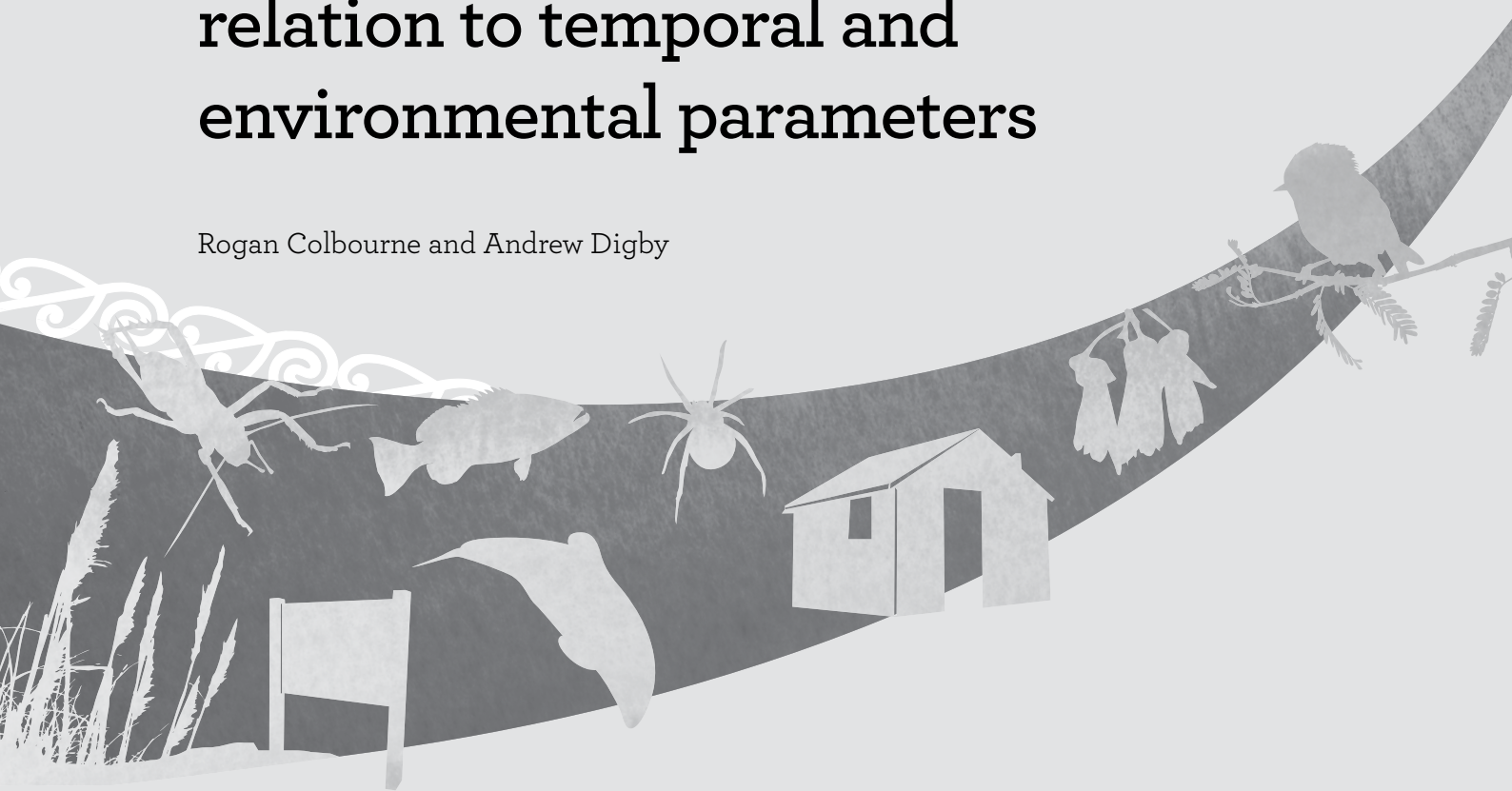




Call rate behaviour of brown kiwi (*Apteryx mantelli*) and great spotted kiwi (*A. haastii*) in relation to temporal and environmental parameters

Rogan Colbourne and Andrew Digby



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Call rate behaviour of brown kiwi (*Apteryx mantelli*) and great spotted kiwi (*A. haastii*) in relation to temporal and environmental parameters

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Abstract

Call rates are often used to monitor populations of cryptic species such as kiwi by providing indices of abundance to determine if a population under study is increasing, stable or declining. Observations using human listeners are limited by biases such as variation in hearing ability and fatigue. Therefore the development of remote recording technology provides an opportunity to collect a great amount of data at little cost and effort. Call rates can also provide insight into kiwi behaviour. To gain a better understanding of how temporal and environmental conditions influence kiwi call rates, we deployed automated acoustic recorders at six sites—five inhabited by brown kiwi (*Apteryx mantelli*) and one inhabited by great spotted kiwi (*A. haastii*). Frequency of calling was clearly related to the breeding season for both species, but the pattern of calling was highly variable between sites and sometimes between years within sites. Brown kiwi call rates peaked in the first 10–40% of the night whereas great spotted kiwi call rates peaked in the second half of the night. Moonlight had no significant effect on male call rates at any site but had a significant effect on brown kiwi females at Whanganui and great spotted kiwi females at Saxon. At all sites, call rates were lower during high winds and heavy rain. Inter-seasonal variations in factors such as the quality of the previous breeding season or environmental conditions (e.g. summer droughts) could affect the ability of males, in particular, to recover to maximum breeding condition, which could, in turn, impact on call rates. Based on these findings, we recommend specific times at which kiwi call rates could be recorded to make monitoring more efficient and reliable. Because of the inherent natural variation in call rates, and the fact that chicks and juveniles rarely call, monitoring by calls is still too crude a method to determine an accurate density of a kiwi population.

Keywords: bioacoustics, nocturnal, vocalisations, kiwi.

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1. Introduction

Kiwi are cryptic nocturnal birds, which makes it difficult to determine their distribution and population size. However, they do have extremely loud calls that can be heard up to 1.5 km away, which reveal information about not only their presence and gender, but also, potentially, their age class (subadult or adult) and/or individual identity. Generally, chicks and juveniles do not call.

Kiwi begin to call when they emerge from their burrows or shelters soon after sunset and continue to call very occasionally/sporadically until sunrise, when they return to their burrows to sleep. True pairs of brown kiwi (*Apteryx mantelli*) often duet, with one calling immediately after their partner has finished, or sometimes by overlapping or alternating with their partner; and, in some instances, this can trigger a wave of calling from nearby territorial pairs. By contrast, there is more overlap in the calls of a true pair of great spotted kiwi (*A. haastii*). Kiwi calls primarily serve to maintain territories (Colbourne & Kleinpaste 1984), but also help to maintain the pair bond and contact between mates—and in great spotted kiwi, which share the incubation of eggs, provide information on the location of the partner who is foraging/incubating.

Brown kiwi begin to breed in late autumn – early winter in Waitangi Forest (Northland), with copulation sounds heard from May to November but most frequently in June (Colbourne & Kleinpaste 1984). During this period, males and females are probably in greater contact with each other, and territory integrity and defence would become particularly important once the nest has been selected. The peak egg-laying period in Northland is from July to September (Colbourne & Kleinpaste 1983), while throughout the rest of the North Island eggs are laid between June and December (Heather & Robertson 2000). Only male brown kiwi incubate the eggs, and so during the first quarter of incubation the eggs are left unattended at night while the males forage; however, as incubation progresses, they sit longer, only leaving the nest for 3–5 hours per night; and once the eggs are close to hatching, some males do not leave the nest for several nights (Colbourne 2002).

Great spotted kiwi lay their eggs mainly between late July and October at Saxon (Northwest Nelson) and Kahurangi (12 km NW of Saxon), although a few continue on until late December (McLennan & McCann 1991). Males and females share incubation of the single egg and so it is rarely left unattended—the male takes the day shift and the female relieves him about an hour after sunset and stays on the egg most of the night (Peat 1990).

Kiwi calls are monitored at many sites across New Zealand to compare the relative abundances of kiwi in different areas and to determine changes in population density over time. However, when carrying out such studies, it is important to consider the temporal variation in kiwi calls both between seasons and during a night. For example, in a study on great spotted kiwi at Saxon, McLennan & McCann (1991) found that the birds called at much the same rate throughout a night, except in mid-summer and autumn, when they tended to call more often in the 2 hours before dawn. The birds' call rates during the first 2 hours of darkness also varied seasonally, with an annual peak over summer (November–February) and a low in late autumn and winter. The results of this study suggested that mid-summer is the best time for surveying populations of great spotted kiwi (McLennan & McCann 1991).

Kiwi call monitoring is also often compromised by unfavourable weather conditions—and even when environmental conditions appear to be similar, kiwi call less on some nights than others in what appears to be an unpredictable way (Colbourne & Kleinpaste 1984). In the past, it has generally been thought that kiwi calls rates are negatively correlated with moonlight. For example, Colbourne & Kleinpaste (1984) noted that brown kiwi were often silent on moonlit nights in Waitangi Forest in Northland; and Kayes & Rasch (1985) also concluded that there was significantly less calling with increasing brightness of the moon at the same site. However, Miles (1995) found no significant relationship between call rates and moonlight in Tongariro Forest,

central North Island; and McLennan & McCann (1991) found no significant difference between call rates of great spotted kiwi on the brightest of nights (full moon overhead and not obscured) and on dark nights at Saxon and Kahurangi Point in Northwest Nelson.

Kiwi call monitoring has traditionally involved the use of trained listeners who manually record the number of calls in a given time period, usually for 2 hours per night (Robertson & Colbourne 2003). However, this is a time-consuming survey method that is prone to observer error. Recent rapid developments in the technology of automated acoustic recording devices have allowed acoustic data to be collected with much greater efficiency, providing much promise for this type of monitoring work. However, the optimal method of deploying recorders is unknown for most species. Therefore, this study aimed to improve our understanding of the calling behaviour of kiwi in relation to temporal and some environmental parameters, to help determine the most effective protocols for acoustic monitoring of their populations. This study primarily focussed on populations of brown kiwi, but a population of great spotted kiwi was also surveyed to determine whether the findings could be generalised to other kiwi species.

2. Methods

2.1 Field recordings

Six Song Meter SM2+ recorders (Wildlife Acoustics, Concorde, MA, USA; Fig. 1) were deployed at five North Island sites for brown kiwi and one South Island site for great spotted kiwi (Fig. 2). Two of these recorders developed faults, resulting in the loss of 2 months of data on Te Hauturu-o-Toi / Little Barrier Island and 2.7 months of data at Saxon; therefore, once replaced, these Song Meters were run for an extra 2 months to compensate for this. Recording was only possible over 8 months at Whanganui due to difficult access, and so these data were used to assess environmental rather than seasonal effects on call rates. We extended the recording at Hodges Bush to a total of 22 months to investigate the repeatability of the seasonal pattern of call rates.

The Song Meters were placed on ridges to gain the maximum listening coverage but were positioned away from the prevailing wind to minimise weather interference. They were set 1.5 m above ground level, screwed onto trees that were no more than 20 cm in diameter and away from forest epiphytes that could cause rustling noise in the wind.



Figure 1. Song Meter SM2+ automated recorder deployed at Hodges Bush, central Northland.

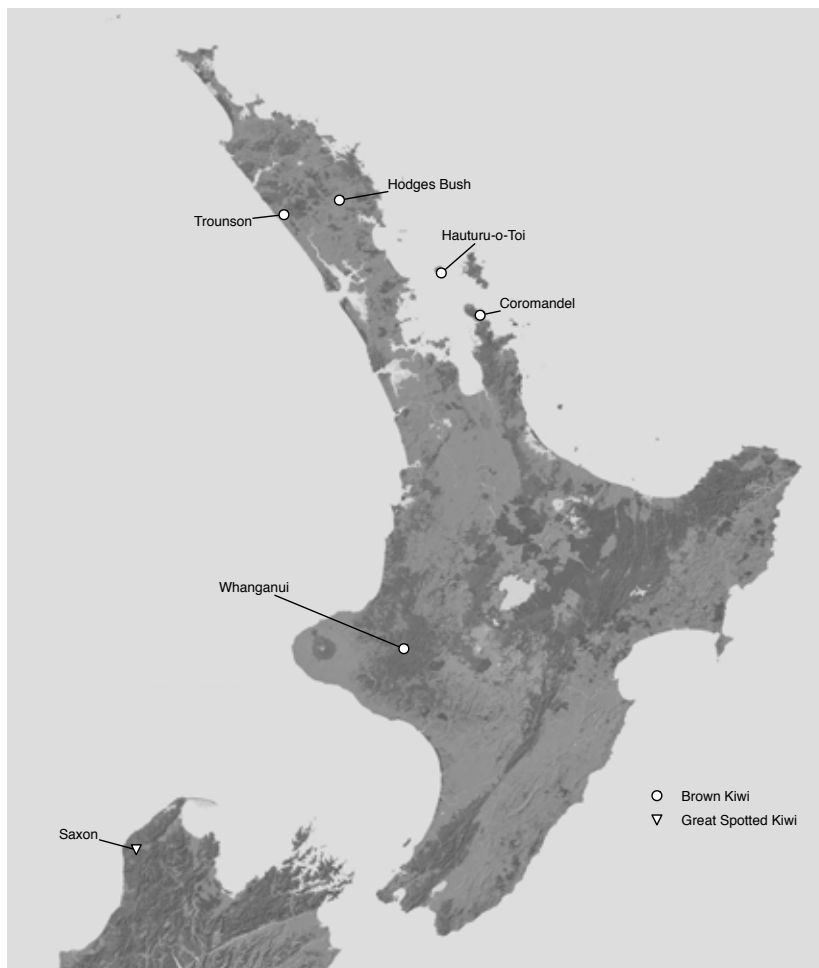


Figure 2. Map showing the locations of the six study sites at which Song Meter SM2+ automated recorders were deployed.

Recordings were conducted from sunset to sunrise on each night. The recordings were made at a 16 kHz sampling rate in stereo and stored as compressed wave (WAC) format files. The Song Meters were powered by an external 12 V battery to enable extended recording time. Each month, the batteries and SDHC cards of each unit were exchanged with freshly-charged batteries and empty SDHC cards.

The Song Meters at Hodges Bush and Trounson were calibrated side by side with a person listening for 2.5 hours and 2 hours, respectively, on calm, dry nights.

2.2 Study sites

Hodges Bush is located 19 km northwest of Whangarei city and is a privately owned 35 ha forest remnant set in hill country farmland, with an adjoining 15 ha radiata pine (*Pinus radiata*) plantation. The recording site ($-35^{\circ} 37' 19''$, $174^{\circ} 9' 18''$) had a listening coverage over about 30 ha of forest/ forest and farmland, which is inhabited by a population of 10 banded pairs of brown kiwi (Peter Graham, Department of Conservation (DOC), pers. comm.). The forest is largely taraire (*Beilsmedia taraire*) and tōtara (*Podocarpus totara*) with an open understorey.

Trounson Kauri Park is located in western Northland, 40 km north of Dargaville. It is a 586 ha block of mature kauri (*Agathis australis*) forest. The recording site ($-35^{\circ} 43' 19''$, $173^{\circ} 38' 2''$) was 150 m inside the northern boundary of the forest and covered about 90 ha of forest and forest margin. About 15 pairs of brown kiwi live within this area (Jeff Hall, DOC, pers. comm.).

Te Hauturu-o-Toi / Little Barrier Island (3083 ha) lies 60 km northeast of Auckland City. The recording site ($-36^{\circ} 12' 58''$, $175^{\circ} 3' 32''$) was within secondary regenerating forest of largely mānuka (*Leptospermum scoparium*) and the listening area covered 35 ha that is inhabited by an estimated five to seven brown kiwi pairs. Cook's petrel (*Pterodroma cookii*) breed on the island and were noisy at night between August and April.

The Coromandel site, near Port Charles, was on an existing kiwi monitoring station (K404; $-36^{\circ} 32' 20''$, $175^{\circ} 27' 50''$). This site is largely covered by cut over forest dominated by mānuka and is situated 1200 m from the sea. The recording site had an effective listening coverage of approximately 110 ha and is occupied by at least seven pairs of brown kiwi (Peter Stewart, pers. comm.).

The Whanganui site is within the Whanganui National Park in the central/lower North Island ($-39^{\circ} 18' 00''$, $175^{\circ} 1' 48''$). It has a low-density kiwi population compared with Northland, with about four pairs of brown kiwi being heard from the recording site (Daniel Hurley, DOC, pers. comm.). The listening coverage is about 80 ha. In this area, tributaries of the Whanganui River run through deeply incised gorges, with many bluffs and V-shaped valleys. The vegetation consists of podocarp hardwood lowland forest, with kāmahi (*Weinmannia racemosa*) and tawa (*Beilschmiedia tawa*) as the main canopy species.

The Saxon site is 900 m west of Saxon Hut on the Heaphy Track, and is about 100 m east of the site used by McLennan & McCann (1991). The recording site ($-40^{\circ} 53' 13''$, $172^{\circ} 17' 58''$) was in the open in red tussock (*Chionochloa rubra*) grassland on a raised river terrace, which sits above tussock-covered riverflats and is surrounded by hills covered in beech forest (*Fuscospora* spp. and *Lophozonia menziesii*). The site had a listening coverage of 70 ha and about five pairs of great spotted kiwi occur in parts of that zone (R. Colbourne, pers. obs.).

2.3 Spectrogram analyses

The WAC files were decompressed into WAV format for analysis using Raven Pro 1.4 (Cornell Laboratory of Ornithology, Ithaca, NY, USA). The recordings were viewed as spectrograms with a 512-sample Hann window and 31.3 Hz resolution (Figs 3 & 4). The kiwi calls were identified manually by drawing Raven 'selection' boxes around each call, and the frequency and temporal limits of each call were then exported from Raven and collated in Microsoft Excel spreadsheets for each site. Kiwi calls that were very strong (judged to be within 100 m) were given a score of 1, those that were very faint were given a score of 3 and those in between were given a 2. This helped to distinguish different kiwi heard over short time frames.

Each kiwi call is a series of repeated notes, or syllables, with males producing consistently higher frequency calls than females (Corfield et al. 2008; Digby et al. 2013). To differentiate between overlapping calls, we used a 5-second rule—if a bird called and then stopped for more than 5 seconds, then that was regarded as one call, whereas if it stopped and resumed within 5 seconds, the multiple calls were regarded as one continuous call.

We also recorded information on background noise in each three-hour WAV file by listening to the sound file and inspecting the background noise levels in the spectrogram. The main noises were wind (a scale of 0-3; 0 = no wind, 1 = light wind, 2 = moderate to strong wind and 3 = severe wind), rain (a scale of 0-3; 0 = no rain, 1 = light rain, 2 = moderate to heavy rain and 3 = torrential downpour), sea noise at Coromandel (a scale of 0-3) and seabird noise (Cook's petrel) on Te Hauturu-o-Toi / Little Barrier Island (a scale of 0-3).

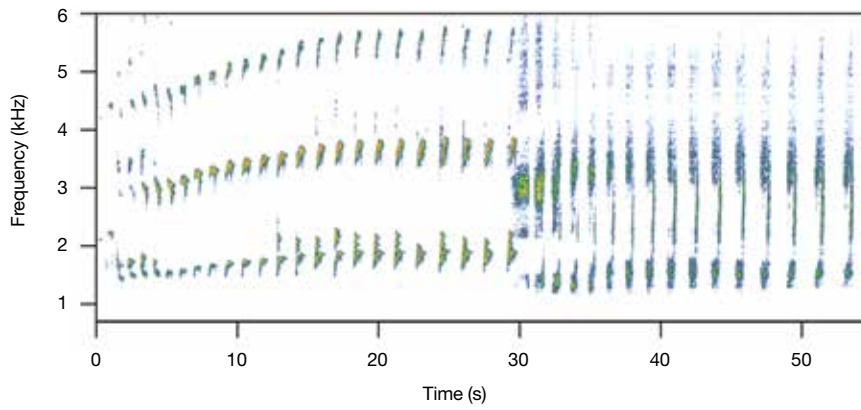


Figure 3. Spectrogram of a pair of brown kiwi calling. The male call appears first, followed by the female call, with no overlap between the two.

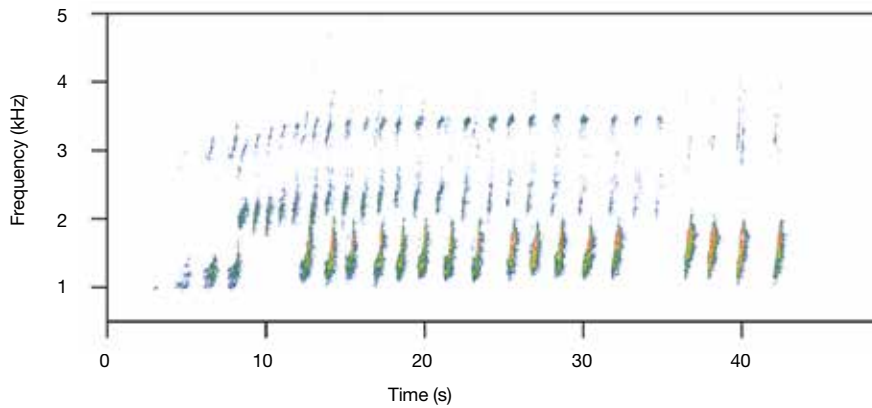


Figure 4. Spectrogram of a pair of great spotted kiwi calling. The female call appears first (lower frequency), followed by the male call completely overlapping.

2.4 Statistical analyses

The relationship between calling activity and time of night was analysed by dividing each night into 10 periods of equal length, to account for changing night length during the year. Thus, time of night was given as a percentage, with each time period ('decile') covering 10% of the night. The number of female and male kiwi calls were summed, and environmental variables were scored for each of these deciles. To assess the available moonlight in each time period, moon phase and altitude were calculated at the middle of each decile using the package *moonsun* (version 0.1.2; Komsta 2010) in R (version 3.01; R Core Team 2013). An altitude-adjusted moon phase was then used, which was set to zero when the moon was below the horizon.

The variation in kiwi call counts between time periods was analysed separately for each site using generalised additive models in R package *mgcv* (Wood 2011). The response variable was the number of counts per decile, while kiwi gender, night number from the start of the observation period, decile, altitude-adjusted moon phase, and two to four environmental parameters (wind and rain for all sites, plus sea noise for Coromandel and seabird noise for Te Hauturu-o-Toi/ Little Barrier Island) were included as explanatory variables. An offset of $\log(\text{decile length})$ was also included to account for variation in the duration of deciles throughout the year. Night number was used rather than year and day of year because of the low number of years recorded at each site. A negative binomial error distribution was used to account for slight overdispersion of the data.

Penalised cubic regression splines were fitted to the night number, decile and altitude-adjusted moon phase to account for non-linear relationships with call rate. A two-dimensional tensor

smoother was also applied to night number and decile to allow for seasonal variation in call rates, with a different smoother being used for each sex. Since there was significant temporal autocorrelation of residuals in the generalised additive models, an auto-regressive moving-average (ARMA) correlation error structure was used with an auto-regressive parameter (p) of 1 and a moving-average parameter (q) of 1 (chosen from inspection of the autocorrelation and partial autocorrelation functions). This was initially applied to deciles within the same night, with zero correlation for deciles on separate nights. Bonferroni-corrected confidence intervals of the autocorrelation function were then used to assess residual independence and if there was still significant autocorrelation, the ARMA(1,1) correlation structure was applied to time periods within groups of 3 nights rather than 1 night. In all cases, this resolved the residual autocorrelation.

All covariates were included in the final model, since preferred informatic-theoretic methods (Anderson et al. 2000) are not possible for generalised additive models with correlation structures in R.

3. Results

Recordings were made over 150 to 562 nights, with over 60 000 calls detected across all six sites (Table 1).

Calibration using trained listeners showed that the Song Meters detected 75% of calls heard (33 out of 44) at Hodges Bush and 73% of calls heard (11 out of 15) at Trounson.

Table 1. Monitoring periods and kiwi calls detected at each study site.

Note: a one-sample proportions test with continuity correction was used to assess whether there was a significant difference between male and female call rates.

SITE	SPECIES	START DATE	END DATE	TOTAL NIGHTS	TOTAL HOURS	MALE CALLS	FEMALE CALLS	M:F	
								χ^2	<i>P</i>
Hodges Bush	Brown Kiwi	23/5/2011	17/3/2013	562	6278	22521	8486	6352	<0.001
Coromandel	Brown Kiwi	14/9/2011	29/10/2012	262	2945	5662	1741	2076	<0.001
Trounson	Brown Kiwi	07/12/2011	18/02/2013	386	3933	6379	1078	3767	<0.001
Te Hauturu-o-Toi / Little Barrier Island	Brown Kiwi	14/12/2011	02/11/2013	394	4224	5991	1726	2356	<0.001
Whanganui	Brown Kiwi	08/11/2012	05/07/2013	150	1696	986	385	262.6	<0.001
Saxon	Great Spotted Kiwi	21/03/2012	23/02/2014	459	5107	3157	3072	1.113	<0.001
Total				2213	24183	44696	16488		

3.1 Temporal variation in call rates

The call rates of both brown and great spotted kmales and females showed significant variation with time of year and time of night (Figs 5 & 6). At all sites, there was a strong association between the timing of peak calling for males and females in terms of both time of year and time of night, although male call rates exhibited larger seasonal fluctuations.

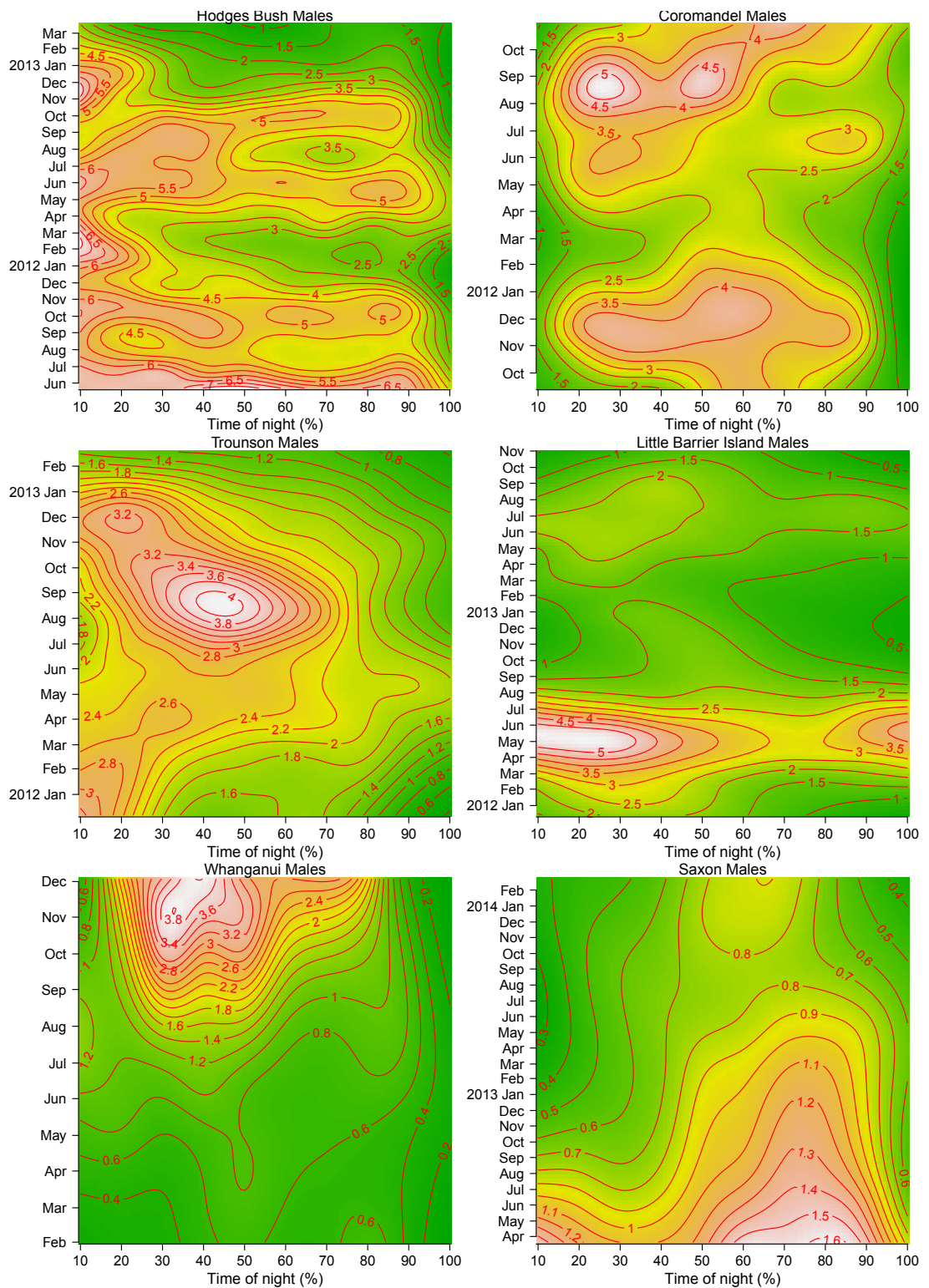


Figure 5. Variation in male brown kiwi and great spotted kiwi (Saxon) call rates (per hour) with time of year and time of night. Shading and contours provide the modelled change in counts, assuming that all other covariates are constant and at their median values.

For brown kiwi, the seasonal variation in call rates was associated with breeding. This was best demonstrated by the clear repeated peaks in calling at Hodges Bush immediately before the June–July egg-laying period. The other brown kiwi sites also showed similar seasonal peaks, but annual patterns were less clear due to the shorter monitoring periods at these sites.

In all brown kiwi populations, peak calling usually occurred in the first half of the night for both sexes. However, calling occurred later in the night during the main incubation periods (July–

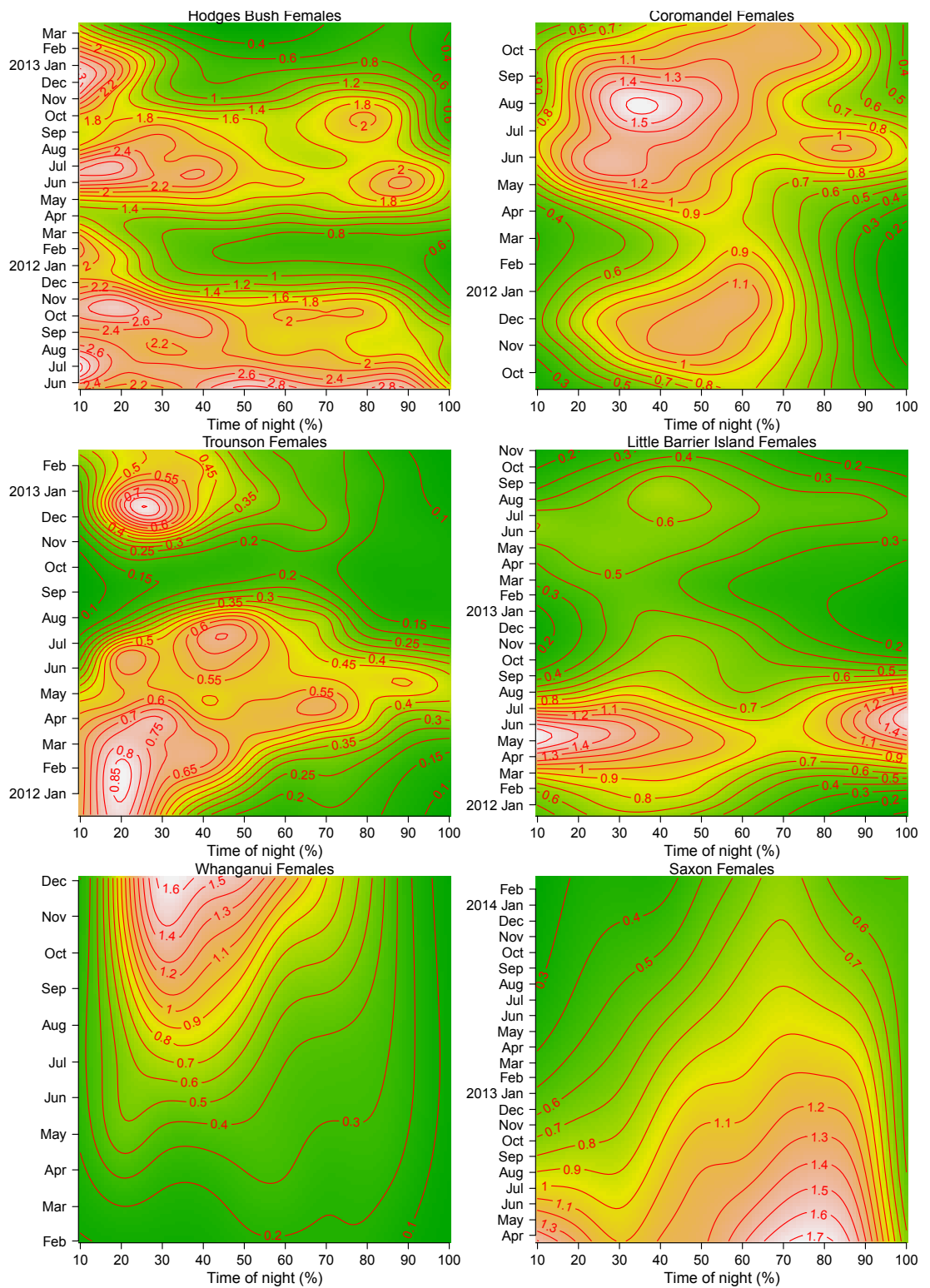


Figure 6. Variation in female brown kiwi and great spotted kiwi (Saxon) call rates (per hour) with time of year and time of night. See Fig. 5 for interpretation.

September and November-February), with this seasonal change being particularly pronounced at Trounson. There was also some variation between sites in when peak calling occurred during the night. At Hodges Bush, call rates peaked in the first 10% of the night, whereas at the other brown kiwi sites the highest rates usually occurred from 10% to 30% of the night outside the breeding period. Calling activity late in the night showed much more seasonal variation than in the first part of the night.

Great spotted kiwi exhibited a very different calling pattern from brown kiwi, with calls demonstrating less seasonal variation and poor repeatability from year to year, and call rates peaking in the second half of the night.

3.2 Environmental variation in call rates

There was variation in the relationship between altitude-adjusted moon phase and call rates between sites (Fig. 7). There was no significant variation in the calling rates of male brown kiwi with moon phase at any of the sites; however, the calling rates of female brown kiwi at Whanganui were related to moon phase. In great spotted kiwi, the calls of both males and females tended to increase with increasing moon phase to about 60% illumination, and then decreased for brighter moon periods; this effect was only significant for females, however.

As expected with acoustic monitoring, increasingly heavy rain led to a reduction in call rates at all sites (Fig. 8 and Appendix 1). In general, this masking effect of rain did not affect one sex more than the other, with the exception of Hodges Bush, where heavy rain masked female calls more than male calls.

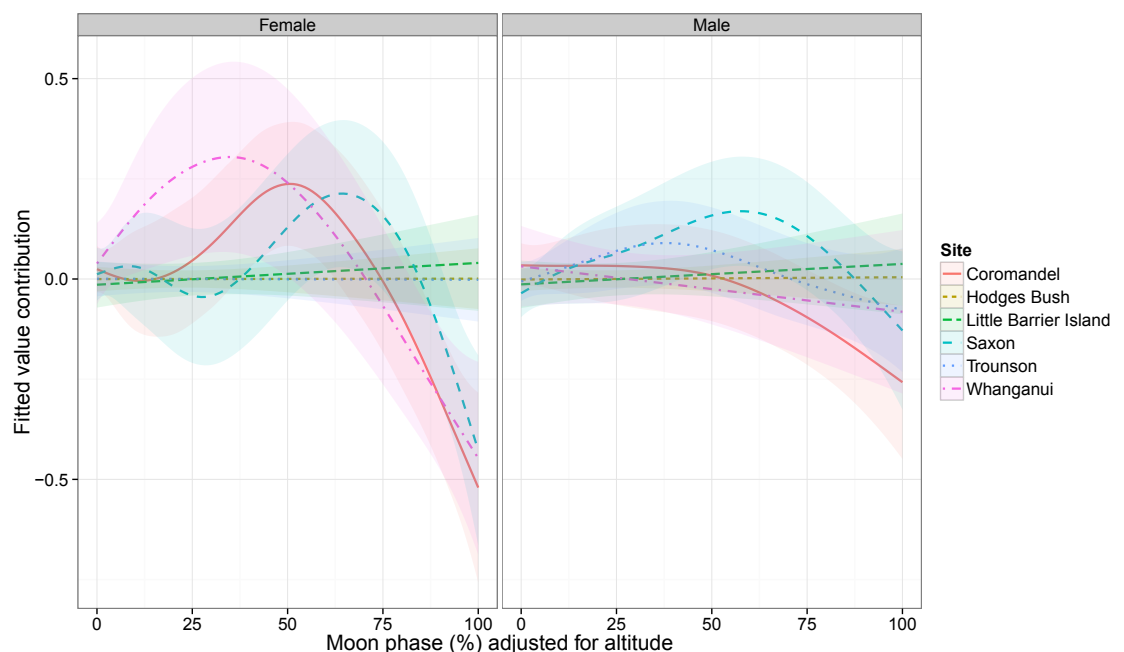


Figure 7. The effect of altitude-adjusted moon phase (set to zero when moon below the horizon) on brown kiwi and great spotted kiwi (Saxon) call rates. Shadings show 95% confidence intervals.

Increasing wind speed also led to lower call rates, although this was generally only significant for higher wind speeds (Fig. 8 and Appendix 1). Female calls tended to be more adversely affected by high winds; however, this effect was only strongly significant for very high wind speeds, and there was no significant effect at Hodges Bush—the site with the most data.

Noise from waves and seabirds did not significantly affect call rates at Coromandel and Te Hauturu-o-Toi/ Little Barrier Island, respectively. Female calls were elevated compared with males during periods of very high sea noise, however (Fig. 8).

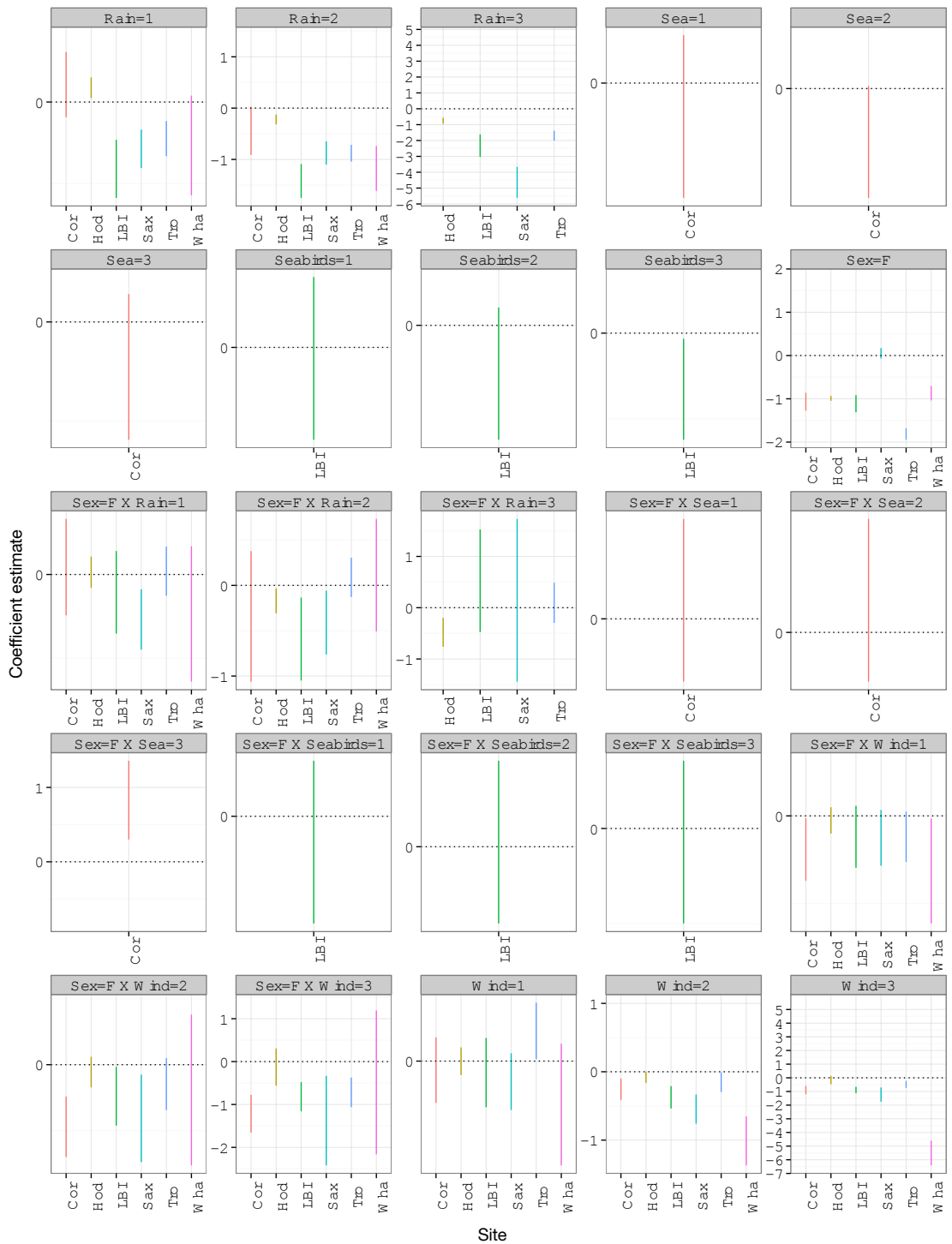


Figure 8. Effect sizes from the generalised additive models showing the influence of sex and environmental conditions on brown kiwi and great spotted kiwi (Saxon) calls detected. Each subplot shows the effect size for each site. Abbreviations: Cor = Coromandel, Hod = Hodges Bush, LBI = Te Hauturu-o-Toi / Little Barrier Island, Sax = Saxon, Tro = Trounson, W ha = Whanganui. Bars display 95% confidence intervals; where these do not intersect zero (equivalent to a score of 0 for the variable of interest), the effect can be considered to significantly affect call rates.

4. Discussion

4.1 Male:female call ratio

4.1.1 Brown kiwi

Male brown kiwi call rates were significantly higher than female call rates at all sites (Table 1), but ratios varied from 2.56:1 at Whanganui to 5.92:1 at Trounson. Similarly, Colbourne & Kleinpaste (1984) found a 2.54:1 call ratio in favour of males at Waitangi Forest, Northland, and Miles (1995) reported 2.78 male to female calls at Tongariro Forest. The sex ratio of adult males and females has been found to be close to unity at Hodges Bush and Trounson (Robertson & Fraser 2009; Hugh Robertson, DOC, pers. comm.), and so the lower detection rate of females was presumably due to them calling less frequently than males rather than them being at lower abundance. Therefore, since females are generally harder to detect, listening periods need to be long enough to detect most females resident within calling range, especially in low-density populations.

4.1.2 Great spotted kiwi

Unlike brown kiwi, there were no sex biases in call rates for great spotted kiwi (Table 1), which is in accordance with results from human listening records (Colbourne 2006). A total of 942 hours listening resulted in 1168 male and 1107 female calls heard, which equates to a male to female call ratio of 1.1:1.

4.2 Temporal variation

4.2.1 Brown kiwi

There was significant seasonal variation in brown kiwi calls (Figs 5 & 6). At Hodges Bush, the peak in calling (May–June) coincided with mating and the start of incubation of the first clutch of the season (median date of the first egg being laid in study areas within 5 km of Hodges Bush was 20 June in 2011; Hugh Robertson, DOC, pers. comm.). The Song Meter at Hodges Bush ran for 22 months, and the peaks and patterns of calling corresponded well between different years. However, there were much lower call rates in December 2012 to March 2013 than in December 2011 to March 2012 and the call ratio of males to females also dropped considerably during this time (Fig. 9). The total number of kiwi remained the same during this period, as adults were monitored by transmitters (Peter Graham, DOC, pers. comm.). This seasonal difference in call rate can possibly be attributed to the very dry ground conditions in Northland in the summer–autumn of 2012/13 when the area was officially declared as suffering from a drought (NZ Herald 2013). This would have made it difficult for birds to probe and feed, which would have had a greater effect on males than females because only males incubate in this species (Colbourne 2002). Thus, males would have continued to lose more weight after the breeding season, reducing their call rate. This drought effect may have been more exaggerated for the Te Hauturu-o-Toi / Little Barrier Island population (Figs 5 & 6) as the calling rates were significantly lower in December 2012 to August 2013 than in the previous season.

There were also changes in the variation of call rates through the night, which were likely related to breeding. Calls occurred later at night during the breeding period, probably because males were incubating and not calling until they emerged from their nests later in the night. However, the time of night at which males come off the nest and start calling is not necessarily the same everywhere. Even within a single population there can be a time synchrony when all neighbouring males come off their eggs after sunset to feed and call, but on the same night only a kilometre away this can be reversed, with males leaving the nest early in the morning (Colbourne 2002). Birds' decisions about when to leave their nests maybe related to differences in micro-habitat, environment or hunger.

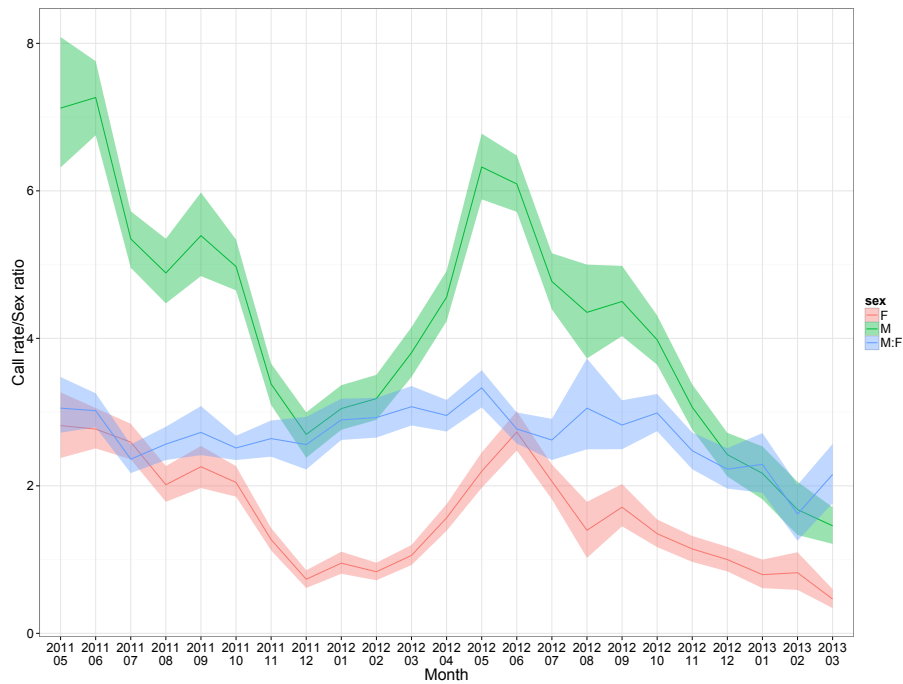


Figure 9. Seasonal variation in brown kiwi call rate and sex ratio (male:female) of calls at Hodges Bush, Northland. The shaded area represents the 95% confidence interval. Note the significant difference in call rates between years in January to March for males and October and March for females and the significant differences in the sex ratio of calls between years in February and March, and trends through late summer in the 2 years.

There were also differences between sites in when peak calling occurred during the night during the non-breeding period. For example, Hodges Bush birds mostly called at the start of the night, while bird calls peaked later at other sites. Hodges Bush contains the densest population of kiwi and so it may be crucial that birds call as soon as they emerge from their shelters to maintain their territories. By contrast, birds in the lower density populations at Coromandel and Whanganui may not have the same urgency for territorial defence and so may spread their calling more evenly through the night.

4.2.2 Great spotted kiwi

We found that the call rate of great spotted kiwi was lowest in August to December, which corresponded with the breeding season. By contrast, the highest call rates were detected in midsummer to late autumn/early winter for females and midsummer to mid-autumn for males (Figs 5 & 6).

Like McLennan & McCann (1991), we found that most great spotted kiwi calling occurred in the hours just before dawn. However, this was only true from mid-summer through to early spring, with call rates being high throughout the second half of the night during the rest of the year for both sexes (Figs 5 & 6).

4.3 Environmental variation

4.3.1 Moonlight

The Best Practice Manual for kiwi (Robertson & Colbourne 2003) recommended that kiwi monitoring should take place only during the darker moon phases and this advice probably still holds, since some negative effects associated with bright moonlight were noted for female brown kiwi at Whanganui and female great spotted kiwi at Saxon. This latter finding differs from that of McLennan & McCann (1991), who found that moonlight had no effect on call rate in great spotted kiwi.

We suspect that environmental factors rather than genetic factors were responsible for the changes in call rate with moonlight, such as whether a population was at carrying capacity or there was an abundance of food.

4.3.2 Wind and rain

The noise from wind and rain can make listening for kiwi extremely trying and uncomfortable for the people listening. Even if kiwi are calling, it is difficult for humans to pick up calls in these conditions because of the sound of wind or rain on the observer's clothing and surrounds. The advantage of acoustic recorders is that spectrograms allow frequency separation, enabling the higher harmonics of calls to be detected above the lower-frequency wind noise. Likewise, in light to moderate rain, kiwi calls can still be seen—although very heavy rain does mask calls (particularly female calls) on spectrograms.

4.4 Future monitoring for kiwi

Since brown kiwi call rates vary at different times of the night during the breeding period, we recommend that all new brown kiwi populations be monitored between May and July, to avoid monitoring during the second half of the incubation period. Thus, for brown kiwi, we recommend that existing monitoring continues to follow the best practice promulgated by Robertson & Colbourne (2003), i.e. monitor populations between April and June, away from the full moon (because females in some populations are affected by the full moon), and avoid windy or rainy nights.

For great spotted kiwi, we recommend that call count monitoring take place between January and April, away from bright phases of the moon, and excluding windy or rainy nights. The highest call rates are recorded in the last 3 hours before dawn, but this is not a practical time for people to listen if a mix of humans and acoustic recorders are being used. Therefore, we recommend staying with the conventional listening period of the first 2 hours after civil twilight ends (45 minutes after sunset).

As a result of the extreme seasonal variation from one year to the next at some sites, we caution against comparing counts over just a few years. There are good seasons and bad, and so sites need to be surveyed a number of times and the results averaged to obtain meaningful monitoring results.

In addition, over the course of a night, kiwi calls tend to be clustered rather than spread out evenly, meaning that counts that are made over short periods are likely to produce highly variable results. Furthermore, the time of peak calling during the night is also highly variable between sites. The main advantages of acoustic recorders over human listeners are that they can record much more data at much less cost for much longer periods each night and for weeks on end. If files are saved securely, the data can also be checked or re-analysed at a later date if there are any queries over the validity of the results. Acoustic recorders can also detect calls under poor conditions of wind and rain, when humans may struggle due to the low-frequency noise overwhelming the senses. However, the acoustic recorder used in this study (Song Meter SM2+) is not currently as good as a human ear under ideal listening conditions.

If acoustic devices are to be used as a tool to monitor long-term changes in populations, it is vital to calibrate them against different models or brands so that better designs and specifications through time do not get mistaken for improvements in the population under study. For example, since this study began, the Song Meter SM2+ has been superseded by the Song Meter SM3 and then the Song Meter SM4. With the rapid development of smart phone technologies, it will only be a matter of time before these devices equal or better the human ear.

For long-term monitoring, it is also important to set recorders at the exact same location, height and orientation of microphones each time counts are repeated. Permanent attachment posts are

probably preferable to attaching them to trees or branches, because trees grow and die, either of which could affect the results. Finally, the individual recognition of calls can provide a better estimate of actual kiwi numbers than numbers of calls—which will be the subject of a further paper.

All these methods are essential to reduce variation from the use of the recording equipment. However, this study has highlighted the considerable variation of call rate from night to night and, at Hodges Bush, from season to season. If the goal is to monitor numbers of kiwi accurately then using recorders alone is too crude a method, does not take into account the lack of delectability of chicks and juveniles, and it should be done in conjunction with other methods such as banding and recapture using trained kiwi detection dogs to remove biases in the captures.

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Appendix 1

Effect sizes for the generalised additive models of call rate variation with sex and environmental conditions at each site

SITE	EFFECT	ESTIMATE	s.e.	<i>t</i>	<i>P</i>
Hodges Bush	(Intercept)	-2.91	0.019	-150.12	0.000
	Sex=F	-0.99	0.029	-34.57	0.000
	Rain=1	0.09	0.032	2.70	0.007
	Rain=2	-0.22	0.049	-4.55	0.000
	Rain=3	-0.76	0.100	-7.56	0.000
	Wind=1	0.00	0.026	-0.02	0.986
	Wind=2	-0.08	0.041	-2.04	0.042
	Wind=3	-0.16	0.156	-1.05	0.292
	Sex=F × Rain=1	0.01	0.048	0.29	0.772
	Sex=F × Rain=2	-0.17	0.070	-2.41	0.016
	Sex=F × Rain=3	-0.48	0.144	-3.33	0.001
	Sex=F × Wind=1	-0.03	0.038	-0.67	0.502
	Sex=F × Wind=2	-0.06	0.059	-0.95	0.342
	Sex=F × Wind=3	-0.13	0.221	-0.58	0.563
Coromandel	(Intercept)	-2.91	0.019	-150.12	0.000
	Sex=F	-0.99	0.029	-34.57	0.000
	Rain=1	0.09	0.032	2.70	0.007
	Rain=2	-0.22	0.049	-4.55	0.000
	Rain=3	-0.76	0.100	-7.56	0.000
	Wind=1	0.00	0.026	-0.02	0.986
	Wind=2	-0.08	0.041	-2.04	0.042
	Wind=3	-0.16	0.156	-1.05	0.292
	Sex=F × Rain=1	0.01	0.048	0.29	0.772
	Sex=F × Rain=2	-0.17	0.070	-2.41	0.016
	Sex=F × Rain=3	-0.48	0.144	-3.33	0.001
	Sex=F × Wind=1	-0.03	0.038	-0.67	0.502
	Sex=F × Wind=2	-0.06	0.059	-0.95	0.342
	Sex=F × Wind=3	-0.13	0.221	-0.58	0.563
Trounson	(Intercept)	-2.91	0.019	-150.12	0.000
	Sex=F	-0.99	0.029	-34.57	0.000
	Rain=1	0.09	0.032	2.70	0.007
	Rain=2	-0.22	0.049	-4.55	0.000
	Rain=3	-0.76	0.100	-7.56	0.000
	Wind=1	0.00	0.026	-0.02	0.986
	Wind=2	-0.08	0.041	-2.04	0.042
	Wind=3	-0.16	0.156	-1.05	0.292
	Sex=F × Rain=1	0.01	0.048	0.29	0.772
	Sex=F × Rain=2	-0.17	0.070	-2.41	0.016
	Sex=F × Rain=3	-0.48	0.144	-3.33	0.001
	Sex=F × Wind=1	-0.03	0.038	-0.67	0.502
	Sex=F × Wind=2	-0.06	0.059	-0.95	0.342
	Sex=F × Wind=3	-0.13	0.221	-0.58	0.563

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Appendix 1 continued

SITE	EFFECT	ESTIMATE	s.e.	t	P
Te Hauturu-o-Toi / Little Barrier Island	(Intercept)	-2.91	0.019	-150.12	0.000
	Sex=F	-0.99	0.029	-34.57	0.000
	Rain=1	0.09	0.032	2.70	0.007
	Rain=2	-0.22	0.049	-4.55	0.000
	Rain=3	-0.76	0.100	-7.56	0.000
	Wind=1	0.00	0.026	-0.02	0.986
	Wind=2	-0.08	0.041	-2.04	0.042
	Wind=3	-0.16	0.156	-1.05	0.292
	Sex=F × Rain=1	0.01	0.048	0.29	0.772
	Sex=F × Rain=2	-0.17	0.070	-2.41	0.016
	Sex=F × Rain=3	-0.48	0.144	-3.33	0.001
	Sex=F × Wind=1	-0.03	0.038	-0.67	0.502
	Sex=F × Wind=2	-0.06	0.059	-0.95	0.342
	Sex=F × Wind=3	-0.13	0.221	-0.58	0.563
Whanganui	(Intercept)	-2.91	0.019	-150.12	0.000
	Sex=F	-0.99	0.029	-34.57	0.000
	Rain=1	0.09	0.032	2.70	0.007
	Rain=2	-0.22	0.049	-4.55	0.000
	Rain=3	-0.76	0.100	-7.56	0.000
	Wind=1	0.00	0.026	-0.02	0.986
	Wind=2	-0.08	0.041	-2.04	0.042
	Wind=3	-0.16	0.156	-1.05	0.292
	Sex=F × Rain=1	0.01	0.048	0.29	0.772
	Sex=F × Rain=2	-0.17	0.070	-2.41	0.016
	Sex=F × Rain=3	-0.48	0.144	-3.33	0.001
	Sex=F × Wind=1	-0.03	0.038	-0.67	0.502
	Sex=F × Wind=2	-0.06	0.059	-0.95	0.342
	Sex=F × Wind=3	-0.13	0.221	-0.58	0.563
Saxon	(Intercept)	-2.91	0.019	-150.12	0.000
	Sex=F	-0.99	0.029	-34.57	0.000
	Rain=1	0.09	0.032	2.70	0.007
	Rain=2	-0.22	0.049	-4.55	0.000
	Rain=3	-0.76	0.100	-7.56	0.000
	Wind=1	0.00	0.026	-0.02	0.986
	Wind=2	-0.08	0.041	-2.04	0.042
	Wind=3	-0.16	0.156	-1.05	0.292
	Sex=F × Rain=1	0.01	0.048	0.29	0.772
	Sex=F × Rain=2	-0.17	0.070	-2.41	0.016
	Sex=F × Rain=3	-0.48	0.144	-3.33	0.001
	Sex=F × Wind=1	-0.03	0.038	-0.67	0.502
	Sex=F × Wind=2	-0.06	0.059	-0.95	0.342
	Sex=F × Wind=3	-0.13	0.221	-0.58	0.563