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Changes in the population size of North Island weka (*Gallirallus australis greyi*) during establishment on Pakatoa Island, Hauraki Gulf, New Zealand

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Abstract Thirty-one North Island weka (*Gallirallus australis greyi*) were released on Pakatoa Island (26 ha), Hauraki Gulf, New Zealand in Aug 1996. The population then fluctuated between *c.*19 and 182 individuals, including *c.*6-55 pairs. The last of the translocated weka died between Jan and Jun 1998, during a drought and after the rodenticide Talon® was laid to kill Norway rats (*Rattus norvegicus*), and only weka <1 year old survived. Most young raised in Dec 2001-Jan 2002 died during a drought in Feb - Mar 2002. The weka population increased during a period of higher rainfall from mid-1998 to Dec 2001. The higher population resulted in smaller home ranges, higher frequencies of diurnal spacing calls, more aggressive behaviour, and a higher incidence of plumage damage. The large fluctuations in population size on Pakatoa I suggests that future translocations of weka should select islands with wetter and less variable rainfall patterns

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INTRODUCTION

The weka (*Gallirallus australis*) is a flightless forest-dwelling rail, endemic to New Zealand. Historically, weka occurred on New Zealand's 3 main islands and on D'Urville I (Buller 1888; Oliver 1955), and they have been deliberately released on many smaller islands by Maori and Europeans as food during muttonbirding or for ship-wrecked sailors (Guthrie-Smith 1936; Wilson 1979; St. Clair & St. Clair 1992).

Weka currently inhabit at least 37 islands of < 30 ha around Stewart Is, off Fiordland and in the Marlborough Sounds (Beauchamp *et al.* 1999), and have survived on islands of <40 ha, e.g., Jacky Lee, Herekopare, Taumaka, for >70 years (Guthrie Smith 1914; Wilson 1959; Stirling & Johns 1969; Beauchamp *et al.* 1999). Wilson (1959) attributed a substantial increase in the density of weka on Jacky Lee I (30 ha, near Stewart I) between 2 visits 8 years apart to the absence of harvesting by muttonbirders. St. Clair and St. Clair (1992) reported "unusually high densities" and "squabbling" among territorial weka on Taumaka I (West Coast, South I) in the absence of harvesting. Both islands have stable, moist climates, deep leaf litter, friable soils enriched with seabird guano, and support dense invertebrate populations, and both have productive inter-tidal zones (Wilson 1959; St. Clair & St. Clair 1992).

Weka released on drier, larger, northern islands have not persisted. Populations introduced to Kawau and Urapukapuka Is died out within 30 and 20 years, respectively (Buller 1892; Edgar 1972; Robertson 1976; Beauchamp 1988). The reasons for these extirpations are unknown.

The North Is weka (*G. a. greyi*) is recognised as nationally vulnerable, and among the objectives of the Department of Conservation's weka recovery plan is further weka releases to islands (Beauchamp *et al.* 1999). Pakatoa I (33 ha; 36°46'S, 175°11'E, in the Hauraki Gulf), from which, in 1996, it was believed Norway rats (*Rattus norvegicus*) had been eradicated,

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was chosen as an island on which to release captive-raised weka. Pakatoa I had no known threatened plants, invertebrates or lizards likely to be at risk from weka introduction. It was hypothesised, using data from a population study of weka on Kawau I (Beauchamp 1997a, *unpubl. data*; Beauchamp & Chambers 2000), that Pakatoa I would: (i) hold *c*.30 adult weka during dry periods, but more adult weka at other times; (ii) that breeding birds would be restricted to areas of vegetation cover (Bramley 1994; Beauchamp *et al.* 2000) and would comprise pairs with overlapping home ranges (A.J. Beauchamp, *unpubl. data*); (iii) that the sub-adult and non-paired adult weka would be more visible and more mobile than paired adults; (iv) that food supplies would not be defended because sources, like Moreton Bay figs (*Ficus macrophylla*), were patchily distributed and able to be used by non-paired birds (Beauchamp 1987a), and other foods, like worms, would not be sufficiently predictable and defendable; and (v) that aggression between weka of all ages would be restricted to parents defending dependent young, as had been found in other studies of populations with overlapping home ranges (A.J. Beauchamp *unpubl. data*; Bramley 1994).

We report on the establishment of a weka population on Pakatoa I, the accuracy of the population biology and density predictions, and how weka behaviour changed in response to variations in population density. We also assess the potential effects of climatic conditions at the times of rapid population changes.

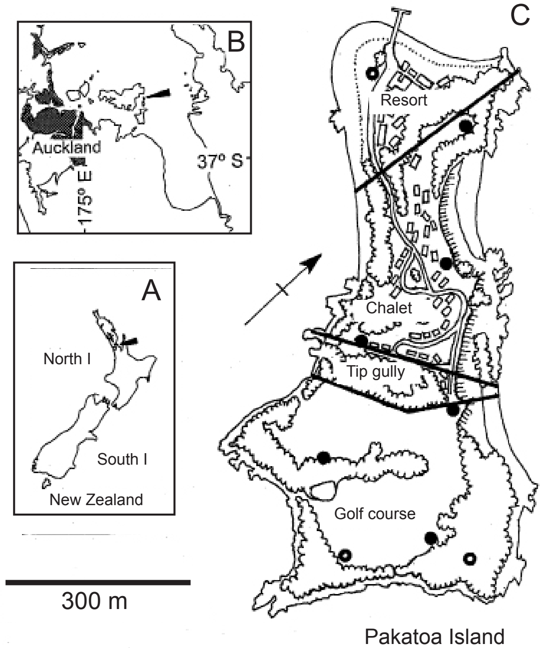

Fig. 1. Location of Pakatoa I, **A**, within New Zealand, and **B**, within the Hauraki Gulf. **C**, detail of island, with zones and locations of spacing call counts: filled circle, principal counts; open circle, occasional counts.

METHODS

Study site

Pakatoa I comprised a tourist complex, golf course, beaches, bush, regenerating fern, and shrubland (Fig. 1). The north-western end of the island had the main facilities of the resort and a road ran from this to the centre of the island where scattered palms (*Phoenix reclinata*) and Moreton Bay figs grew. An organic waste tip and recycling centre was located in a gully below the main water tanks. Norway rats were observed here on 17 Nov 1997 and a rodent poison, Talon®, was laid from late Dec 1997 to Jun 1999. A 9-hole golf course was maintained in the south-west and a pond was established in the lower reaches of a forested gully in 1995 to supply irrigation for the golf course. The golf course grass was cut short throughout the study, while the surrounding steep bluffs were retained in coastal bush and rank kikuyu (*Pennisetum clandestinum*). Irrigation of the golf course ceased when the resort closed in 2001.

Field methods

On 3 Aug 1996, 4 captive-reared adults (2 ♂♂, 2♀♀), 25 sub-adult (12 ♂♂, 13 ♀♀), and 2 wild-reared adults (1 ♂, 1 ♀) North I weka, originally from Kawau I, were released on Pakatoa I. All adults were birds retired from a captive rearing programme and others had been held in aviaries for up to 8 months (G. & E. Staples, *pers. comm*.). All weka released were fitted with numbered stainless steel leg bands and unique colour-band combinations. Some weka bred on the island were colour banded: 10 in Jul 1999; 2 in Dec 1999; 9 in Dec 2000; and 13 in Dec 2001.

The identity, activity, and breeding success of pairs was checked during 11 visits from 31 Aug- 1 Sep 1996, 12-13 Oct 1996, 9-10 Dec 1996, 18-19 Mar 1997, 7-8 Nov 1997, 17-19 Nov 1998, 25-29 Jul 1999, 10-12 Dec 1999, 1-3 Dec 2000, 14-16 Dec 2001, and 26-28 Apr 2002. Count methods were established during the 1st visit and full census information was collected during all subsequent visits. JH and RH were present during all visits and AJB present on the 1st 2 visits and then all visits after 1998.

Daily rainfall and soil moisture deficit data were taken from a weather station 7 km to the east of Pakatoa I, on nearby Waiheke I. These data were used to identify drought periods (defined as ≥15 days with <0.1 mm rain each day), and dry spells (rainfall did not exceed 1 mm on each of 15 consecutive days; Mosley & Pearson 1997). Severe drought or dry periods were defined as those when the soil moisture deficit index exceeded 120 (0, wet;

150, dry). On Kawau I, a soil moisture deficit index of 120 coincided with a period when humus under leaf litter in a gully dried out, and weka could not locate earthworms. The patterns in soil moisture deficit were assessed in relation to predicted lower rainfall and lower temperatures accompanying intense El Niño conditions, and greater incidence of north-easterlies and higher rainfall during La Niña conditions in the Hauraki Gulf (Mullan 1996; McKerchar *et al.* 1997).

Population census and composition

During each visit, we searched all the grass margin on the upper part of the island and the beaches for weka sign and corpses. From 1998, all the main bush areas were checked for weka sign: AJB collected weka faeces and estimated ages of young birds seen.

The number and composition of pairs was established from our observations of the movements and behaviour of banded and unbanded individuals (Beauchamp 1987a). The location of sightings of uniquely marked adults and sub-adults were mapped relative to land-marks, such as numbered chalets and trees. The movements of all colour-banded and uniquely plumaged sub-adult weka were plotted. Unique plumage characters included neck and head crests, more pronounced frontal bands, unusually pale plumage, and unusual tail or wing feather breaks or markings. Other identifying features included limps or foot deformities, unusual leg colour patterns, and dark brown irides.

All weka were counted and mapped at least 4 times a day in the grassed chalet area (Fig. 1) from Jul 2000, and their age, pair status, and sex were recorded. Elsewhere, the number of non-paired weka was established by mapping observations and then assigning the maximum number of weka seen on each trip. On the golf course, the maximum number of non-calling weka seen at dusk was used to estimate the number of non-paired weka.

The numbers of pairs and lone adult weka were estimated during each visit by mapping the pairs with dependent young, the locations of adults giving spacing calls during the day, and the locations of all weka calling near the 4-6 sites surveyed during the 30 min immediately before and after sunset (Beauchamp & Chambers 2000; Fig. 1). Birds at 3 key sites, the water tanks above the resort and the 2 sites on the margins of the rubbish tip gully, were always counted on the 1st night of a visit. Birds were counted twice at these sites if call rates were exceptionally low from the earlier day's observations or if the weather was bad (see Beauchamp & Chambers 2000). Weka were then counted at the other 3 principal sites, the mid-chalet pohutukawa (*Metrosideros excelsa*), the upper bush tongue in the middle of the golf course, and the top of the golf course (Fig. 1). If the number and location of calls indicated that greater coverage was needed then the 3 secondary sites were added. The densities of weka in the 4 regions (resort, chalet, tip gully, golf course; Fig 1) were then calculated, using the areas with overhead cover. The bush margins and most covered areas were traversed each trip by AJB to search for weka feeding sign, establish the breeding status of pairs, and to recover faeces. JH and RH walked the coastline on each trip. Diurnal spacing call rates were derived from all calls counted in each period that AJB was in the field, regardless of the area. Longevity was estimated from sightings of individually colour-banded weka.

The minimum polygon sizes of breeding pair home ranges and non-paired weka foraging ranges were estimated from those pairs and birds with >5 sightings each trip. Sightings were plotted onto maps in PolyMEDIA (2002) and the areas were calculated.

Behavioural interactions

All chasing, fighting, and "parallel-walking" (Beauchamp 1987a) between colour-banded adults and their neighbours were recorded. AJB recorded whether weka seen with dependent young had damaged plumage. From Jul 1999, adult weka with and without dependent young were caught and weighed, their moult scored, and damage to remiges, rectrices, and body feathers scored.

Breeding

Breeding periods were defined by AJB using the date of hatching estimated from the plumage and soft part characteristics of those young weka seen (Beauchamp 1987a, 1998), and using measurement, plumage, and moult patterns of young birds caught in Jul 1999, Dec 1999, 2000, 2001, and in Apr 2002. Weka could be aged to month of hatching when under 180 days old and then to within the 1st year (Beauchamp 1998). The number of dependent young and their ages were estimated from the location and types of calls given by dependent young, or by sightings of dependent young (Beauchamp 1987a).

Foraging and diet

Weka diet was assessed by AJB watching weka in the chalet region at ranges of <10 m between 0800 h and 0930 h, and by counting rates of taking worms, collecting the regurgitations produced by weka under observation, and dissecting recently-produced (still moist) faeces collected from all areas of the island in Oct 1996, Nov 1998, Jul 1999, Dec 1999, Dec 2001, and Apr 2002. Soil moisture during sample collection was recorded by parting leaf litter along the track through the upper kanuka (*Kunzea ericoides*) forest area of the rubbish tip gully and classifying the humus zone as dry if there were patches of no moisture, moist if the humus

Table 1. Soil moisture deficit (SMD) index at Waiheke I, Hauraki Gulf, New Zealand,1985-2004. Scale range: 0, wet; 150, dry soil.

Period	Days >120 mm SMD in summer	Drought and dry periods during summer	Length of dry periods when SMD >120 mm (days)	SMD Dec-Feb (summer) mean, SD	SMD Mar-May (autumn) mean, SD	SMD Jun-Aug (winter) mean, SD	SMD Sep-Nov (spring) mean, SD
1985-2004	-	-	-	90.1, 38.8	62.7, 41.0	3.2, 6.5	32.8, 29.5
1995-1996	-	-	-	-	-	-	46.9, 35.7
1996-1997	6	0		75.4, 35.8	86.7, 27.1	1.6, 2.3	24.7, 27.1
1997-1998	50	2	20, 21	120.7, 23.4	64.6, 25.3	1.9, 2.6	28.1, 28.1
1998-1999	25	2	16, 15	92.1, 38.0	70.1, 39.5	1.9, 2.9	17.7, 11.5
1999-2000	21	0	-	98.8, 25.7	66.9, 39.9	3.7, 3.8	38.6, 26.3
2000-2001	9	0	-	74.0, 40.5	30.0, 31.0	3.1, 3.3	34.7, 22.7
2001-2002	0	1	25	44.4, 39.1	74.0, 17.0	-	-

was moist with no film of water, and wet if there was a film of water. Faeces were stored dry. For examination, they were moistened with water and separated into 2 fractions using a 250 µm sieve. The fine portion was examined at 30× magnification for worm chaetae, and the coarse portion for other invertebrates, and vegetation and seeds, at 15× magnification.

RESULTS

Weights and post-liberation survivorship

Mean weight of females at release on 3 Aug 1996, was 734 g (SE_{mean} = 174, range 550-1040 g) and of males 947 g (SE_{mean} =167, range 710-1240 g). The median age of females at first breeding was 237 days (range 222-1697 days, n = 9) and for males was 275 days (range 208 - 2041 days, n = 10). In late Aug 1996, 2 pairs had formed and at least 15 birds gave spacing calls indicating at least 95% of the mature weka survived the transfer.

Climate

Weka were released onto Pakatoa I during a developing La Niña phase of the Southern Oscillation (NIWA 2005), which lasted until early 1997, when it was replaced by a strong El Niño event until mid-1998. A moderate La Niña event then prevailed until mid-2001, from when a weak El Niño event lasted to the end of the study (NIWA 2005). Soil moisture deficits during the 1997-98 summer were higher than the average for 1985-2004; the summers of 1997-98 and 1998-99 were dry to droughty (Table 1). The 1999-2000, 2000-2001, and early 2001-2002 summers were characterised by more regular rainfall, with no droughts, and the years between had average or low soil moisture deficits (Table 1).

Population changes since liberation

The population increased, with continuous breeding being recorded until Dec 1997 (Table 2). On 5 visits between Oct 1996 and 1998 (mostly El Niño conditions), mean counts of adult and independent sub-adult weka were 25.6 (SE_{mean} = 6.8), but 111.2 (SE_{mean} = 23.5) for the 5 visits in 1999 and 2002 (La Niña and neutral conditions). The estimated annual survival rate of paired adults was 74%. The weka population then declined during the drought in Jan-mid-April 1998, during which period Talon® (brodifacoum) poison was laid to eradicate Norway rats (*Rattus norvegicus*), which had re-appeared on the island in Nov 1997. All paired adults died, and by Jul 1999 all surviving weka were <1 year old, and hence just reaching breeding age (Beauchamp *et al.* 2000). No estimate of adult survivorship was possible for 1998-99 (all banded weka had died before Nov 1998; Table 2), but the number of pairs increased, and 27 birds caught in Jul and Dec 1999 included a range of age classes, which indicated high survivorship.

In 1999-2000 and 2000-2001 survivorship of paired adults exceeded 70% (n = 20). Weka ceased breeding again in mid-Jan to mid-Feb 2002, and most of the younger, non-paired birds died. Breeding started again in Mar 2002. During the breeding periods, adult males exceeded 830 g, and females 620 g (Table 3).

Table 4 shows the changes in population density of pairs in the 4 study areas over time (Fig. 1). Birds bred 1st in the chalet area, where the buildings and surrounding vegetation provided extensive cover. The minimum-polygon estimated home ranges of breeding pairs in the chalet area decreased significantly as the population increased (2-sample unequal variance $t_{1,3}$ = 3.512, P<0.05). From Oct 1996 to Jul 1999, mean home range size of pairs was 0.64 ha (SE_{mean} = 0.10, n =11); the ranges of 3 pairs overlapped by at least 20%. Home ranges were much smaller in Dec 2000 and Dec 2001 (mean = 0.26 ha, SE_{mean} = 0.04, n = 12) and the home ranges of

Table 2. Composition of population and breeding information for North I weka (*Gallirallus australis greyi*) on Pakatoa I, Hauraki Gulf, New Zealand, 1996-2002.

Month/year	Minimum number of pairs	Number of known breeding pairs	Age of dependent young (days)	No. of dependent young	Dependent young pair^{-1} (mean, SE_{mean}, range, *n*)	Unpaired, independent weka	Minimum total
Dec 1996	2	1	21	>13	-	15	34
Mar 1997	6	4	40-50	9	-	24	45
Nov 1997	-	-	-	9	-	-	47
Nov 1998	6	2	-	4	2.0, 0.8, 1-3, 2	3	19
Jul 1999	6	4	21-40	>10	2.0, 0.8, 1-3, 4	23	45
Dec 1999	13	8	14-35	>24	2.3, 0.5, 1-3, 8	22	82
Dec 2000	15	10	10-70	>14	1.2, 0.4, 1-2, 9	73	107
Dec 2001	23	15	1-50	>35	1.5, 0.5, 1-2, 12	101	182
Apr 2002	55	2	14-100	>2	-	28	140

Table 3. Weights (g) of breeding adult North I weka (*Gallirallus australis greyi*) on Pakatoa I, Hauraki Gulf, New Zealand, 1999-2001.

Date	Males	Females
Jul 1999	940, 1030, 1110	710, 770, 810
Dec 1999	920, 960, 980, 980, 1000, 1040	760, 720
Dec 2000	910, 980, 1020, 1030, 1040, 1080	760, 870
Dec 2001	980, 1040	620, 650

9 pairs overlapped with their neighbours by 5 - 60%. Changes in home range size could not be calculated in other regions because of the low numbers of sightings.

Non-breeding sub-adult and adult weka

Conservative estimates of the number of non-breeding weka present in each study period is given in Table 2. Some non-paired weka traversed at least half the island during a single visit, but most were more sedentary. Marked non-paired weka with 6-11 sightings each during any 1 visit in the 1998 to 2002 period occupied minimum-polygon ranges of 1.73 ha (SE_{mean} = 0.24, range 0.3 - 2.4, *n* = 7).

In the chalet area, more unpaired (independent, <1-year-old) than paired birds were seen (Table 5). The numbers of unpaired weka present were minimum estimates based on sightings of marked and unmarked weka, and the numbers of paired weka were estimates from sightings and evening spacing call counts, so were not analysed statistically. Sighting of adults were also biased towards those with dependent young. Thirty-eight of 45 sightings of paired males, and 20 of 25 paired females in the chalet area, were of birds with young.

The distributions of non-paired and sub-adult weka changed with changes in ground moisture. During Dec 1999 (dry), groups of 6, 8, and 9 weka were seen at the tip compost heap, 4-6 (*n* = 4) around the Moreton Bay figs, and a group of 10 was seen near leaks in the water pipe at the top of the Tip Gully. In Dec 2001 (moist), weka were dispersed; no groups were seen. In Apr 2002, only 1 group of 7 weka was seen, under figs.

Table 4. Population densities (pairs ha^{-1}) of North I weka (*Gallirallus australis greyi*) in different study areas on Pakatoa I, Hauraki Gulf, New Zealand, in 1997-2002. Numbers in parentheses, area (ha) of overhead cover in each region.

	Study area (area of overhead cover, ha)			
Date	Resort (4.4)	Chalets (9)	Rubbish tip gully (1.5)	Golf course (6.1)
Mar 1997	0.0	0.8	0.6	0.2
Nov 1997	0.0	0.4	1.4	0.4
Nov 1998	0.0	0.4	1.4	0.2
Jul 1999	0.0	0.5	2.6	0.9
Dec 1999	0.0	0.7	2.6	0.8
Dec 2000	0.2	1.2	2.6	1.5
Dec 2001	0.2	2.5	6.0	4.0
Dec 2002	0.4	1.4	4.6	2.0

Behavioural interactions

In Mar 1997, adults with dependent young chased sub-adults, and "boom" and spacing calls were heard (Beauchamp 1987a). There was no obvious damage to the wing and tail feathers of 4 adults and 6 <1-year-old birds in sub-adult, non-definitive basic plumage, all breeding, handled in Jul 1999. Two paired males (14%, *n* = 14) had scarred necks, which indicated that they had been fighting. Independent sub-adult males (mean 980 g, SE_{mean} = 65, *n* = 5) were similar in weight to adult males (Table 3).

Table 5. Status of pairs, and sight recoveries of North I weka (*Gallirallus australis greyi*) in the chalet area, Pakatoa I, Hauraki Gulf, New Zealand, 1999-2002. *, includes pairs in the rubbish tip area that used part of the chalet area; sightings ratio, unpaired:paired weka (weka counted, number of surveys).

Date	Pairs present*	Pairs with dependent young	Paired weka ♂♂	Paired weka ♀♀	Unpaired weka ♂♂	Unpaired weka ♀♀	Sightings ratio
Jul 1999	7	3	7	4	7	2	-
Dec 1999	5	5	5	5	7	5	1.93:1 (85, 9)
Dec 2000	12	9	10	8	10	1	1.32:1 (102, 11)
Dec 2001	22	10	14	4	8	4	1.85:1 (74, 9)
Apr 2002	16	2	9	4	9	3	2.00:1 (63, 7)

Table 6. Occurrence of food items in faeces of North I weka (*Gallirallus australis greyi*) on Pakatoa I, Hauraki Gulf, New Zealand.

		Samples						
		Oct 1996	Nov 1998	Jul 1999	Dec 1999	Dec 2000	Dec 2001	Apr 2002
Samples (*n*)		7	10	10	8	10	10	10
Soil moisture		-	Dry	Moist	Dry	Moist	Wet	Moist
Vegetation								
Shoots		-	-	4	3	-	1	1
Grass		4	6	-	4	10	8	8
Seeds	Figs (*Ficus* sp.)	-	-	3	6	3	2	2
	Gahnia spp.	3	4	-	-	-	-	-
	Palm seeds	-	2	-	-	4	5	1
	Other fruit cases	-	3	4	1	2	3	6
Flower parts		1	7	-	-	-	2	1
Invertebrates								
Coleoptera	beetles	5	7	9	8	9	4	6
	larvae	1	1	3	3	-	1	-
Orthoptera	crickets	-	-	2	-	2	-	2
	weta	-	-	1	-	-	-	-
Hymenoptera	native bees	-	-	-	-	6	1	-
	ants	1	1	4	-	-	2	2
Lepidoptera	caterpillars	-	1	-	1	2	2	-
Hemiptera	cicada	-	-	1	-	-	-	-
Diptera	flies	-	3	1	1	4	2	1
	larvae	-	-	2	-	-	-	-
Arachnida	spiders	3	-	1	1	2	2	3
	harvestman	3	1	-	2	2	1	1
	pseudoscorpion	-	-	1	1	-	-	-
Isopoda	woodlice	1	3	-	-	-	-	-
Amphipoda	hopper	-	1	-	-	3	3	1
Diplopoda	millipedes	1	1	-	-	3	-	-
Mollusca	snails	-	-	1	-	-	1	1
Oligochaeta	earthworms	6	10	5	5	10	9	9

Non-paired weka postured, "boomed," and made contact calls (Beauchamp 1987a) at the dump, and left the tip face when threatened or when pairs with dependent young appeared.

In Dec 1999–Jan 2001, 13 of the 15 paired weka handled had extensive body and head scarring and had lost primaries and tail feathers. During 1999 and 2000, paired weka with dependent young <50 days old chased unpaired weka, both when the young were with the adults and when the adults were foraging alone. The males of 3 pairs fought 3 times and "parallel-walked" in the open areas away from major shared food resources and where home ranges had previously overlapped. No fights were seen in Dec 2001, but most young were >50 days old and most pairs kept to dense cover. In Apr 2002, 4 of 7 weka handled had substantial damage to recently-renewed contour and primary feathers.

The average rate of spacing calls recorded during the day (0700-1900 h) in Dec 1999, 2000, and 2001, when birds were breeding was 1.4-1.7 calls individual^{-1} day^{-1}. The average call rate was only 0.2 calls individual^{-1} day^{-1} in Apr 2002 when the population density was high, but there was no breeding.

Foraging areas, and exposure to predation

Birds were more conspicuous in daylight in the chalet area than on the open golf course or at the beach (Fig. 1). All 31 chalets were on raised foundations and they provided cover for weka between the figs and palms and the cliff edges. Birds also foraged within 10 m of cover around the cliff tops and within the rubbish tip. Weka foraged >10 m from cover over the entire golf course and amongst the cast seaweed on the beaches during morning rain in Jul 1999. A minimum of 16, 28, 31 and 20 individuals used the golf course from dusk and during moonlit nights in Dec 1999, 2000, 2001 and Apr 2002, respectively.

Adult weka were generally only seen during the day when they were feeding dependent young. Pairs with dependent young generally ventured < 100 m to food patches such as figs, and were found there only occasionally despite their foraging constantly. Sightings of banded weka, and faecal analyses showed that the use of patchy foods was confined to pairs within 200 m of that food source.

Food resources generally did not appear to be limiting: pairs raised multiple clutches during periods of favourable, moist, weather conditions. In 1999-2001, all adult weka handled, including those with dependent young, weighed 20-33% more than the critical survival values found on Kapiti I (Table 3; Beauchamp 1987a). Stress bars were seen only in Dec 2000, on the primaries of 2 adults raised in 1999. The bars were laid down when these birds were *c*.40-60 days old (Beauchamp 1998), and were probably caused by food stress during fledging.

The association of feeding birds with cover may have been in response to the presence of Australasian harriers (*Circus approximans*), which were seen on all visits except that in Dec 2001. Harriers were not seen to kill weka, but in Jul and Dec 1999 and in Apr 2002, we observed harriers approach from the sea and surprise adult weka and their dependent young on the cliff top.

Diet

The main food of weka on Pakatoa I were earthworms (Table 6). During moist weather, 92% of faeces ($n = 37$) each contained 100s to 1000s of earthworm chaetae. When the soil was dry, chaetae were present in only 55% ($n = 18$) of faeces and were less abundant (low 10s to 100s in each). When soils were damp, weka ate a worm every 66 s in Jul 1999 ($n = 4$ weka, 19 min), 27 s in Dec 2001 ($n = 3$ weka, 20 min), and every 20 s in Apr 2002 ($n = 3$ weka, 20 min).

There were few (median 4, range 0-12, $n = 67$) identifiable invertebrates, other than worms, in the faeces. There were significantly fewer invertebrates in faeces collected in winter (when soils were moist) than in summer (Wilcoxon sign ranked test, $P = 0.028$). Most of the insects were <5 mm long, but some larger beetles and beetle larvae (Elateridae, Carabidae or Scarabaeidae), crickets, cicadas, and native bees (*Leioproctus fulvescens*) were eaten. A regurgitation collected in Oct 1996 contained the remains of at least 11 carabid larvae and 2 scarabaeids.

Fleshy fruits and vegetation were more common in faeces collected when soils were drier in Nov 1998 and Dec 1999 (Table 6). Moreton Bay fig seeds and fruit casings dominated 3 faeces collected in Nov 1998, and 7 faeces collected in Dec 1999 consisted mainly of fruit cases of palms and figs. Five of 6 regurgitations contained palm seeds. In Apr 2002, figs were only a minor component in 20% of the faeces and nightshade seeds were more common in 60% of faeces. At other times, most of the vegetable matter present was grass or leaf litter that was probably ingested accidentally while the bird was foraging for invertebrates.

Seeds of the sedge *Gahnia* spp. were present in 40 and 42.8% of the faeces collected in Oct 1996 and Jul 1999, respectively, and may have been substitutes for stones as stomach grit.

DISCUSSION

Changes in composition of the population

As predicted, the mean annual adult population on Pakatoa I when the soils were dry was <30 weka, but during moist summers the island's carrying capacity reached at least 142 individuals. The declines observed in the drought in 1997 and 1998 were higher than the annual losses recorded in other North I weka populations (Beauchamp & Chambers 2000; A.J. Beauchamp, *unpubl. data*). However, the age classes that died were not consistent with those on Kawau I when Talon® was used during moist autumn conditions. On Kawau I, proportionally more sub-adult and unpaired adult weka were poisoned than paired adults, and no weka appeared to have starved (Beauchamp 1997b; A.J. Beauchamp, *unpubl. data*; Beauchamp & Chambers 2000). Paired weka were less exposed to sites where the poison was laid, and where there were poisoned rats.

It was expected that a similar proportion of weka would have been killed on Pakatoa I, because unpaired and paired weka have similar mobility. The complete absence of paired breeding adults on Pakatoa I from late 1997 to mid 1998 suggests that they died because they entered summer in low weights after breeding, and starved, rather than that they were poisoned. The young weka may have survived because they were heavier than the adults during late summer and were not poisoned (Beauchamp 1987a, 1997b). The losses resulted in a population of immature weka <9 months old that had to mature and pair before they could breed.

After 1998, many weka pairs included a 1st year bird. In other, stable, populations 0-3% of the pairs included a 1st-year bird (Beauchamp 1987a, b).

The population increase between Nov 1998 and Dec 2001 exceeded any annual rates of increase documented in other weka populations (Beauchamp 1987a; Beauchamp & Chambers 2000). The increase resulted from both high fecundity and low adult mortality, and happened when breeding adults were well above starvation weight (Beauchamp 1987a). Food supplies did not, therefore, appear to be limiting population growth at this time. Consequently, during some periods the carrying capacity of Pakatoa I far exceeded expectation.

Changes in weka behaviour with population density

As expected, weka occupied overlapping home ranges as did birds on Kawau I (A.J. Beauchamp, *unpubl. data*) and at Rakauroa, Gisborne (Bramley 1994). Contrary to prediction, the population displayed more aggressive interactions than the birds on Kawau I. Pairs with dependent young chased other weka from foraging areas, which suggests that resources were limiting. The wide distribution and constant presence of other paired and unpaired weka, and the patchy nature of some shared foods (figs) and feeding areas (rubbish tip) meant resources could not be monopolised on Pakatoa I.

As the population density of weka increased on Pakatoa I, the proportion of weka with damaged plumage increased. The incidence of plumage damage during 1998-2001 was higher (88%, n = 15 captures) in paired adults on Pakatoa I, than it was on Kawau I in 1992–2000 (2%, n = 564 captures), Kapiti I in 1979-88 (11%, n = 900 captures), or at Double Cove, Marlborough Sounds, in 1996-88 (13%, n = 55 captures). In addition, the frequency of "parallel-walking" or fights observed after Dec 1999 was 0.09 h^{-1} on Pakatoa I during 32 h of observation, higher than the 0.017 h^{-1} on Kapiti I in 350 h in 1981-1982 (A.J. Beauchamp, *unpubl. data*), and the behaviour was seen only once in 340 days of observation on Kawau I during 95 trips in 1992-2003 (A.J. Beauchamp, *unpubl. data*). On both Kawau and Pakatoa Is unpaired, independent weka generally congregated at, and moved between, patchy resources with few aggressive interactions, and plumage damage was less obvious.

The diurnal rate (1.4 - 1.7 calls individual^{-1} day^{-1}) of spacing calls during periods when population densities were high and birds were breeding on Pakatoa I was also far higher than that recorded in other studies. Spacing calls are given when pair members meet each other after a period of separation, by parents separated from their mates and dependent young, and after disputes with neighbours or transient weka (Beauchamp 1987a). On Kawau I, where home ranges overlapped and disputes with other weka were rare, daytime call rates of 0-0.5 calls individual^{-1} day^{-1} were recorded over 7 days in 1996-2002, during similar times to those of each visit to Pakatoa I (A.J. Beauchamp, *unpubl. data*). The high rate of calling on Pakatoa I may have reflected the proximity of aggressive pairs while the adults were searching for, and in some instances defending, food.

The higher incidences of plumage damage and call rates suggested that population interactions were more frequent than in other populations that had overlapping home ranges, but in which overall population density was lower (A.J. Beauchamp, *unpubl. data*), or in territorial populations where interactions involved fewer physical contacts (Beauchamp 1987a).

Historical increases and the timing and location of future liberations

The weka population on Pakatoa I between Jul 1999 and Dec 2001 expanded during a La Niña-dominated weather pattern, which maintained easterlies and wetter-than-average summers over the upper North I. The conditions favoured an abundance of earthworms near the surface, and an ample supply of palm fruit and figs.

Weka became restricted to an area near Gisborne on the East Coast of the North I, after the sustained 1914 -1918 drought (Guthrie-Smith 1927; Boady 1950; Stidolph 1955). The weka population there expanded in 1954-56 and 1958 during the most substantial La Niña-associated weather patterns (McKerchar 1994), on the East Coast since the 1914-18 drought (Allan *et al.* 1996).

Napier rainfall records are considered to reflect those of the East Coast Region (Grant 1968, 1996) and show 152 meteorological droughts (≤ 0.1 mm rainfall over ≥15 consecutive days; Mosley & Pearson 1997) and 89 "dry spells" (≤1 mm day^{-1} for ≥15 consecutive days; Mosley & Pearson 1997) in 76 years of records to 1950 (Boady 1950). Grant (1968) found that from 1890 to 1968 the incidence of rainfalls that recharged soil moisture on the East Coast (>57 mm) declined substantially in springs and summers after 1905-06, and became less frequent during the entire year from 1930. Consequently, is not surprising that recent reductions in the range and population density of North I weka populations in the East Cape and Bay of Islands were associated with prolonged droughts (Beauchamp 1997a; Beauchamp *et al.* 1998).

The diets of weka at Gisborne and at Rakauroa (Carroll 1963a; Bramley 1994) were very similar to those on Pakatoa I, with high relative importance on earthworms, larger beetles, vegetation and seeds throughout the year, and with higher frequency of beetles and other invertebrates in summer. Dry weather tended to restrict the availability, and hence consumption, of earthworms (Bramley 1994).

Weka attempted to breed throughout the year on the East Coast (Monckton 1958; Sibson 1958; Bramley 1994), but Carroll (1963b) recorded peaks in breeding attempts between Jun and Sep in 1952-62. Weights of paired females (*c*.800 g in winter; *c*.640 g in summer; Carroll 1963b) were similar to those on Pakatoa I. Weights of females in winter on Pakatoa I and on the East Coast were higher than those of birds during the period of highest breeding activity on Kapiti I in 1983-84, whereas summer weights were close to those recorded when breeding ceased on Kapiti I in all other seasons between 1979 and 1984 (Beauchamp 1987a). It is possible that wetter weather on the East Coast in the summers of 1954-56 enabled female weka to find foods such as earthworms, maintain high weights, survivorship, and to have higher fecundity, which allowed the weka population to increase. However, the population expansion may have coincided with other ecological changes, such as reduced predation pressures, or increased food supply resulting from natural or human-induced changes (van Epenhuijsen *et al*. 2000).

During the 1990s, predation of dependent young, adults being killed on roads and by predators, and a general lack of undisturbed cover prevented the weka population at Rakauroa from breeding successfully and expanding (Bramley 1994, 1996), whereas during the higher rainfall years after 2000, the weka population recovered to 1991 levels despite no increase in available habitat and no predator control, according to surveys led by P. Jansen in 1991 and F. Kemp in 2003 (P. Jansen, F. Kemp, *pers. comm*.).

The breeding data from Pakatoa I, habitat use information from Pakatoa I and Rakauroa (Bramley 1994), and dietary information from the present and earlier studies (Carroll 1963a; Bramley 1994) suggest that future weka liberations are likely to enjoy greater success in areas with undisturbed cover and less severe drought patterns. Transfers are most likely to be successful if establishment is attempted during periods with moist summers, in the north and east of the North I when La Niña weather patterns prevail and during El Niño events in other areas of New Zealand, such as Golden Bay, in the northwestern South I. The Pakatoa I population data indicate that weka populations can increase rapidly when the climate is suitable, but will decline during protracted, and severe short, droughts. Established populations should be monitored during and after drought periods to determine if they have declined and to establish if birds need to be introduced to assist recovery (Beauchamp *et al.* 1999).

Mammalian predators have historically been cited as a key factor preventing or hindering expansion after declines (Bramley 1996). The importance of cats (*Felis catus*) and stoats (*Mustela erminea*) in inhibiting expansion during different climatic conditions is currently under investigation (F. Kemp, *pers. comm*.). Current work suggests that rabbit (*Oryctolagus cuniculus*), mustelid, and cat populations should be assessed before any weka translocation is considered. When ferrets (*Mustela putorius*) are present, both ferrets and rabbits should be controlled (S. Sawyer, *pers. comm*.) to improve the chances of success (Bramley 1994, 1996; Beauchamp *et al.* 2000).

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