

The detection, breeding behaviour, and use of mangroves (*Avicennia marina australasica*) by banded rails (*Gallirallus philippensis assimilis*)

A.J. BEAUCHAMP

17 Bellbird Ave, Onerahi 0110, New Zealand

Abstract: This study assessed how tall mangroves were used by a pair of banded rails with dependent young during three breeding seasons and the intervening periods. Banded rails were territorial and resident all year, raised their young under the mangrove canopy predominantly in dense pneumatophores, and sub-canopy seedlings and saplings. Foraging rails did not follow the tide as it covered and uncovered the flats. Young less than 20 days old were left in cover and delivered food. Young then followed parents as they strolled throughout the site, swam, flew short distances, and climbed mangroves. Rails bathed in and drank saline water and ate worms and crabs. The dependence period of broods was 45–49 days, and in one season, a young bird stayed within the natal site until it was 59 days old.

Beauchamp, A.J. 2022. The detection, breeding behaviour, and use of mangroves (*Avicennia marina australasica*) by banded rails (*Gallirallus philippensis assimilis*). *Notornis* 69(2): 99–111.

Keywords: Rallidae, weka, weasel, breeding, mangroves

INTRODUCTION

Banded rail (*Gallirallus philippensis assimilis*) is frequently cited as a volant relative of the weka (*Gallirallus australis*) and used in morphological and physiological comparisons between flightless and flighted forms (McNab 1994; Lamb 2004). The *Gallirallus* group of rails is thought to colonise offshore islands repeatedly and evolve flightless forms (Livezey 2003; Kirchman 2009, 2012; Garcia-R *et al.* 2017). Flightlessness evolves where genetic changes produce morphologies that can be selected for and confer physiological and ecological advantage (McNab 1994; Kirchman 2009; Shen *et al.* 2009; Sackton *et al.* 2019). However, flightless

Gallirallus species have frequently died out when people have colonised islands (Kirchman 2012; Sayol *et al.* 2020), while flighted rails have remained, or established, including the *Gallirallus philippensis* group on Tonga (Kirchman & Steadman 2005). In New Zealand, humans and a suit of human-assisted introduced mammalian predators have reduced the distribution of weka (Beauchamp *et al.* 1999; King 2017) and banded rails (Guthrie-Smith 1925; Elliott 1983). However, it is unclear why flighted banded rails are now more habitat constrained than flightless weka (Bull *et al.* 1985; Beauchamp *et al.* 1999) and why saltmarsh and mangrove forests (*Avicennia marina australasica*) comprise the remaining habitats of most of the New Zealand banded rail population (Bellingham 2013).

Received 1 September 2019; accepted 3 June 2021

Correspondence: wekaman@xtra.co.nz

Historically, banded rails utilised the widespread terrestrial wetland habitats in New Zealand (Guthrie Smith 1925; Oliver 1955; Turbott 1967). However, during the 1930s, rail distribution declined (Oliver 1955), and by the 1970s, the mainland population was predominantly restricted to coastal wetlands in Golden Bay, South Island, and coastal wetlands, especially mangroves, in the North Island (Bull *et al.* 1985). Nevertheless, banded rails continued to use terrestrial habitats on Aotea/Great Barrier Island, where mustelids are absent.

Observing banded rails in mangrove forests is difficult because New Zealand mangrove forests can be structurally complex (Lundquist *et al.* 2017), and banded rails are cautious and cryptic, and blend into tall (15 cm high) pneumatophores or patches of mangrove seedlings and saplings. The actual level of use of mangroves by rails has not been determined (Morrissey *et al.* 2010; Boffa Miskell Ltd 2017), but Botha (2011) found that mangroves had up to three times the footprint density of saltmarshes at Ohiwa Estuary. Banded rail home ranges are estimated to be 1.5 ha per pair in Nelson saltmarshes (Elliott 1983) and up to 4 ha per pair in mangroves (Bellingham 2013).

The breeding biology of banded rails is well known until the week after chicks leave the nest (Elliott 1983). Banded rails use grassed sites for nesting, incubate from the last laid egg, and the egg hatching is synchronous. The young leave the nest within 24 hours, and brood nests are used (Elliott 1983). Chicks feed independently at 5–7 days old in saltmarsh and when they are also provided with supplementary food (Dunlop 1970; Elliott 1983). After that time, there are anecdotal records about the biology of the chicks and parents but no detail on parental care and relationships with habitat use (Dunlop 1970).

Dunlop (1970) identified six call types associated with pair communication, breeding and territorial defence. A “sharp squeak, *kuk/chik, coo, coo-aw-oo-ooaw*” was used for warning, post-chase advertisement and chick communication, and partner/chick location, respectively. Dunlop (1970) also described sharp squeaks repeated at 15–20 seconds associated with walking as a “mating call”. Other studies have described a low pitched and potentially angry growly *coo*, a grunt given during nest defence and explosive hisses from adults when chicks are chased (Marchant & Higgins 1993). Downy chicks also *peep* and are communicated with by soft cooing by parents (Dunlop 1970).

Year-round breeding takes place in the tropics (Robinson 1994; Tarburton 2018), and seasonal breeding occurs in temperate climates (Dunlop 1970; Marchant & Higgins 1993), with an estimated two clutches per year in Nelson, New Zealand (Elliott 1983). One pair in Samoa hatched on average 4.2 (range 3–5, $n = 5$) chicks per clutch, of which

1.3 (range 1–3) fledged (Robinson 1994). Eviction of these broods averaged 44 days (range 34–63 days; Robinson 1994). At Little Goat Island, Pumicestone Channel, Queensland, Australia, pairs were seen with 1–6 young ($n = 12$) per clutch when young appeared at 2–21 days old (Dunlop 1970). At Nelson, New Zealand, one clutch became independent at 29 days after both parents died (Elliott 1983).

Infrequently, a group or pair of rails living in mangroves is more tolerant of humans than others. For example, during 2005 and 2006, walkers often saw a bird at the boardwalk behind the public baths in central Whangarei (AJB *unpubl. data*). At Sandspit, near Warkworth, during 2013–2021, 2–14 rails foraged within 10 metres of the mangrove margin after long-term predator control occurred around the mangroves (AJB *unpubl. data*). From late 2015, a more tolerant pair lived around the Limeburners Creek boardwalk.

In this paper, I provide information on the habitat use by this pair and developing banded rail chicks, the parental behaviour and care of those young, and the calling of both the adults and young during three breeding attempts and intervening periods.

METHODS

Study Area

This study took place near Whangarei sewerage ponds (Fig. 1), beside a 186 m long boardwalk in mangroves at mid-Limeburners Creek, Kioreroa Road (35.745°S, 174.322°E). The Limeburners Creek boardwalk extended from the southern section of the rest area to the stream margin over a tidal flat occupied by eight-metre-tall *c.* 60–80-year-old mangroves (Fig. 2). Much of the open understory was covered with 0.1–0.15 m high pneumatophores and seedlings up to 0.2 m tall in winter, and visibility was 15–50 m. Beside the creek, part of the tidal flats bed was up to 0.3 m higher and was covered in 0.5–2.0 m sapling and seedling mangroves. The visibility within these mangrove seedlings and saplings was 2–7 metres. The tidal flats were covered and re-exposed about 1–2 hours before and after high tide via channels west of the boardwalk (Fig. 2). The raised tidal flat margin along the creek remained exposed during the lowest high tides (2.3 m chart datum at Marsden Point) and was heavily holed with tunnelling mud crab (*Helice crassa*) burrows. The inner margin between the boardwalk entrances also contained dense seedling and saplings (Fig. 2C). In addition, there were two small (*c.* 100 m²) areas with oioi (*Leptocarpus similis*), one on the western margin near the road and the other between the boardwalk entrances. The remaining creek banks were planted with low native shrubland and flax (*Phormium tenax*) and included the weed pampas (*Cortaderia selloana*).

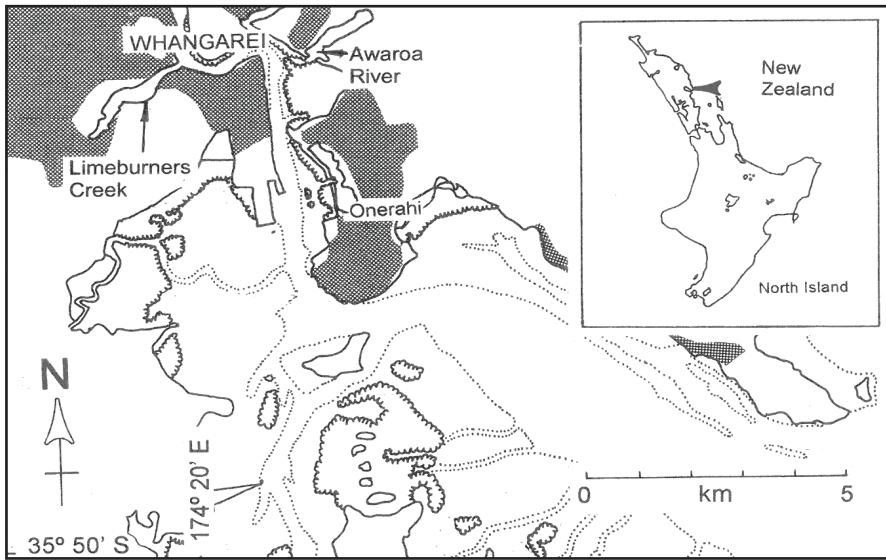


Figure 1. The location of banded rail breeding and survey sites in Whangarei Harbour, New Zealand.



Figure 2. The habitat and location at first detection of adult banded rails at Limeburners Creek, Whangarei. A) during young dependency 2018–19; B) after young dependency; C) during young dependency 2019–20; D) during young dependency in 2020–21. Filled squares are where birds were first seen, and filled dots are where birds were first heard. Open squares are where birds of the southern pair were seen, and open dots heard in November 2020. In C, the ++ regions show the extent of the sapling understory.

Table 1. Survey effort, detection and location of banded rails when they had dependent young at Limeburners Creek, Whangarei. For detection; nil = not detected, juv = dependent young, comms = communication calls, *chit-it* = *chit* and *chit-it* calls, terr = territorial call and squeak = warning squeak. For visibility; open = first detected in an open area with or without seedlings, closed = first detected in an area of saplings.

Young age (day)	2018–2019 Breeding season				2019–2020 Breeding season				2020–2021 Breeding season			
	Start time	Detection	contact, total time (mins)	visibility location	Start times	Detection	contact, total time (mins)	visibility location	Start times	Detection	contact, total time (mins)	visibility location
1	16:40	seen	10, 16	open middle	-	-	-	-	17:20	nil	0, 42	-
2	-	-	-	-	17:40	squeak	7, 34	closed outer	17:30	seen	7, 32	open outer
3	-	-	-	-	-	-	-	-	16:40	seen	10, 72	closed middle
4	-	-	-	-	18:00	squeak	0, 51	closed outer	17:05	seen	53, 86	closed outer
5	-	-	-	-	-	-	-	-	18:20	comms	1, 40	closed outer
6	-	-	-	-	-	-	-	-	10:47	terr	4, 73	closed middle
7	-	-	-	-	-	-	-	-	07:35	seen	37, 60	open middle
8	-	-	-	-	17:00	nil	0, 20	-	-	-	-	-
9	17:20	nil	0, 20	-	-	-	-	-	12:30	nil	0, 53	-
9	-	-	-	-	-	-	-	-	16:40	seen	22, 78	closed inner
10	-	-	-	-	17:00	nil	0, 20	-	18:40	squeak	1, 40	closed inner
11	-	-	-	-	17:05	nil	0, 47	-	12:30	nil	0, 60	-
11	-	-	-	-	-	-	-	-	17:50	seen	1, 67	closed inner
12	-	-	-	-	14:00	seen	70, 75	open middle	10:45	seen	3, 55	open outer
13	-	-	-	-	14:45	nil	0, 69	-	17:20	seen	22, 40	closed inner
14	-	-	-	-	-	-	-	-	-	-	-	-
15	17:55	nil	0, 20	-	10:15	seen	28, 75	open middle	17:05	squeak	2, 60	open middle
15	-	-	-	-	15:27	seen	77, 93	closed outer	17:05	squeak	3, 87	closed inner
16	-	-	-	-	17:36	seen	22, 74	open middle	-	-	-	-
17	-	-	-	-	-	-	-	-	07:40	seen	30, 40	open inner
17	-	-	-	-	-	-	-	-	17:30	comms	44, 65	open outer
18	-	-	-	-	-	-	-	-	16:55	seen	3, 20	closed outer
19	-	-	-	-	-	-	-	-	17:05	nil	0, 70	-
20	-	-	-	-	-	-	-	-	07:40	squeak	15, 50	closed outer
20	-	-	-	-	-	-	-	-	17:00	nil	0, 60	-
21	14:10	squeak	80, 90	closed outer	16:15	seen	22, 95	open outer	-	-	-	-
22	17:00	seen	17, 30	closed outer	14:30	nil	0, 63	-	07:35	nil	0, 30	-
22	-	-	-	-	-	-	-	-	17:35	nil	0, 26	-
23	15:40	nil	0, 100	-	17:45	seen	1, 55	open middle	-	-	-	-

Table 1. *continued*

Young age (day)	2018–2019 Breeding season				2019–2020 Breeding season				2020–2021 Breeding season				
	Start time	Detection	contact, total time (mins)	visibility location	Start times	Detection	contact, total time (mins)	visibility location	Start times	Detection	contact, total time (mins)	visibility location	
24	-	-	-	-	17:23	seen	5, 47	closed	inner	16:35	nil	0, 80	-
25	16:40	juv & comms	54, 56	closed	outer	seen	6, 45	closed	inner	11:15	nil	0, 63	-
26	17:20	seen	8, 25	open	middle	seen	25, 85	closed	inner	-	-	-	-
27	16:48	seen	10, 100	closed	inner	squeak	1, 58	closed	outer	-	-	-	-
28	13:00	squeak	20, 90	closed	inner	nil	0, 73	-	-	17:10	nil	0, 45	-
29	-	-	-	-	16:26	seen	19, 79	closed	outer	-	-	-	-
30	-	-	-	-	16:10	seen	32, 60	open	outer	-	-	-	-
31	18:20	squeak	12, 20	closed	inner	seen	43, 63	open	middle	-	-	-	-
32	17:30	juv & comms	5, 60	closed	outer	squeak	0, 12	closed	outer	15:15	nil	0, 60	-
32	-	-	-	-	16:40	squeak	10, 62	open	outer	-	-	-	-
33	19:00	juv & comms	70, 75	closed	outer	squeak	43, 45	open	inner	-	-	-	-
34	10:15	squeak	2, 34	closed	inner	squeak	63, 63	open	middle	-	-	-	-
34	19:40	nil	0, 35	-	-	-	-	-	-	-	-	-	-
35	07:30	nil	0, 30	-	14:05	nil	0, 46	-	-	-	-	-	-
35	17:18	squeak	10, 72	closed	inner	nil	0, 36	-	-	-	-	-	-
36	-	-	-	-	18:22	seen	7, 61	open	inner	-	-	-	-
37	-	-	-	-	14:23	seen	9, 67	closed	inner	-	-	-	-
38	-	-	-	-	17:48	seen	44, 83	open	outer	-	-	-	-
39	-	-	-	-	11:02	nil	0, 38	-	-	12:56	nil	0, 72	-
41	18:30	squeak	10, 30	closed	inner	seen	26, 60	open	inner	-	-	-	-
42	12:40	nil	0, 60	-	18:35	seen	48, 80	open	inner	-	-	-	-
42	15:58	squeak	25, 62	closed	inner	-	-	-	-	-	-	-	-
43	16:00	seen	55, 110	closed	outer	-	-	-	-	-	-	-	-
44	15:40	chit-it	19, 45	closed	inner	comms	13, 53	open	middle	18:28	nil	0, 41	-
45	18:00	nil	0, 20	-	17:02	seen	25, 128	open	outer	-	-	-	-
46	16:20	squeak	66, 90	closed	outer	squeak	41, 49	closed	outer	-	-	-	-
47	-	-	-	-	19:00	seen	26, 50	open	middle	-	-	-	-
48	-	-	-	-	18:10	chit-it	4, 70	closed	middle	-	-	-	-
49	-	-	-	-	18:50	seen	24, 75	open	middle	-	-	-	-
50	14:08	squeak	4, 60	closed	inner	seen	6, 52	open	outer	-	-	-	-

Survey method

I visited the Limeburner Creek boardwalk and neighbouring sediment ponds (Fig. 2) at least weekly from 10 October 2015. I walked the boardwalk at <2 km/hr, 1–8 times per survey, stopped at all corners and searched out to 50 m using Nikon 8x20 binoculars. Banded rails were only detected ten times in 145 single-pass surveys until November 2018. Then, after chicks were seen on 5 November 2018, I increased the number of times the boardwalk and pond margins were checked to 2–6 times each survey.

In the 2018–19 parental care period, surveys occurred when the mangrove-covered flats were submerged by the tide when the young rails were 15, 31, 33, 35, 42, 43, 44, and 45 days old (Table 1). All other surveys occurred when the mudflats were exposing, exposed, or covering.

I noted the location of detection, the duration of observation, the routes undertaken by the birds, the number of birds present, the behaviours of adults and young, the food items eaten, and the calls given. I also recorded the calls from birds when they were 3–10 metres from the boardwalk on an Olympus Linear PCM recorder LS-10 and the characteristics of the calls were assessed on Raven Lite (Charif *et al.* 2010).

I visited the site 29 times each year to record the behaviour and calls given after young fledged and until moult commenced (until the 28 February 2019 and 24 March 2020) to determine if there were further breeding attempts (post-breeding period). This time was chosen because a pair and two half-grown young were seen near the boardwalk on 28 March 2016 (AJB *unpubl. data*). I also visited the site 19 times between 1 April 2019 and 31 August 2019 and 18 times between 19 April 2020 and 28 August 2020 (non-breeding period) to assess whether the site was permanently occupied.

The chicks were aged using the presence/absence of an egg tooth, colour of downy plumage and size (Dunlop 1970), and chick mobility and behaviour. Notes were kept on the plumage of the first young as they developed and used to check later clutches. The larger adult was assumed to be the male (Marchant & Higgins 1993).

RESULTS

Detection and habitat

Rail parents with 4, 1, and 3 young were seen from the Limeburners Creek boardwalk during 22, 29, and 16 days of the parental care period in the 2018–19, 2019–20, and 2020–21 seasons, respectively (Table 1). When detected, a pair was present with the young 26 times and one parent 23 times. The only time I saw three adults with young was on a territorial boundary where all three birds were

calling because a weasel (*Mustela nivalis vulgaris*) was c. 5 m from them.

Rails were detected significantly more often than not during the chick dependency periods ($\chi^2 = 16.50$, $df. = 1$, $P < 0.001$, $n = 83$) and before moult started at 1 March 2019 and 3 February 2020 ($\chi^2 = 5.76$, $df. = 1$, $P < 0.025$, $n = 34$). However, during the two non-breeding period rails were equally likely to be detected or missed ($\chi^2 = 0.017$, $df. = 1$, $P < 0.01$, $n = 61$).

The average time to detection of the breeding birds with chicks 21–50 days old during the 2018–2019 breeding season (mean = 10.4 minutes, $SD = 9.65$, $n = 21$) did not differ from that in the 2019–2020 season (mean = 14.1 minutes, $SD = 14.3$, $n = 36$; $t = -1.03$, $df. = 55$, $P = 0.31$). During the three parental care periods banded rails were first seen or heard in similar proportions ($\chi^2 = 7.89$, $df. = 5$, $P > 0.05$, $n = 65$); however, rails were initially located significantly more often in saplings ($\chi^2 = 11.88$, $df. = 5$, $P < 0.05$, $n = 65$) until I learned how to approach the birds without unduly disturbing them. Consequently, when first seen in the open, parents continued activity without apparent distress ($n = 11$, 41%), but also gave the warning squeak when near young ($n = 10$, 37%) or when they entered the sapling margins ($n = 4$, 14%), or when they returned to sites where young were resting and I was present ($n = 2$, 7%).

Parental care when young were 1–20 days old

It was difficult to find rails when they had young that were less than 20 days old. In 2018–19 chicks were only seen once, on 5 November 2018 at 1650h (Table 1). Then, four small black downy chicks were seen. They were assumed to be 1–2 days old due to their size, the presence of egg teeth on their bills, and their stumbling walking when led by a parent eight metres into saplings. The chicks were fed three times on crabs and brooded for 12 minutes. The other parent gave a warning squeak, disappeared into saplings and circled back in silence to the brooding bird, and the family moved into the mangrove saplings.

On 21 December 2019, I saw a chick beside a preening adult in saplings. The chick was downy grey-black with no egg tooth. The parent remained silent and only moved when the chick exposed itself. The chick followed the parent and swam a five-metre water gap that the parent had flown over. The parents and chick had not been located during five visits to the site after the predicted hatch date (Table 1). The chick was only seen three times in the remaining first 20 days and was left in saplings and fed by parents. Adults walked past me in the open in silence but then gave many warning squeaks as they entered the saplings. They also gave low volume *chit* and communication calls during movements.

Three 2-day-old chicks were seen with parents on 22 October 2020 (Table 1) and seven subsequent occasions. Both parents generally raised the chicks in silence but gave very soft communication calls (*purr*) when the chicks were two and 18 days old. Rails left chicks in three sunny hiding spots in dense saplings or fallen logs, and delivered food to them from within the surrounding *c.* 20 m. The chicks were brooded/covered by the female on day seven when disturbed in open habitat, and while the male attempted to lure me away from them, giving warning squeaks. At other times the male moved throughout the territory, only gave single warning squeaks to indicate threats ($n = 3$). These calls were not responded to by female or chicks. At 17 days old, the chicks ran to cover when they heard steps or other people on the boardwalk and without any calling by parents. The chicks were not following foraging parents when they were all lost to either a weasel or an extreme rainfall and hail event when between 18 and 20 days old.

Parental care days 21–50 days old

Parents and young were more visible when young exceeded 21 days old (Table 2). At this time, young rails were still downy-grey, but the wing overcoverts were visible. Then, parents and young always walked while foraging and often covered 20 or more metres a minute. Young moved behind and within 1–3 m of feeding parents and fed from the parent's bill and on food that the parent dropped. Adults gave soft calls, and occasionally low amplitude warning grunts when they passed within 10 m of me (Fig. 3C). Foraging was most often from within the mangrove sapling area and its margins (Fig. 2) and only once targeted the tidal margin of the covering flats. When chicks were inactive, adults foraged up to 50 m from them within the sapling area. Young started to forage for themselves at 21–23 days old, and from day 42, the young fed over 20 metres from parents (Table 2).

Table 2. The timing of behaviours by parent and juvenile banded rails in two breeding periods at Limeburners Creek, Whangarei. Records in brackets are less certain due to a lack of sightings in the period specified.

Activity	Juvenile age (day)	
	2018–2019	2019–2020
Chick brooding	2	not seen
Juveniles started to feed alone	23	21
Juveniles swam between sites	31, 43	12, 33
Juveniles last fed by adults	25	36
Juveniles started foraging independently	23	21
Juveniles started wing flap and dash	21	15
Juveniles climbed mangroves	31, 32, 33	not seen
Juveniles gave last <i>peep</i> calls	43	42
Juveniles gave wavering calls	21–43	15–42
Juveniles deliberately drinking seawater	not noted	21–50
Juveniles last foraged with adults	43	44
Juveniles last interacted with adults	46–(49)	45
Juveniles last foraged at natal site	50	59
Juveniles tail flicking started	25	30
Juveniles gave <i>chit-it</i> call	not heard	(50)–54
Juvenile gave warning squeak	not heard	(57)–59
Adult gave food calls	21–34	13–34
Adult lead away display and soft calling ends	21	16
Adult gave close deep distress calls	not heard	15–21
Adult chased young	not seen	45
Adult climbed mangroves	21, 33	not seen
Adult swam in the creek channel	21, 31	not seen
Adult courtship chase and feeding	not seen	51, 52
Adult territorial activity southern boundary	not seen	45–58
Adult flying in the understory	21, 25	12, 33, 42, 48

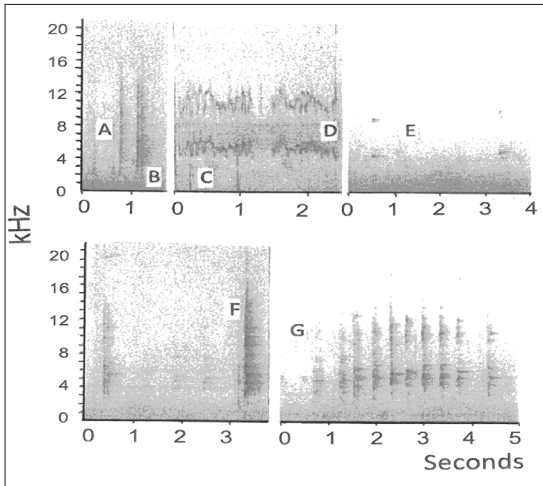


Figure 3. Spectrogram of the calls given by banded rails at Limeburners Creek. A, communication call; B, *chit-it*; C, close warning grunt call; D, chick later wavering call; E, chick out of site peep call; F, Warning call; and G, rapid territorial calls.

Adults and young bathed in seawater on the incoming tide ($n = 7$) and deliberately drank seawater ($n = 6$). In the 2018–19 breeding season, when young were 31 and 33 days old, adults and young climbed six-metre-high mangroves, and when young were 31 and 43 days old, they swam along the mangrove creek margin. Each time, the young swam with their head, upper back and tail out of the water, while the parents swam with a third of their body above the water. On day 33, the family of rails remained in the outer mangroves and called there until half an hour after sunset.

Young rails jumped while flapping their wings over the outer drainage channels when they were 25 days old. Wing-stretching showed that the remiges were *c.* 80–90% of total length at 37 days old.

In 2018–19, four young rails were last seen with parents when 27 days old and when young foraged predominantly independently of parents. Then, from 31–47 days old, only two young were seen with parents. In 2019–20, only one chick was seen with parents, and from 45–59 days old, it remained in the natal area with little interaction with its parents (Table 2).

Young at 47 days old, had a red-brown nape and grey front band and resembled small adult weka. Then, from 52 days old, the upper unbanded breast developed light bars and the pale orange-brown patch typical of independent young rails. By day 59, the nape cap became a light rusty colour on the margin, and the wings appeared fully developed. The mid proximal upper mandible changed from dark grey to maroon grey at 37 days old to reddish-brown at 59 days old.

I assumed the parents of all three clutches were the same because of their tameness, consistent use of the same areas between seasons (Fig. 2), consistent number and size of young seen during the season, and the location of sites of territorial defence. However, I did not see the parents or young of the third clutch after 10 November 2020, during what should have been the remaining dependency period of these young (from 20–50 days old; $n = 9$ surveys, Table 1).

Foraging and food use

Mud crabs were the most sought-after food, and rails ate 18 of them during eight surveys. Crabs were the only food item that rails ran to catch, and were caught on exposed mudflats and within the water in the stream channel. When young were less than 15-days-old parents took crabs to dry areas and broken them up for the chicks. After this, crabs were given whole to young.

Worms were the principal food item consumed. Chicks and juveniles ate 44 worms during 13 surveys. Adults raised worms in their bills *in situ* so that the following young could catch up and take them at adult's side. Adults always carried worms to <20 day-old young, and sometimes carried worms over 50 m to sites where older young were resting ($n = 5$).

When the 2019–20 juvenile was 52 days old, it searched with an open bill in dirty shallow water-filled pools for worms and appeared to be using its tongue for detection. Small items, likely snails, were also taken by adults and the juvenile from the tide-moistened bases of mangrove trunks and boardwalk supports.

Call use by adults and young

Adults gave four long-distance call types as part of territorial defence, pair and chick communication (Tables 3 & 4). There was also an additional call syllable *cheo* (not recorded, likely the *coo aw oo oow*, Dunlop 1970) given throughout the year before multiple repeat *chit* calling.

During parental care, the most frequent call was a single warning squeak which carried at least 120 m (Tables 3 & 4; Fig. 3F). The squeak was given when I was detected on-site but had not first located the birds, when I moved erratically near the adults, and when adults entered dense saplings after they were previously seen in the open. This call was only responded to three times by the partner, and then with communication and *chit-it* calls (Fig. 3A & B). The warning squeak never resulted in young rails running or freezing. Groups of warning squeaks repeated at *c.* 0.3–30 second intervals also occurred after territorial disputes and when a weasel was

Table 3. Number of banded rail calls groups where the activity could be assigned at Limeburners Creek, Whangarei. Danger nearby, included people and dogs on the boardwalk and mustelids. Response to other stimulus, included other bird species distress calls, emergency services alarms, heavy truck breaking.

Activity	Warning squeak			Communications call			<i>Chit-it</i> calls			Territorial calls	
	Pair contact	Danger nearby	Response to other stimulus	Pair contact	Young contract	Post defence	Pair contact	Young contract	Post defence	Physical conflict	Vocal defence
Incubation	0	0	0	0	0	1	1	0	1	1	0
Parental care	2	25	10	13	10	4	8	17	2	2	4
Breeding season lacking young	2	5	6	8	0	7	7	1	7	1	7
Non-breeding period	0	0	2	4	0	2	2	0	3	0	6

Table 4. Presence of calls types (% of surveys) given by banded rail adults during the breeding season where dependent young were present at that site, where dependent young were absent during the breeding season, and in the non-breeding period at Limeburners Creek, Whangarei. January 2019 – October 2020. *n* = number of surveys.

	Surveys calls types heard (%)				Surveys lacking calls (%)		
	Warning Squeak	Communication calls	<i>Chit & chi-it</i>	Territorial calls	Rails not detected	Rails seen but not calling	Surveys (<i>n</i>)
Breeding season							
1 September – 31 March							
Incubation	0	8	17	8	67	0	12
Young <20 days old	37	9	23	11	34	9	35
Young ≥21–50 days old	38	22	27	3	19	9	64
Other times	14	19	19	10	41	9	80
Overall breeding season	25	17	22	8	34	8	191
Non-breeding season							
1 April – 31 August							
	8	17	14	17	44	8	36

nearby. These calls continued for up to 25 minutes after I left the immediate vicinity.

Groups of communication calls were given every *c.* 1–5 seconds when pairs were together in dense saplings (Fig. 3A; Table 3), and while pairs were separated when each tending part of the brood. These calls ceased when the pair re-established visual contact (when the young were 1, 23, and 33 days old).

The only other adult call that carried more than 30 m was a *chit-it* call (Fig. 3B; Table 3). This call was given by a separated parent trying to locate its partner and young, or as a response to warning squeak calls from neighbours or partners.

Parents gave repeated soft contact calls every few seconds when walking with older young. A short-range food call (increasing frequency *geer*) was given by adults when presenting food, and a parent gave a *guik* call every second as it swam in front of two 31-day-old young to the shoreline.

Warning grunt calls (Fig. 3C) were also given by the adult when feeding juveniles 3–10 metres from me beside the boardwalk (Table 2).

From 15 days old, young gave a call like the wavering jerky end of dependence period calls of weka (Fig. 3D; Table 2; Table 5), initially only when presented with food by parents, and then from days 21–34 continuously when parents were present. Louder *peeps* were given by young while foraging with adults (Fig. 3E). These calls carried over 50 metres and were given almost continuously along with parental communication calls as rails fed in dense saplings.

Calls used in response to a neighbour calling and territorial behaviour

The boardwalk pair only responded seven times (*n* = 227 surveys) to the immediate calls by neighbours between 25 November 2018 and 18 February 2021.

Table 5. Calls used by banded rails and weka during equivalent activities

Activity	Banded rail call	Weka call
Territorial defence	"Chi-dik", 'kuk" "cick"* <i>chit</i> , <i>chit-it</i> #	Booming <i>doon-doon-doon</i> repeated
Pair or individual spacing	A rapidly repeating group of communication calls #	Spacing call duet, <i>coo-eet</i> , repeated up to 40 times
Warning calls	<i>Kuk</i> *, or high intensity and modulating high pitched <i>squeak</i> #	<i>Kuk</i> , <i>Squeak</i> often repeated multiple times where dependent young are present
Partner close contact calling	soft <i>coo</i> or communications calls #	Contact call and boom and soft <i>uh</i>
Nest and breeding readiness	Guttural rising <i>Urrrrrrr</i> repeated	Guttural rising <i>Urrrrrrr</i> repeated
Chick leading	Soft <i>coo</i> *, <i>chit-it</i> , <i>guik</i> repeated and adult to chick food call	<i>put-put-put</i> call
Adult to chick food calling	<i>Chit</i> * and food call <i>uurha</i>	Food call rising <i>uurha</i>
Chick out of sight	<i>Peep</i>	<i>Peep</i> or silence
Chick late foraging with parents	#	Wavering calls constant when near parents
Chick close contact defence	Loud <i>coo</i> * <i>growl</i> #	<i>growl</i> repeated <i>grrrrh</i>

* Dunlop 1970, not heard in this study, #, see Fig 3.

Two of these responses were associated with police sirens, one to a drone flying over the site and three with close conflict on the western boundary (Fig. 2D).

In the post-breeding period between 20 January 2020 and 9 March 2020, there was considerable activity in the western margin of the home range. This activity included call groups, with six or more combined communication call or *chit* notes repeated together three to a second (territorial calls; Fig. 3G) before and after chases. The behaviour was indicative of a boundary dispute but may have also included a pair challenge, because it was associated with courtship feeding and a courtship chase.

No pair duet or individual calling took place at dawn or the early evening through the year.

DISCUSSION

Most data collected in this study derive from observations of three broods with the same parents, so may not represent how all banded rails behave within mangroves. The other breeding pair present in the 2020–21 season, only occupied saplings.

This study showed that banded rails were generally secretive and extremely mobile ground-based foragers. There was little leaf litter under mangroves, so foraging was predominantly undertaken by investigating under objects, probing at objects, fishing about in small puddles or dashing at visible food items. Some foraging occurred within the water of the creek margin, but most foraging was from the exposed mangrove

forest floor. Banded rails delivered worms and crabs to young. The territories were submerged twice a day by the tide and were always moist. There was no apparent competition for food resources on the mangrove forest floor with New Zealand kingfishers (*Todiramphus sanctus*), Eurasian blackbirds (*Turdus merula*), song thrush (*Turdus philomelos*), or mallards/grey ducks (*Anus platyrhynchos/superciliosa*). Rats (*Rattus norvegicus*) emerged from hollow standing mangrove trunks in the late evenings.

Food appeared to be abundant. Banded rails did not follow the flush or ebbing tide or were pressed for foraging areas or time. Rails were first detected near the creek margin 30 or more minutes after tidal-flat exposure. Up to one metre long short-finned eels (*Anguilla australis*) were always near the head of newly advancing flushing tides and could have been a predation issue for young rail chicks (McDowall 1990). Adult rails generally flew over drains and channels and only swam when chicks could not fly or would not see where adults hand flown. On most occasions, adults and young moved inland in advance of the tide.

The noisiest and potentially the riskiest time for banded rail young at Limeburners Creek was when they were 18–43 days old, when they could not fly, and communication between young and parents lasted up to 80% of the time. Similar long periods of noisy calling occurred between parents and young during the hour before sunset at Awaroa River (75–77% of the time) on 9 and 12 February 2019 (AJB unpubl. data). Five of the eight young I followed at Limeburners Creek disappeared during this time.

The appearance of a weasel in the mangroves two days before the loss of the chicks and adults in 2020–21, suggests that predation was the cause. It is likely that the two young that disappeared in early December 2018, at 27 days old, died; because young of this age were still dependent on some parental feeding, and independent young would still have been expected to be within the parental territory.

Banded rails, like weka, had specific locations where they left chicks while they foraged for food. All of these sites were near or within logs or dense sapling cover. During the first 20 days, the pair foraged within 20 metres of young and carried food to them instead of calling them from cover. The male roamed more widely and only called when there was another person on the boardwalk or to locate the female if she had moved chicks on. The female answered these calls with a single communication call. Unlike weka, banded rails did not call when they met after separation, and there were no equivalents of the territorial boom or the spacing call (Table 5, Beauchamp 1987), which are used in pair greetings and to define ownership of space (Beauchamp 1987; Beauchamp & Chambers 2000).

At Limeburners Creek, the banded rails used a similar group of calls during pair communication and territorial defence to those described in Queensland (*G. p. mellori*, Dunlop 1970). These included the “*kuk*” or “*chik*” calls, which like the *chit* and *chit-it* calls in my study were associated with keeping other rails away, partner communication and boundary defence (Table 5). In addition, banded rails used a call, like the distant food calls and breeding readiness calls in weka (Table 5), while breaking up crabs near chicks (Dunlop 1970). Dunlop (1970) also described the sharp squeak, given every 15–20 seconds, as associated with mate finding and warning of an unexpected factor. This description appears to cover both the warning squeak and the communication calls. Rails in both areas gave calls that started with a burst of squeaks up to three a second and then slowed to 20 or more seconds apart. Calls like this occurred during and after territorial defence.

Dunlop (1970) reported that the single squeak given when birds were surprised was a directed warning call to the group, not the partner alone, and seldom induced a response. The banded rail young in my study did not appear to treat this call as an indication of imminent danger. Multiple repeated warning squeaks and communication calls occurred when the weasel was present, but chicks only moved when the parents sort cover. Similar warning squeaks and multiple communication calls occurred on 20 November, 12 December, 22 December 2019, and 7 & 28 February, 9 March, and 28 August 2020 at adjoining banded rail

sites, but chick presence was only confirmed once (AJB *unpubl. data*). The lack of any speedy reaction to predators is considered a reason for losses in other rail populations (Bunin & Jamieson 1995).

In contrast, North Island weka (*G. a. greyi*) often gave similar harsh warning squeaks, once when surprised, but multiple times when dependent young were present but frequently up to 100 m away. This call was also occasionally taken up by nearby non-paired weka and pairs with and without young (AJB *unpubl. data*). Young between 3–41 days old ran and occasionally hid. However, the South Island weka (*G. a. australis*) and those of a mixed population on Kapiti Island (Beauchamp 1987; Trewick *et al.* 2017) very occasionally gave this call when weka were surprised, and seldom gave it when they had dependent young unless those young were hiding a few metres away (Marchant & Higgins 1993). This call was never taken up by neighbouring pairs (AJB *unpubl. data*).

The study indicated that adult banded rails also reduced their vulnerability by reducing actions that would make them visible. For example, no banded rails foraged on the margin of the oxidation ponds in daylight. Also, rails foraged within 6–10 metres of cover at Sandspit where mammalian predator control was present (AJB *unpubl. data*), and at Ohiwa Harbour when it was not (Botha 2011).

Most of the calls described by Dunlop (1970) in Queensland, Australia, were given by New Zealand banded rails and appeared to have similar functions. However, in both populations there was no equivalent to the loud spacing calls, or mate finding calls of weka which are often heard in the evenings (Table 5; Beauchamp 1987, 1997). There was calling that would allow predators to find banded rails within the mangroves. However, this calling appears to be of less than that described for other populations of banded rails (Lachish & Goldizen 2004) and the related terrestrial Roviana Rail (*Gallirallus roviiane*; Kirchman 2012) that give lengthy territorial calls (Frank Lambert, XC404084. Accessible at www.xeno-canto.org/404084).

In conclusion, banded rails in New Zealand are vulnerable to nest and chick predation from introduced rats and mustelids in saltmarsh and swamp habitats (Guthrie-Smith 1925; Elliott 1983). Even when predator control occurs, banded rails tend to stay within 10 m of cover. There is limited competition for the resources under mangroves, and banded rails can use mangroves because they can drink saline water, eat saline foods, and utilise a habitat with predictable food supplies. In mangroves, rails have limited calling behaviour that may further reduce the attention of mammalian predators near that habitat, especially outside of the time that young are between 18 and 43 days old.

ACKNOWLEDGEMENTS

I thank Katrina Hansen, Neil Fitzgerald, an anonymous reviewer and Craig Symes for comments on earlier drafts of the paper, which substantially improved this paper.

LITERATURE CITED

- Beauchamp, A.J. 1987. A population study of the weka *Gallirallus australis* on Kapiti Island. Unpubl. PhD thesis. Victoria University of Wellington, Wellington, New Zealand.
- Beauchamp, A.J. 1997. The decline of the North Island weka (*Gallirallus australis greyi*) in the East Cape and Opotiki Regions, North Island, New Zealand. *Notornis* 44: 27–35.
- Beauchamp, A.J.; Butler, D.J.; King, D. (Eds). 1999. Weka (*Gallirallus australis*) recovery plan 1999–2009. Department of Conservation Threatened Species Recovery plan 29. Wellington.
- Beauchamp, A.J.; Chambers, R. 2000. Density changes of adult North Island weka in the Mansion House Historic Reserve, Kawau Island: 1992–1999. *Notornis* 47: 82–90.
- Bellingham, M. 2013. Banded rail. In Miskelly, C.M. (ed.) *New Zealand Birds Online*. www.nzbirdsonline.org.nz Accessed: 25 September 2020.
- Boffa Miskell Ltd. 2017. Use of mangrove habitat by banded rail (*Gallirallus philippensis assimilis*). Waikato Regional Council Technical Report 2017/24.
- Botha, A. 2011. Foraging distances and habitat preferences of banded rails in the Ohiwa Harbour. Bay of Plenty Regional Council Environmental Publication 2010/06. Whakatane, Bay of Plenty Regional Council.
- Bull, P.C.; Gaze, P.D.; Robertson, C.J.R. 1985. *The atlas of bird distribution in New Zealand*. Wellington, The Ornithological Society of New Zealand.
- Bunin, J.S.; Jameson, I.G. 1995. New approaches toward a better understanding of the decline of takahe (*Porphyrio mantelli*) in New Zealand. *Conservation Biology* 9: 100–106.
- Charif, R.A.; Waack, A.M.; Strickman, L.M. 2010. Raven Pro 1.4 User's Manual. Ithaca, New York, Cornell Lab of Ornithology.
- Dunlop, R.R. 1970. Behaviour of the banded rail, *Rallus philippensis*. *The Sunbird* 1: 3–15.
- Elliott, G.P. 1983. The distribution and habitat requirements of the banded rail (*Rallus philippensis*) in Nelson and Marlborough. Unpubl. MSc thesis, Victoria University of Wellington. Wellington, New Zealand.
- King, C.M. 2017. Contemporary observations of predation on buff weka (*Gallirallus australis hectori*) by ferrets in the South Island during the nineteenth century. *Notornis* 64: 52–55.
- Garcia-R, J.C.; Joseph, L.; Adcock, G.; Reid, J.; Trewick, S.A. 2017. Interisland gene flow among populations of the buff-banded rail (Aves: Rallidae) and its implications for insular endemism in Oceania. *Journal of Avian Biology* 48: 679–690.
- Guthrie-Smith, H. 1925. *Bird life on island and shore*. London, William Blackwood & Sons.
- Kirchman, J.J. 2009. Genetic tests of rapid parallel speciation of flightless birds from an extant volant ancestor. *Biological Journal of the Linnean Society* 96: 601–616.
- Kirchman, J.J. 2012. Speciation of flightless rails on islands: a DNA-based phylogeny of the tropical rails of the Pacific. *The Auk* 129: 56–69.
- Kirchman, J.J.; Steadman, D.W. 2005. Rails (Aves: Rallidae: *Gallirallus*) from prehistoric sites in the Kingdom of Tonga, including a description of a new species. *Proceedings of the Biological Society of Washington* 118: 465–477.
- Lachish, S.; Goldizen, A.W. 2004. Responses to neighbours and non-neighbours in the buff-banded rail (*Gallirallus philippensis*): no dear-enemy relationships. *Australian Journal of Zoology* 52: 369–378.
- Lamb, J.M. 2004. Changes in feather microstructure associated with the occurrence of flightlessness. Unpubl. MSc thesis. Portland State University, USA.
- Livezey, B.C. 2003. Evolution of flightlessness in rails (Gruiformes: Rallidae) phylogenetic, ecomorphological and ontogenetic perspectives. *Ornithological Monographs* 53: 1–654.
- Lundquist, C.; Carter, K.; Hailes, S.; Bulmer, R. 2017. *Guidelines for managing mangrove (mānawa) expansion in New Zealand*. NIWA Information Series No. 85. National Institute of Water & Atmospheric Research Ltd.
- Marchant, S.; Higgins, P.J. 1993. (eds) *Handbook of Australian, New Zealand, and sub-Antarctic Birds. Vol. 2, Raptors to Lapwings*, [*Gallirallus philippensis* Buff-banded rail.] Pp 495–506, Melbourne, Oxford University Press.
- McDowall, R.M. 1990. *New Zealand freshwater fishes, A natural history and guide*. Auckland, Heinemann Reed MAF publishing group.
- McNab, B.K. 1994. Energy conservation and the evolution of flightlessness in birds. *American Naturalist* 144: 628–642.
- Morrisey, D.J.; Swales, A.; Dittmann, S.; Morrison, M.A.; Lovelock, C.E.; Beard, C.M. 2010. The ecology and management of temperate mangroves. *Oceanography and Marine Biology: An Annual Review* 48: 43–160.
- Oliver, W.R.B. 1955. *New Zealand Birds*. Wellington, A.H. & A.W. Reed.
- Robinson, A.C. 1994. Breeding pattern in the banded rail (*Gallirallus philippensis*) in Western

- Samoa. *Notornis* 42: 46–48.
- Sayol, F.; Steinbauer, M.J.; Blackman, T.M.; Antonelli, A.; Faurby, S. 2020. Anthropogenic extinctions conceal widespread evolution of flightlessness in birds. *Science Advances* 6: eabb6095. doi: 10.1126/sciadv.abb6095
- Shen, Y-Y; Shi, P.; Sun, Y-B.; Zang, Y-P.; 2009. Relaxation of the selective constraints on avian mitochondrial DNA following the degeneration of flight ability. *Genome Research* 19: 1760–1765.
- Sackton, T.B; Grayson, P.; Cloutier, A.; Hu, Z.; Liu, J.S.; Wheeler, N.E.; Gardner, P.P.; Clarke, J.A.; Baker, A.J.; Clamp, M.; Edwards, S.V. 2019. Convergent regulatory evolution and the loss of flight in paleognathous birds. *Science* 364: 74–78.
- Tarburton, M.K. 2018. Evidence for year-round breeding of birds in the Samoan Islands in the context of the Australasian and South Pacific regions. *Notornis* 65: 92–108.
- Trewick, S.A.; Pilkington, S.; Shepherd, L.D.; Gibb, G.C.; Morgan-Richards, M. 2017. Closing the gap: Avian lineage splits at a young, narrow seaway imply a protracted history of mixed population response. *Molecular Ecology* 26(16): 4197–4210. doi: 10.1111/mec.14323
- Turbott, E.G. 1967. *Buller's birds of New Zealand*. Christchurch, Whitcoulls Publishers.