulnerable) and LR (low risk). Taxonomy follows Daugherty et al. (1994).

2. Inventory phase

2.1. Ancient faunas discovered

Tuatara have long been viewed as part of an ancient element in the fauna (e.g. Robb, 1986), but the lizards (especially skinks) were traditionally viewed as very recent (Pliocene-Pleistocene) additions to a relatively small fauna of cosmopolitan waifs and strays derived through overwater dispersal from Australia and the Pacific (Towns, 1974; Hardy, 1977; Robb, 1986).

Subsequently, ancient origins were proposed for the geckos and skinks (Towns et al., 1985) on the basis of extensive radiation and phylogenetic distinctiveness (endemism), a proposition strengthened by taxonomic and genetic studies (Towns et al., 1985; Hutchinson et al., 1990; Daugherty et al., 1990c; Hickson et al., 1992; Patterson and Daugherty, 1995). Closest links appear to be with the fauna of New Caledonia (Bauer, 1990; Hutchinson et al., 1990; Hitchmough, 1997), supporting evidence either for land connections or islands in close proximity between New Zealand and New Caledonia during the Early and Middle Miocene (Herzer et al., 1997).

Tuatara and 37% of the New Zealand lizard species are now totally or mainly confined to islands (Daugherty et al., 1994). Like tuatara, some of the lizards have widely disjunctive distributions between islands (Towns et al., 1985). For example, the northern and southern populations of Duvaucel's gecko (*Hoplodactylus duvaucelii*) are separated by a 413 km (straight line) gap and populations of McGregor's skink (*Cyclodina macgregori*) are separated by a gap. However, there are extensive subfossil remains of tuatara in caves, sand dunes and Maori midden sites on the North and South Islands (Whitaker, 1978; Fig. 1), remains of Duvaucel's gecko throughout the North and in the South Island, and McGregor's skink in deposits around the North Island (Worthy, 1987, 1991; Holdaway and Worthy, 1996; Worthy and Holdaway, 1996). These remains indicated extensive range contractions of species of tuatara and large nocturnal lizards that apparently postdate the arrival of humans 1000–2000 years BP (Towns and Daugherty, 1994; Holdaway, 1996). Because of these range declines, reptile faunas, especially on the North Island, underwent dramatic diversity reductions. For example, the fauna of the northern third of the North Island fauna once comprised tuatara, six species

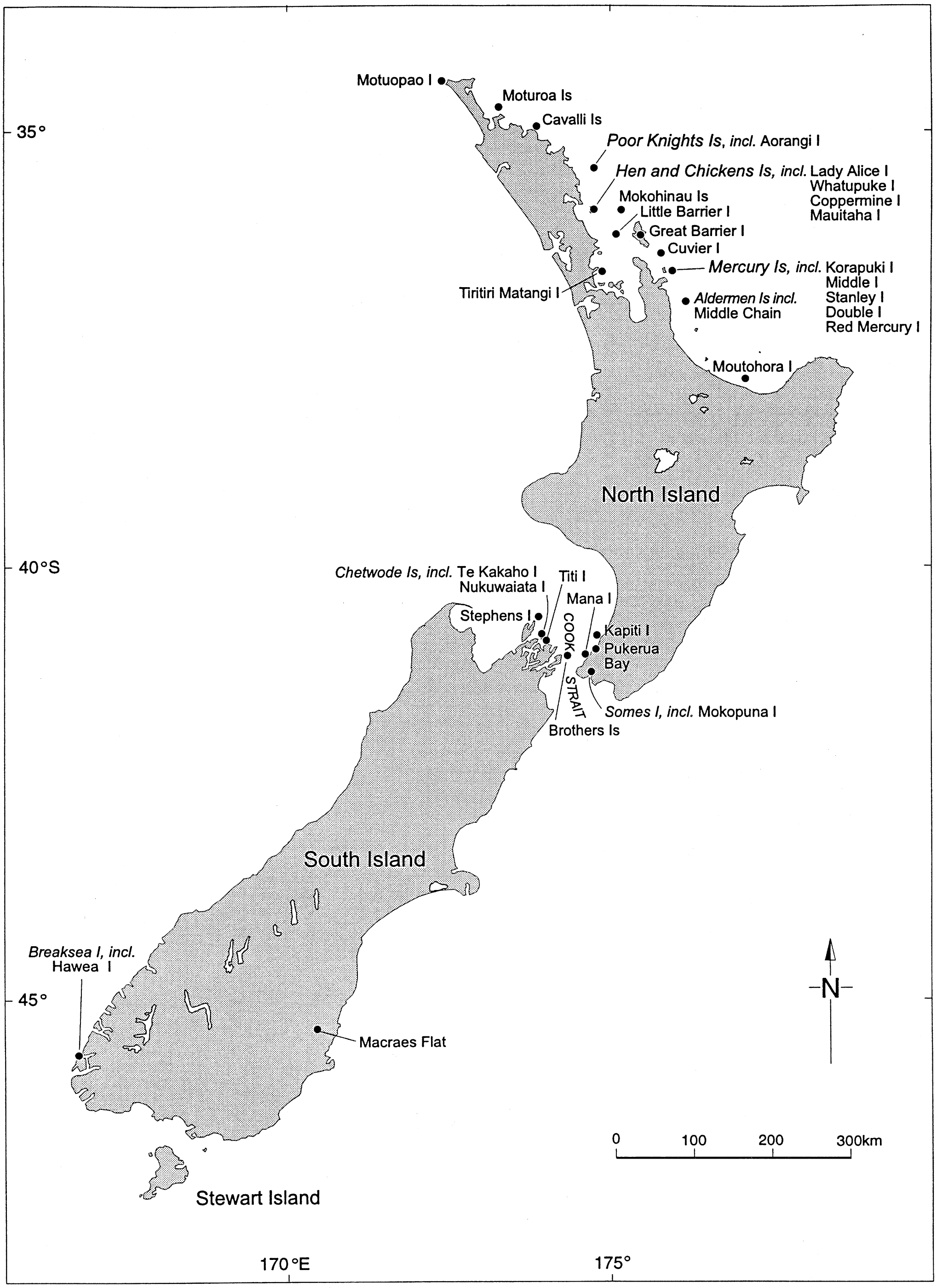

Fig. 1. Map of localities mentioned in the text and tables.

of geckos and 11 species of skinks (including at least six sympatric species of *Cyclodina*). Today tuatara are absent from these areas, and only four species of geckos and four or five species of skinks remain (a 56% reduction); and some of them, such as *Oligosoma suteri* and *Oligosoma moco,* are now confined to scattered, isolated sites (Towns and Daugherty, 1994).

The significance and origins of these relict island populations of reptiles were clarified with the application of genetic techniques, beginning in the early 1980s. Allozyme analysis of island populations of tuatara indicated very low levels of divergence among populations of the northern subspecies (*Sphenodon p. punctatus*) even though they were scattered through a range of 334 km. These analyses also confirmed likely subspecific divergence between a northern and southern (Cook Strait) form of tuatara and confirmed the existence of a previously described species (*S. guntheri*) comprising ca.

300–400 individuals confined to 4 ha North Brothers Island (Daugherty et al., 1990c; Thompson et al., 1993; N. Nelson, personal communication). Like tuatara, selected lizard species showed virtually no measurable allozyme divergence, even between island populations up to 500 km apart (Towns and Daugherty, 1994 and references therein). Allozyme analyses and studies using DNA have also enabled resolution of cryptic species complexes in skinks (Daugherty et al., 1990c; Hickson et al., 1992) and geckos (Hitchmough, 1997).

Understanding the origins of the island populations of lizards and tuatara has particular relevance to their conservation. The subfossil deposits have enabled documentation of range declines and, in some cases, indicate previous distribution patterns. The subfossil data have also enabled separation of primary endemics — derived from allopatric speciation in isolated locations — from secondary endemics (pseudoendemics) derived as relict survivors of range declines (Daugherty et al., 1990a; Towns and Daugherty, 1994). However, the genetic studies indicated *how* the scattered island populations were derived. Rather than originating on the islands by chance oceanic dispersal, the low levels of recorded divergence indicated that many species were once vicariantly distributed members of large gene pools subsequently isolated into subunits by rising sealevels during the last glaciation (Towns et al., 1997).

In sum, 10 years ago, the size, status and antiquity of the reptile fauna were being clarified and the extent of declines of tuatara and many lizard species (especially those on islands) were documented. However, the likely agents of decline were largely postulated through circumstantial comparisons of historic and present distributions and contemporaneous comparisons of islands with introduced predators compared with those without (Whitaker, 1978; Craig, 1986; Towns and Daugherty, 1994). Tests of these predictions — such as removal of pests from islands or defined land areas — appeared beyond reach, but this changed with a series of new initiatives beginning in the mid 1980s.

3. Management phase

3.1. Rodent eradication and recovery plans

Despite previous predictions of a tide of predators spreading to islands, there are now >90 islands from which predators have been removed (C.R. Veitch, personal communication). The earliest successes were with the largest organisms and included, by 1925, the removal of cats (*Felis catus*) threatening the tuatara population on Stephens Island. However, since the mid 1980s, attention has shifted towards the smaller, and more difficult, mice (*Mus musculus*), Norway rats, Pacific rats and ship rats (*R. rattus*), while also attempting their eradication over increasingly large islands (Towns and Ballantine, 1993). By 1998, rodents had been removed from at least 25 islands covering a total area of almost 4000 ha (Table 2). These campaigns against rodents have provided either measurable or potential benefits for tuatara, two species of *Naultinus* geckos and six species of *Hoplodactylus* geckos, five species of *Cyclodina* skinks and seven species of *Oligosoma* skinks. Aside from reducing threats of the further spread of rodents, these successes have demonstrated that preventative measures against rodent invasion can be instigated and that species previously extirpated can be reintroduced to areas from which predators have been removed.

Alongside recently improved pest management has been the initiation of recovery plans for threatened species. So far, five plans have been completed for nine of the 13 terrestrial reptiles requiring most urgent action (Table 1). Only two plans are for single species; the rest are for taxonomic groups (such as tuatara) or sympatric species (such as Otago and grand skinks). One plan is near completion for all twelve species of *Oligosoma* skinks. The New Zealand plans are not legally enforceable but instead are statements of intent — usually within a 5–10-year timetable. Such plans have the advantage of flexibility to respond to changing circumstances or improved data. The plans involving tuatara and lizards on islands have been particularly effective (Table 3) by defining technical advances needed in predator eradication, developing methods for successful hatching and raising tuatara for release onto islands, and re-establishing tuatara and skinks in *Cyclodina* on islands cleared of introduced predators (Towns, 1992). Some of these successes, and also intractable difficulties encountered with conservation of the threatened species, are described below in a series of case studies.

3.2. Rehabilitation and restoration of tuatara

In addition to revealing the existence of *Sphenodon guntheri*, genetic studies revealed divergence — consistent with previous subspecific distinctions on morphological grounds — between the northern populations of *Sphenodon punctatus* scattered among about 25 islands and the four southern populations on four islands in Cook Strait (Daugherty et al., 1990b). The vulnerability of *S. guntheri*, sporadic breeding success with *S. punctatus* in captivity (all originating from Stephens Island in Cook Strait), and the precarious status of eight populations of the northern subspecies on islands inhabited by Pacific rats, emphasised the need for management that took a national view of tuatara conservation (e.g. Cree et al., 1994). Consequently, the recovery plan for tuatara (Cree and Butler, 1993) sought to ensure the prevention of further extinctions of any populations of tuatara and the maintenance (and

Table 2
Islands in New Zealand from which introduced predatory vertebrates have been removed in order to protect reptiles, and the resident reptiles likely to benefit[a]

Pest and island	Area (ha)	Resident species of reptiles
Gallirallus australis		
Te Kakaho	81	*Hoplodactylus maculatus, Oligosoma lineoocellatum, O. zelandicum*
Mus musculus		
Mana	217	*H. chrysosireticus, H. maculatus, Cyclodina aenea, C. macgregori, Oligosoma nigriplantare polychroma, O. zelandicum*
Rattus exulans		
Mokohinau Islands (>7)	96	*H. duvaucelii, H. pacificus, C. aenea, C. ornata, O. moco, O. smithi. O. suteri*
Cuvier	170	*Sphenodon p. punctatus, H. maculatus, H. pacificus, C. aenea, O. moco, O. smithi, O. suteri*
Double	32	*H. duvaucelii, H. maculatus, C. aenea, O. moco, O. smithi, O. suteri*
Korapuki	18	*H. duvaucelii, H. maculatus, C. aenea, O. moco, O. smithi*
Lady Alice	155	*S. p. punctatus, H. duvaucelii, C. aenea, C. ornata, O. moco, O. smithi. O. suteri*
Middle Chain	23	*H. duvaucelii, O. moco*
Motuopao	30	*C. aenea, O. moco, O. smithi*
Red Mercury	225	*S. p. punctatus, H. maculatus, C. aenea, C. oliveri, O. moco, O. smithi, O. suteri*
Stanley	100	*S. p. punctatus, H. duvaucelii, H. maculatus, C. aenea, O. moco, O. smithi*
Tiritiri Matangi	196	*C. aenea, O. moco*
Whatupuke	102	*S. p. punctatus, H. duvaucelii, H. maculatus?, C. aenea, O. smithi, O. suteri*
R. exulans + G. australis		
Nukuwaiata	195	*H. duvaucelii, H. maculatus, O. lineoocellatum, O. zelandicum*
R. rattus		
Mokopuna	1	*O. lineoocellatum, O. n. polychroma*
Somes	26	*H. maculatus, C. aenea, O. lineoocellatum, O. n. polychroma*
R. norvegicus		
Breaksea	170	*O. acrinasum*[b]
Hawea	9	
Moutohora	143	*H. maculatus, C. aenea, O. infrapunctatum*
Titi	36	*H. maculatus, O. zelandicum, O. lineoocellatum*
R. exulans + R. norvegicus		
Kapiti	1970	*H. granulatus, H. maculatus, Naultinus elegans punctatus, C. aenea, C. ornata, O. n. polychroma, O. zelandicum*
Felis catus		
Stephens	150	*S. punctatus, H. maculatus, H. stephensi, N. manukanus, O. infrapunctatum, O. lineoocellatum, O. n. polychroma, O. zelandicum*
Sus scrofa		
Aorangi	110	*S. p. punctatus, H. duvaucelii, H.* sp. ("Poor Knights"), *C. oliveri, C. ornata, C.* sp. ("Poor Knights"), *O. moco, O. smithi, O. suteri*
Total	4255	

[a] All pest organisms identified here are introduced mammals except *Gallirallus australis* (weka), a native rail liberated by people on some islands. Distribution data from Pickard and Towns (1988), details of eradication methods and references in Veitch (1995). This list is a selection from at least 90 successful eradication campaigns on islands, but for many islands, benefits to reptiles have not been identified or their faunas have not been surveyed.

[b] Recolonised naturally.

possible enhancement) of all genetic stocks (subspecies or above). Achievement of these goals was assisted by successful hatching and rearing of tuatara artificially and the rehabilitation (the removal of existing threats) and restoration (reintroducing tuatara to historic sites) of populations on islands.

3.2.1. Hatching and rearing of tuatara

Critical answers to questions about breeding success and vulnerability came from intensive studies of reproductive biology and nesting physiology of tuatara. These studies revealed that few females (only about 8–46%) are gravid in any one year (Newman et al., 1994; Newman and Watson, 1985) because the females may take up to 4 years to produce a clutch of eggs (Cree et al., 1992). The eggs are also vulnerable to predation because they are laid in rookeries, sometimes over several nights during which time the eggs may be left exposed or only partly buried. In addition, eggs may be dug up and scattered by other females competing for the

Table 3
Recovery plans for New Zealand reptiles (data for tuatara provided by P. Gaze, personal communication)

Recovery plan	Author	Strategic achievements
Whitaker's and robust skink (*Cyclodina whitakeri, C. alani*)	Towns (1992)	Eradication of Pacific rats from Stanley and Red Mercury Islands Three new populations of Whitaker's skinks and four new populations of robust skinks on islands freed of rats Completed ecological study of mainland population of Whitaker's skink New goals developed in *Cyclodina* skink plan
Chevron skink (*Oligosoma homalonotum*)	Towns and McFadden (1993)	Completed surveys of Little Barrier Island Major study commenced on habitat use and potential for predator control
Tuatara (*Sphenodon punctatus, S. guntheri*)	Cree and Butler (1993)	*S. p. punctatus* Successful captive breeding of four populations threatened by rats Removal of rats from five (possibly six) of the nine islands where they threatened tuatara Eradication of rats from four additional islands/island groups within the historic range of tuatara and to which they can be reintroduced Repatriation of one population following removal of rats and reintroduction of a second where recorded historically New research on rat-tuatara-seabird interactions New research on diets of tuatara on islands inhabited by seabirds
		S. guntheri Successful incubation and rearing in captivity Introduction of new population to island freed of rats
Otago and grand skinks (*Oligosoma otagense, O. grande*)	Whitaker and Loh (1995)	Purchase of two new reserves in native tussock grassland Completion of study on effects of agricultural development Completion of study on mark-recapture techniques Commencement of major study on effects of grazing and predation
Striped skink (*O. striatum*)	Whitaker (1998)	Commencement of studies on vulnerability to cutaneous water loss

same nest site (Cree and Daugherty, 1990). These studies and detailed work on physiological effects of the nest environment in the field (Thompson et al., 1996), enabled development of artificial egg incubation methods (Thompson, 1990) and set the scene for the effective management to follow.

Studies of Stephens Island *S. punctatus* showed that egglaying can be induced using the hormone oxytocin (Thompson et al., 1991), and the eggs raised in incubators with high hatching success (Thompson, 1990). The eggs have been incubated in vermiculite at −400 kPa in temperatures ranging from 18 to 23°C, and hatching success ranged from 85.7 to 92.2%. Like some other oviparous reptiles, both species of tuatara show temperature-dependent sex determination. At an egg incubation temperature of 18°C, hatchlings are female, but there is a tendency towards males at warmer or fluctuating temperatures that reach >22°C (Cree et al., 1995b).

3.2.2. Rehabilitation and restoration

The 25 populations of northern tuatara were estimated at about 10 000 individuals, probably one quarter of the size of the southern subspecies on Stephens Island (Cree et al., 1994). The lower number of northern tuatara reflects the predominance of the subspecies on small islands (the exceptions being two populations in the Poor Knights Islands), and recruitment failure on the remaining large islands, all of which were inhabited by Pacific rats (Cree et al., 1995a), a species known to feed on young tuatara (Newman, 1988). Since 1990, three initiatives have changed the prospects for most of these populations.

First, Pacific rats have been eradicated from five of the nine islands where they co-existed with tuatara and on a sixth (Coppermine Island) the campaign against Pacific rats is still under way (Table 4). The two largest islands, Hen and Little Barrier, are probably within the capabilities of existing eradication methods and an attempt at eradication of Pacific rats from Little Barrier Island is likely within the next five years (Anon., 1995). Before eradication of rats was attempted on Red Mercury, Stanley and Cuvier Islands (the smallest relict populations), all tuatara that could be captured were removed and held in captivity. Although some individuals appeared post-reproductive (Cree et al., 1994), all

Table 4
Management of island populations of tuatara (*Sphenodon* spp.) that have indicated recruitment failure, with estimates of population sizes from Cree and Butler (1993)

Location (ha)	Estimated population	Action	References
Sphenodon punctatus			
Lady Alice (155)	Up to 1000	Pacific rats eradicated 1994	Towns (2000)
Mauitaha (26)	< 5	Nil	R. Pierce (personal communication)
Whatupuke (102)	Few hundreds	Pacific rats eradicated 1993	Towns (2000)
Coppermine (80)	Low hundreds	Pacific rat eradication failed 1992 Eradication attempted 1997	
Hen (500)	Low hundreds	Nil	
Little Barrier (3083)	Few tens	Successful captive breeding in rat-proof enclosure on site	
Cuvier (170)	< 10	Six adults removed, breeding in captivity Pacific rats eradicated in 1993	Towns et al. (1995)
Stanley (100)	Few tens	Fifteen adults removed, breeding in captivity Pacific rats eradicated in 1991	Towns et al. (1993)
Red Mercury (225)	Few tens	Eleven adults removed, breeding in captivity Pacific rats eradicated in 1992 12 juveniles (captive bred) and nine adults repatriated in 1996	Towns et al. (1994), G. Ussher (personal communication)
Moutohora (173)	Historic only	Norway rats eradicated in 1986 32 adults reintroduced from neighbouring Moutoki Is in 1996	Owen (1998), G. Ussher (personal communication)
Sphenodon guntheri			
Titi (32)	?	Norway rats eradicated in 1975 50 juveniles (captive bred) and 18 wild adults released in 1995	N. Nelson (personal communication)

tuatara populations have now produced viable clutches of eggs.

Second, through artificial incubation and collaboration by several New Zealand zoos and other institutions (including a museum and wildlife parks), young tuatara have been, or are being, raised in captivity. For example, 10 young tuatara from the Cuvier Island population (from six adults) are now being raised in captivity (M. Bell, personal communication). Similarly, should Pacific rats be successfully removed from Little Barrier Island, there is now an expanding population of young tuatara derived from eggs laid by the few remaining adults at present occupying an 18×12.2 m rodent-proof "tuatarium" on the island. The eggs have been artificially incubated and the hatchlings raised in captivity. Repatriation of tuatara removed from islands previously inhabited by rats is now under way. The first release was of nine adults and 12 juveniles returned to Red Mercury Island in 1996, and the return of tuatara to Stanley and Cuvier Islands is planned within the next 5 years.

Third, tuatara have been reintroduced to Moutohora Island as a site where there are only historic records of their presence (Owen, 1998). The establishment of new populations has also been attempted for *S. guntheri* on Titi Island, where both wild caught adults and captive reared juveniles have been released.

In total, the existing successful eradications of rats have provided over 1000 ha of useable habitat for northern tuatara. Should *S. guntheri* successfully establish on 32-ha Titi Island, this too would represent a significant increase over the <4 ha of habitat presently occupied on North Brother Island (Cree et al., 1991; Thompson et al., 1992).

3.3. Rehabilitation and restoration of lizards on islands

Several eradications of introduced mammals have been undertaken in which lizards were viewed from the outset as the primary beneficiaries. Amongst these was the eradication of Pacific rats (in 1986) and rabbits, *Oryctolagus cuniculus*, (in 1987) from Korapuki Island (Table 2). By studying the response of resident shoreline lizards (using rocky beach habitats not affected by rabbits), the likely effects of Pacific rats on resident lizards were determined.

3.3.1. Rehabilitation of resident lizards

The species showing the most rapid response to removal of rats was the shore skink *Oligosoma smithi*. Shore skinks are small (usually <10 g), diurnal lizards that commonly persist on islands invaded by rodents. However, when rats were removed from Korapuki Island, the capture frequency of shore skinks increased by up to 3600% over 9 years (Towns, 1994; unpublished data). The rates of increase and the capture frequencies varied by location on Korapuki Island and depended on the size of the rocks and stones along the beaches. Some of the most rapid changes in capture frequency were found where rocks were large (> 25 cm length). Changes here reflected movement of adults (especially pregnant females) into what appeared to be favourable basking sites (Towns, 1996). The variable responses of shore skinks to habitat availability by site, size and sex, indicate previous selective effects of Pacific rats related to their ability to penetrate interstices between rocks. The larger the rocks, the larger are gaps between them, and the more vulnerable to predation by rats the lizards are likely to be. Since the larger geckos and skinks inhabit the sites with largest rocks, it is hardly surprising that these species are often the ones missing from islands inhabited by introduced predators (Towns, 1996). However, the work has also shown that the effects of invading rats on islands can be predicted to some extent by assessing the quality of refuge sites available to resident lizards.

3.3.2. Restoration of extirpated lizards

Removal of rodents from islands has enabled the re-establishment of 12 species of lizards as part of island restoration exercises (Table 5). The first of these was on Korapuki Island. Three *Cyclodina* skinks, all nocturnal ground-dwelling species, are present on rat-free Middle Island, but apparently died out on neighbouring Korapuki Island. The rarest of these species, and the first New Zealand lizard deliberately reintroduced, was Whitaker's skink (*C. whitakeri*).

Whitaker's skink is nocturnal and lives in seabirds burrows, amongst tree roots or between rocks. It appears highly sensitive to ambient conditions (being rarely captured at temperatures below 15°C), and may have a clutch size averaging two offspring produced biennially (Towns, 1994). As of 1988, Whitaker's skinks were known from two islands near Korapuki Island, and a bouldery talus slope on the mainland North Island about 500 km further south. The combined area of these three locations was less than 20 ha.

Twenty-eight Whitaker's skinks were released from Middle Island onto Korapuki Island between 1988 and 1990. Although the animals' condition factor (weight versus snout-vent length) on Korapuki was significantly higher than from two other populations, expansion rates for the Korapuki population in the first 5 years were estimated as only 5–9% per annum (Towns, 1994). The main impediment to more rapid expansion appears to be the low annual reproductive output of one per female. This is offset by longevity of adults; 10 years after release adults originally from Middle Island are still present on Korapuki Island at ages of at least 16 years (Towns and Ferreira, in press). However, even if adults live 20 years, total life-time productivity of these lizards may be only 16 offspring (Towns, 1994). Low productivity and high longevity are risky strategies when faced with efficient predators such as rats (Daugherty et al., 1993), but this strategy is found in tuatara and many threatened geckos and skinks from New Zealand (Cree, 1994). These characteristics need to be considered in the design of reintroduction attempts because of extended periods where the new populations are at risk of failure, as well as the long periods required before success can be determined.

3.4. Habitat management on the mainland

The tuatara and many lizards, whose populations are now increasing on islands, were once inhabitants of the mainland. Unlike islands, where threat *removal* may be an option, the mainland North and South Islands present problems of threat *control* which can be site-specific and difficult to resolve. Two examples are provided below.

3.4.1. Conservation in an "urban" refuge: Pukerua Bay

A 12.3 ha area of reverting coastal scrub and forest on the mainland at Pukerua Bay on the southern North Island (Fig. 1) is inhabited by a species of gecko and four species of skink, including the only mainland population of Whitaker's skink. The core Whitaker's skink habitat is a bank of greywacke boulders, bound by the native scrambling liane *Muehlenbeckia complexa*.

Table 5
Translocations of lizards to islands as part of ecological restoration programmes after removal of rodents

Island	Year commenced	Species	Reference
Hawea	1988	*Oligosoma acrinasum*	Thomas and Whitaker (1995)
Korapuki	1988	*Cyclodina whitakeri; C. alani, C. oliveri, O. suteri*	Towns (1994, 1999)
Lady Alice	1997	*Hoplodactylus pacificus, Cyclodina* sp. ("Mokohinau"), *C. macgregori*	Towns (1999)
Mana	1998	*H. duvaucelii, Naultinus elegans, O. lineoocellatum*	C. Miskelly (personal communication)
Motuopao	1997	*H.* sp. ("Matapia"), *C. alani*	Towns (1999), R. Parrish (personal communication)
Red Mercury	1994	*C. alani, C. whitakeri*	Towns (1999)
Stanley	1995	*C. alani, C. whitakeri*	Towns (1999)

The whole area was grazed periodically by sheep (*Ovis aries*) until 1987, when they were excluded by a stock-proof fence. The site is adjacent to Pukerua Bay township and is now a gazetted Scientific Reserve.

A 6-year intensive study of the site from 1983 indicated that the number of Whitaker's skinks was critically low: an estimated 260–330 animals in no more than 0.5 ha (Towns and Elliott, 1996). Threats to this population came from grazing, predation and fire (Fig. 2).

Threats from grazing involved direct and indirect erosion of the boulder slopes occupied by Whitaker's skinks. Direct erosion was caused by sheep walking over the slopes, and indirect erosion through sheep grazing which reduced the capacity of *Muehlenbeckia* to stabilise the boulders. The more destructive effects of grazing were in large part resolved by construction of the fence, but this did not overcome occasional incursions by goats (*Capra hircus*) and the problems caused by resident populations of Australian brush-tailed possums (*Trichosurus vulpecula*) and rabbits.

Predator guild manipulations in dynamic environments represent singular challenges and may lead to unforeseen outcomes (Towns et al., 1997). At Pukerua Bay, the presence of rabbits is likely to encourage cats from the neighbouring township into the areas occupied by lizards. Cats in New Zealand feed on rabbits (Fitzgerald, 1988) but can also be voracious predators of lizards (Daugherty and Towns, 1991; E. Murphy, personal communication). Cats and weasels (*Mustela nivalis*) are probably also attracted to the area by a large population of mice, which undergoes periodic irruptions (Towns and Elliott, 1996), when seed and invertebrates

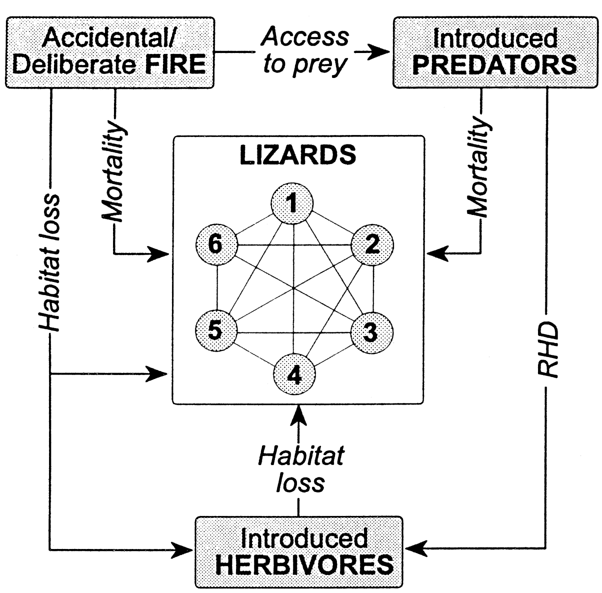

Fig. 2. Schematic summary of various influences of land management on a hypothetical lizard assemblage of six species (numbered). Lines between species imply direct or indirect interactions.

in rank pasture become particularly abundant (Newman, 1994). Mice also prey on lizards (Newman, 1988; 1994). Predation of Whitaker's skinks by weasels at Pukerua Bay has now been documented (Miskelly, 1997). One solution could be to lay anticoagulant poison against mice (C. Miskelly, personal communication), thereby reducing the site's attractiveness to weasels. The toxins may also reduce weasel numbers through secondary poisoning via "toxic" mice (e.g. Alterio, 1996, Alterio, et al. 1997). Unfortunately, secondary poisoning could affect the neighbours' domestic cats, and a sudden reduction in mouse numbers could lead to prey switching by predators with an increased impact on lizards.

Fire is the third problem and is a function of human population pressure (the site is part of a popular coastal walk), reduced grazing, rank grass and a proliferation of woody coastal shrubs (Towns and Elliott, 1996). The risks from fire have been reduced somewhat through regulated fire bans.

Whitaker's skinks at Pukerua Bay remain in a parlous state. The species once probably inhabited seabird burrows and root tangles in coastal forest and was part of a much larger fauna of reptiles that included tuatara. The forest has largely been removed, and the burrowing petrels, shearwaters and tuatara have long since been extirpated from the mainland by predators. The talus slope presently inhabited by Whitaker's skinks apparently provides thermal conditions that mimic those of burrows (Towns and Elliott, 1996), while also providing a refuge that predators find difficult to penetrate. However, there is limited capacity for the skinks to expand into similar habitat elsewhere in the area, and if they leave the deep boulders, they are likely to be preyed on by cats, weasels, mustelids and rodents. If the species is to survive at this locality, the area is going to require indefinite high levels of habitat management and innovative public relations programmes that involve the local community. The need for such initiatives was identified in a Whitaker's skink recovery plan (Towns, 1992), but to date it is one aspect of the plan that has seen little progress (Towns, 1999).

3.4.2. Conservation in a rural setting: Macraes Flat

Although reptile faunas in the North Island have been severely depleted by predation, there are some locations in the South Island where lizard assemblages appear to be relatively intact (Towns and Daugherty, 1994). One of these is on and amongst extensive outcrops of fractured schist rock in middle altitude (500–600 m.a.s.l) native tussock (*Chionochloa rigida*) grassland on the eastern South Island. At Macraes Flat (Fig. 1), these scattered sites are inhabited by an undescribed *Hoplodactylus* gecko and up to six species of *Oligosoma* skinks. The two largest skinks, *O. grande* (up to 27.0 g) and *O. otagense* (up to 45.0 g) (Coddington and Cree, 1997), are threatened species now restricted in distribution to about 8% of their potential former range (Whitaker and Loh, 1995). The species in *Oligosoma* are to some degree separated by habitat, with *O. chloronoton* predominantly amongst grassland in damp valleys, *O. otagense* on bluffs and canyons near streams, *O. grande* and *O. maccanni* on exposed outcrops, *O. nigriplantare polychroma* widespread in grassland and *O. inconspicuum* widely distributed in damp, well vegetated sites (Towns et al., 1985; A.H. Whitaker, personal communication; see also Patterson, 1992).

Conservation of such lizard assemblages presents particular difficulties. There is no habitat occupied by *O. grande* and *O. otagense* that remains unmodified by farming, so it is not possible to identify historic community composition and levels of abundance as management targets. In addition, why the range of some species has declined remains unclear. Threats to the lizards at Macraes Flat resemble those at Pukerua Bay (Fig. 2) but differ in detail and history.

Within the range of *O. otagense* and *O. grande*, traditional landuse over the past century was extensive pastoral farming of sheep and cattle (*Bos taurus*) in native grasslands which were burned periodically to encourage growth of more palatable shoots. The frequency and intensity of the fires has varied, so their direct effects on lizards inhabiting rock outcrops remain unclear, but some grassland species of skinks showed 28% reduction in abundance after a low-intensity burn (Patterson, 1984). The fires almost certainly changed the character of vegetation cover, and in combination with grazing may have greatly reduced the extent of shrubby vegetation, the fruits of which are eaten by *O. otagense* and *O. grande* (Whitaker, 1987). Over the last 15 years, land management has changed to ploughing and/or fertilising and oversowing of native grasses with exotic species, and higher densities of stock. This has further reduced the shrub component, reduced the density of ground cover against predators (Coddington and Cree, 1997), and encouraged increased stock to shelter near outcrops where they further modify the remaining native vegetation (Whitaker and Loh, 1995), possibly resulting in densities of *O. grande* lower than in adjacent native grassland (Whitaker, 1996).

The effects of fires and grazing can be investigated by manipulating grassland management, and this is now possible through the purchase of key areas of grassland habitat (Table 3). However, responses by the guild of introduced predators to these changes remain uncertain. Rabbits, cats, rats, mice and mustelids are all present in this area, and increased cover of tussock, leading to periodic high levels of seed production, may encourage irruptions of mice, with onstream effects similar to those identified for Pukerua Bay. One recent complication was the widespread clandestine release of rabbit haemorrhagic disease (RHD). If rabbit predator densities are high, sudden declines in rabbit abundance following infections of RHD could lead to prey switching from rabbits to lizards (Fig. 2).

Periodic population estimates of *O. otagense* and *O. grande* at a series of sites have indicated no evidence of population declines over 8 years (Coddington and Cree, 1997). However, even in the most productive sites, the densities of *O. otagense* and *O. grande* were only 186/ha and 350/ha respectively, on rock (Coddington and Cree, 1997). At such low densities, and given the annual reproductive output of female *O. otagense* and *O. grande* of only 2.34 and 2.17, respectively (Cree, 1994), it is conceivable that efficient predators (such as cats) could depopulate entire discrete areas (e.g. Whitaker and Loh, 1995).

In sum, although there are many similarities between the threats to the *Oligosoma* skinks of Macraes Flat and those facing the Whitaker's skinks at Pukerua Bay, there is greater potential for in situ conservation at Macraes Flat. First, there are at least vestiges of native habitat (grasslands) and extensive rocky areas that are either occupied now by the large *Oligosoma* skinks, or that could be occupied in the future, given appropriate land management. This is not the case at Pukerua Bay, where Whitaker's skinks, by good fortune, have located a habitat refuge but from which there is limited capacity to expand. Second, populations of the *Oligosoma* skinks have survived at Macraes Flat despite the presence of a guild of predators, fires and changes in land use. These populations are probably still large enough to produce measurable responses to experimental habitat management. By comparison, Whitaker's skinks persist under constant threat from fire and predators and the population is so small, that their responses to habitat manipulation cannot be measured (Towns and Elliott, 1996). On the other hand, Whitaker's skinks are being effectively managed on islands from which predators have been removed, and there are prospects for considerable reduction in their vulnerability to extinction (Towns, 1999). In contrast, habitats equivalent to Macraes Flat do not exist on islands. There is no second option for these large South Island *Oligosoma* species or for the ecosystems they inhabit. They must be effectively managed in a rural, mainland context if they are to survive in the wild.

4. Conclusion

The terrestrial reptile fauna of New Zealand is extraordinary because of the survival of an ancient Order represented by tuatara and because of an endemic and unusually diverse fauna of lizards. When its present recovery plan was completed, tuatara had already received the benefits of almost 100 years of strict protection. However, the decline in populations of tuatara between 1895 and 1984 clearly demonstrated that protection without identification and resolution of agents of decline (Caughley, 1994) can result in a sinking lid for the species (Daugherty et al., 1992). Raised prospects for the group came with recent shifts to more aggressive and effective habitat management, removal of predators and propagation in captivity. These shifts were made possible through information provided by genetic, environmental, physiological and behavioural research, a change of focus in the captive breeding community from reptiles as display items to one of husbandry for conservation (Cree et al., 1994), and by changes in legislation that combined previously fragmented responsibilities for habitat and species protection under one agency: the New Zealand Department of Conservation (Daugherty et al., 1992).

The tuatara and many lizard species have benefited from aggressive island restoration projects involving the removal of a range of introduced pests. However, the eradication campaigns reviewed here are only those confirmed as successful. Rodent eradications are either recently completed or are planned for some very large islands. For example, a campaign in 1996 against *Rattus exulans* and *R. norvegicus* on 1970 ha Kapiti Island appears to have been successful (I. McFadden, personal communication), and campaigns on islands of up to 3000 ha are planned. Given the successes to date, there are prospects for considerable increases in abundance of tuatara and lizards on many islands.

Frequently, the removal of problem organisms from islands is the beginning, rather than the end, of a slow and complex process of habitat restoration with uncertain outcomes (Simberloff, 1990; East et al., 1995). For example, following the release of Whitaker's skinks on Korapuki Island, 9 years of monitoring were required before there was robust evidence that the population was expanding (Towns and Ferreira, in press). Field studies of the biology of this and other New Zealand reptiles indicate that tuatara, Whitaker's skinks and large geckos such as *Hoplodactylus duvaucelii* have such low female annual reproductive output (Cree, 1994), that population expansion rates may be less than 10% per annum (Towns, 1994). A population viability analysis (VORTEX) predicted that without predation, density-dependent effects or possible competitive effects from related species, Whitaker's skinks could take up to 70 years to reach a modest density of around 650/ha in 15 ha of habitat on Korapuki Island (Towns, unpublished data). With other biotic and abiotic influences factored into the simulations, tuatara and some lizards reintroduced to large islands from which predators have been removed may take centuries — and possibly millennia — to reach carrying capacity (N. Nelson, personal communication).

Predators that may have extirpated tuatara and lizards from islands may also have destroyed large ground-dwelling invertebrates, including weta (Orthoptera: Stenopelmatidae) and darkling beetles (Coleoptera: Tenebrionidae) (Towns et al., 1997). These flightless species are amongst the most common prey for tuatara (Walls, 1981) and some large lizards (I. Southey, unpublished data). Comprehensive, long-term restoration projects that include invertebrates as well as vertebrates are now under way in New Zealand and should eventually result in a resurgence of complex plant–invertebrate–reptile–seabird island systems (e.g. Towns et al., 1990; Miskelly, 1997). We estimate that these island rescue projects could result in at least some expanding populations for 56% of the rarest New Zealand reptiles identified in Table 1.

The biggest challenges rest with the remaining 44% confined to the mainland and which lack habitats on islands. An example is the black-eyed gecko (*Hoplodactylus kahutarae*) found only in the northern South Island on rock bluffs in alpine areas above 1000 m in elevation (Whitaker, 1984). The species inhabits extraordinarily difficult terrain in locations with a harsh and unpredictable climate. Determining their status — before clarification of management options — will require many years of effort.

The conservation programmes for reptiles on islands may provide information applicable to situations on the mainland. For example, removal of predators from islands can provide experimental tests of predictions that rare species on the mainland are restricted in abundance by pressure from introduced predators. However, even if these predictions are verified, the Pukerua Bay example indicates that solutions could raise their own problems of unpredictable indirect effects to the neighbours' domestic animals. Nonetheless, studies with declining endemic birds such as kokako (*Callaeas cinerea*) have shown that intensive localised control of predators can have dramatic effects on nestling survival and ultimately population density (Innes et al., 1999). At present, the emphasis of such projects for birds is on reducing the intensity of control to minimise costs. So far, there have been no studies to determine the levels of predator control required to produce measurable responses in resident lizards. The work on islands indicates, however, that the intensity of predator management required for lizards may be even higher — therefore more expensive — than is presently applied to birds.

Nonetheless, management of introduced organisms should have positive results in parts of the South Island where lizard assemblages appear to be largely intact, but affected by decades of predation and habitat modification. There are thus optimistic prospects for the assemblage of *Oligosoma* skinks at Macraes Flat, either in situ or in locations where these species were almost certainly present, and improved habitat quality could enable their return. Bleaker prospects face the highly fragmented lizard faunas of the mainland North Island, where about half of the previous members are now confined to islands. Even so, there is hope that some of these may eventually be restored from islands to the mainland (Towns, 1999) following innovative new approaches to predator management such as protecting discrete forest areas with predator-proof fences and fencing the base of peninsulas, then managing them as insular ecosystems.

Conservation of New Zealand reptiles has thus undergone a shift from absolute protection of species — characterised by Daugherty et al. (1992) as benign neglect — to aggressive management, including restoration of island ecosystems. Perhaps the next wave of achievements will be applying the lessons learned on islands, and largely away from the public view (Mansfield and Towns, 1997), to easily accessible sites on the mainland. Such a move to management of mainland ecosystems may represent higher risks than on islands, but for many species there are no other choices. Future initiatives are also likely to involve partnerships between Government agencies and private landowners or Maori groups (Mansfield and Towns, 1997), such as the existing co-management agreement between the Department of Conservation and Ngati Koata on Stephens Island (Anon., 1994). But if these projects are to enjoy stable funding, some at least will need to be conducted where they either demonstrate to the public effective management or provide opportunities for the public to participate in rare reptile conservation.

Acknowledgements

We wish to thank Keri Neilson, Don Newman, Mandy Tocher and Tony Whitaker for their useful comments on the manuscript, Jaap Jasperse for editorial assistance, and Nicki Nelson and Graham Ussher for making available the results of their postgraduate studies. The manuscript was improved by referees' comments from Ian Atkinson, Craig Miller and Mike Thompson.

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