The secret life of wild brown kiwi: studying behaviour of a cryptic species by direct observation

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Abstract: Kiwi possess many unusual features that make them interesting subjects for behavioural study. However, their nocturnal, cryptic nature has meant that studies to date rely on data collected indirectly. Infrared technology has enabled us to observe kiwi directly and here we present the first study of wild brown kiwi (*Apteryx mantelli*) behaviour by direct observation. We used handheld infrared video cameras to obtain c. 6 hours of video footage of kiwi over 19 months. Kiwi used native forest and exotic pasture habitats while active at night and spent most of their time foraging (75%). Prey capture rates were significantly higher in pasture than forest. The remaining 25% of time was spent walking, vigilant, engaged in comfort behaviours, escaping disturbance, and investigating obstacles. Direct social and courtship interactions were observed rarely. The senses of hearing, olfaction and touch seemed most important to kiwi. Touch was used for investigating terrain and negotiating obstacles. Hearing was used in response to sounds made by observers, conspecifics and other sources. Olfactory search behaviours (OSBs) were used in the direction of these sounds, and olfaction was also apparently used to assess odours on the ground. We observed no behaviours that appeared to be guided by vision. Behavioural repertoire size and diversity increased in winter, due to increases in OSBs towards conspecifics and other odour sources, and rarely observed behaviours. Prey capture rates also increased near-significantly in winter and microhabitat use was more diverse. Female kiwi at our study site had 30% longer bills than males, and probed into soil substrates on average 30% deeper. No other fine-scale behaviours that might reduce competition between kiwi sexes were observed.

Keywords: *Apteryx*; foraging; habitat use; hearing; microhabitat; nocturnal; olfaction; radio-telemetry; sensory systems; touch

Introduction

Kiwi (Apterygidae) are a family of five species of ground-dwelling birds (Burbidge et al. 2003), endemic to New Zealand. They possess features that make them ideal model organisms for studying a range of aspects of behavioural and sensory ecology. For example, kiwi appear to have foregone vision as a major sense (Martin et al. 2007) and instead possess auditory, tactile and olfactory specialisations that are unusual among birds and appear attuned to nocturnal activity (Wenzel 1968; Cunningham et al. 2007; Martin et al. 2007; Corfield 2009). Kiwi also exhibit reversed-sexual-size dimorphism (Robertson et al. 2003) that may have evolved under intense competitive pressure. Evidence for such pressure includes reports of high kiwi population densities from the 1800s (40–100 birds km^{-2}; Buller 1877 and 1888, in McLennan et al. 1996), current high densities of kiwi in some protected areas (e.g. Paerata Wildlife Management Reserve, 40 birds km^{-2}; Potter 1989; Potter & Cockrem 1992), and that kiwi were originally part of a suite of ground-foraging insectivorous birds, many of which are now endangered or extinct (Wilson 2004). Kiwi further possess a breeding system where females lay large rich eggs, which are incubated under a variety of social breeding arrangements including male-alone incubation (McLennan 1990). The mating system of kiwi appears to range from complete monogamy, through to co-operative breeding, depending on species and population (Colbourne 1991; Taborsky & Taborsky 1999; Ziesemann et al. under review).

Kiwi are generally nocturnal and often live at low densities (e.g. one per 100 ha; McLennan & Potter 1992) in thickly vegetated habitats, making them difficult to observe directly. For this reason the majority of studies of wild kiwi behaviour have been carried out indirectly using radio-telemetry and have focused on territoriality, spacing and large-scale habitat use (McLennan et al. 1987; Potter 1990; Miles 1995; Taborsky & Taborsky 1995, 1999). Foraging behaviour has so far been inferred from diet studies that have relied on analysis of faeces (e.g. Kleinpaste 1990; Miles 1995; Shapiro 2005). More recently, smart transmitter technology has allowed remote data collection on aspects of breeding behaviour such as incubation patterns (pers. obs.). Rarely have researchers been able to spend time directly observing kiwi apart from brief encounters (e.g. Colbourne & Kleinpaste 1983; Taborsky & Taborsky 1995). For this reason, we lack systematic descriptions of fine-scale wild kiwi behaviour and microhabitat use. The development of small hand-held infrared video cameras, as well as lightweight infrared lights, now provides opportunity for the direct observation of nocturnal animals.

In this study we used direct observation via infrared cameras to observe free-living brown kiwi (*Apteryx mantelli*) behaviour and microhabitat use over a period of 19 months. A major purpose of the study was to typify fine-scale behaviours exhibited by free-living kiwi when active at night in forest and pasture habitats. Here we provide detailed descriptions of these behaviours and assess the data for differences between sexes, seasons and habitat types. We also use our results to make inferences about the sensory systems used by kiwi.

Methods

Study site and kiwi population

We carried out our research on South Ponui Farm, Ponui Island, New Zealand (1770 ha; 36 55' S, 175 11' E). The study was concentrated in an area comprising two forested gullies (Red Stony Hill Gully and Pipe Gully) and surrounding pastureland in the southeastern corner of a large native forest fragment (Fig. 1). Within the fragment, ridges were thickly vegetated with scrub and remnant kauri trees (*Agathis australis*), while gully floors contained tall forest with an open understorey that was extensively browsed by livestock. Raupo (*Typha orientalis*) swamps extended some distance along the gully floors. Shapiro (2005) provides further detail of vegetation cover.

Brown kiwi were translocated to Ponui Island in 1964 (Miles & Castro 2000) and kiwi density on the island is now estimated at about one per hectare (Cunningham et al. 2007). Between 30 and 36 kiwi within the study area carried radio-transmitters during the course of this study, representing an estimated 25% of the birds using Pipe Gully and 50–70% of birds using Red Stony Hill Gully.

Kiwi morphometrics

Measurements from 30 radio-tagged kiwi (13 females, 17 males) were taken in April 2008. We used Kinchrome® Vernier callipers to measure bill length (following Robertson et al. 2003) and tarsus width to the nearest 0.1 mm and a Pesola® spring balance to weigh the birds to the nearest 5 g. Average difference in bill length between males and females was calculated for use in comparing probing depths. Measurements were also used to assess degree of sexual dimorphism.

Obtaining video recordings of kiwi

We made 11 trips ($n = 6$ nights) to the study site between January 2007 and September 2008 (approximately every second month) to video-record kiwi. Video recording was attempted for between 4 and 8 h from dusk every night (66 nights), except under severe adverse weather conditions. Recordings were made using Sony Handicams (DCR-HC40E and DCR-HC96E) with NightShot™ function and infrared spot lamps (IRLamp6, Bat Conservation and Management Inc.). Lamps and cameras were handheld; lamps were powered from 12V batteries carried in backpacks. Kiwi did not visibly react to the infrared light from the lamps.

Each evening, teams of two people walked set routes through the study site, including areas of forest (2 km) and pasture (1.6 km) (Fig. 1). Walking routes were biased by habitat as we avoided swamps and scrubby ridges due to the difficulty of obtaining clear footage in these areas. Kiwi were located by the rustling sounds they made when walking or foraging, and were recorded from the time they were first encountered until they moved out of view into thick vegetation or out of camera range. Kiwi were not followed when they left the area in which we were video-recording them. Radio-telemetry (Yagi aerial, TR4, Kiwitrack, Havelock North, NZ) was used to identify kiwi observed to be wearing a transmitter.
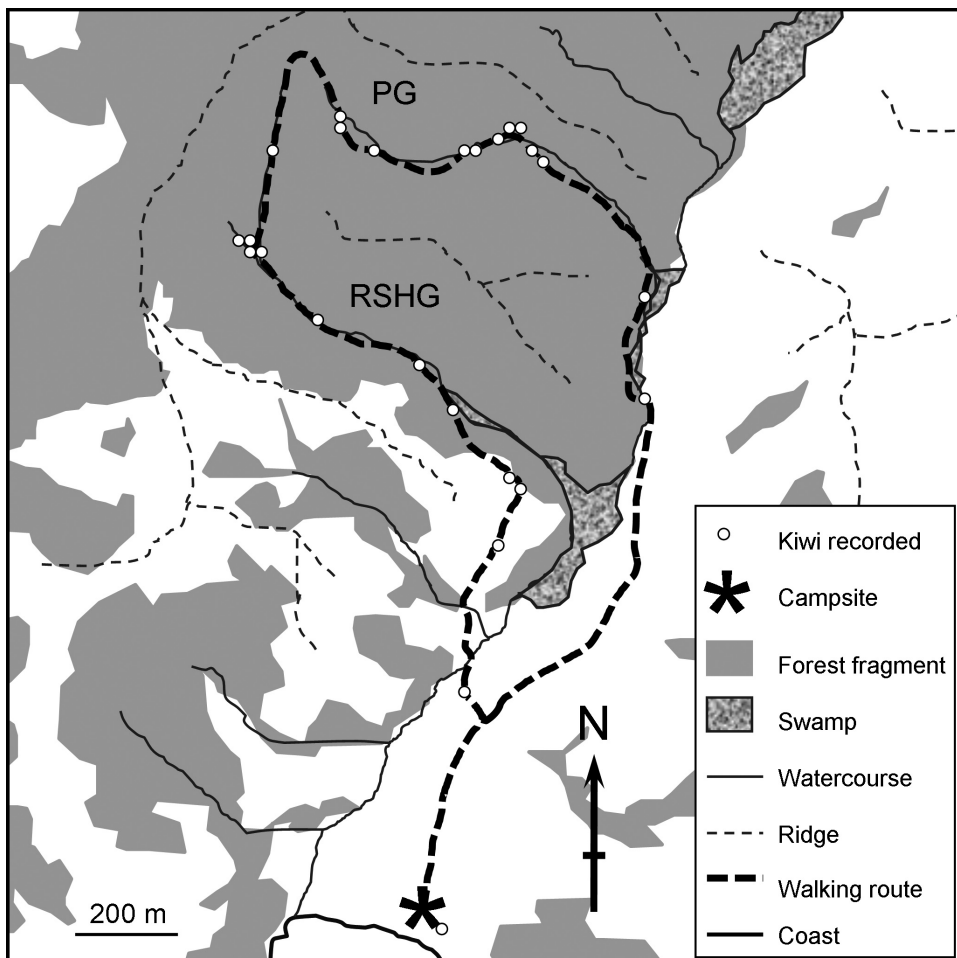

Figure 1. Map of the study area showing walking routes, locations of video-recorded kiwi encounters used in the analyses, and our campsite. PG = Pipe Gully, RSHG = Red Stony Hill Gully.

Assigning sex to untagged kiwi

Male and female kiwi at our study site were dimorphic in terms of bill length (see Results), and this feature can be used to sex kiwi (Robertson et al. 2003). However, we could not determine an accurate scale for directly measuring bill length from video recordings. Instead we developed a 'bill length ratio' measurement (BLR) that allowed sexing kiwi from video footage. The BLR is the ratio of the distance between the cere and eye to bill length (Fig. 2). When applying the BLR, it is important to correctly locate the top of the cere and to ensure the bird is in full lateral view. We therefore chose the clearest lateral-view still frames of each video-recorded kiwi and imported these into ImageJ (National Institute of Health 2008), which allows accurate measurement from photographs. We took five repeat eye–cere and bill-length measurements from each bird and used the averages to calculate each individual's BLR.

To calibrate the measurement, we compared the BLRs of adult tagged kiwi of known sex for which we had clear video still frames or photographs in lateral view ($n = 6$ males; 8 females). Males had an average BLR of 3.70 ± 0.22 SD, range $3.40 – 3.99$, 95% confidence interval $3.26 – 4.13$; females average BLR 5.17 ± 0.52 SD, range $4.28 – 5.88$, 95% confidence interval $4.15 – 6.19$. Because the average BLRs of male and female kiwi were significantly different (Wilcoxon rank sum W-test, $W = 21$, $P = 0.002$) and there was no overlap in range or confidence interval, we assigned female sex to individuals with BLRs ≥ 4.15. Males and juvenile birds, which overlap in bill measurements, could not be distinguished using BLR, so these were treated as a single category.

Assigning identity to untagged kiwi

Untagged kiwi of the same sex, videoed on different occasions, were assumed to be the same individual unless plumage was distinctively marked (some had pale feathering on the head), size was markedly different, or they were filmed in widely separated areas (e.g. top versus bottom of a gully, different gullies).

Data extraction from video recordings

All videos were screened for quality and bird identity before transcription. Poor quality videos (very dark, blurry, or kiwi obscured by vegetation) were discarded from analysis. Where multiple videos of the same individual kiwi had been obtained, data were transcribed from the highest quality video only, in order to avoid pseudoreplication. Where videos of an individual were of similar quality, the longest sequence was used. Videos were transcribed using the freeware video editing program VirtualDub™ (Lee 2008), which allowed us to step through recordings frame by frame.

Habitat and season

Habitats were broadly described as 'pasture' or 'forest' based on vegetation type. The year was divided into 'summer' (November–March) and 'winter' (May–September), because these categories better reflected the weather conditions on Ponui Island during our study than did the standard four seasons (pers. obs.).

Behavioural variables

Behaviours were typified by close examination of video recordings. Time spent engaged in each of six behaviour states (foraging, walking, comfort, vigilant, escape, investigation of obstacles) and detailed aspects of behaviours relating to these states were recorded (Table 1). Depths of probes into soil and leaf litter were measured relative to bill length, using the following scale: 1 < half bill, 2 ≥ half bill, 3 entire bill including cere, 4 part of face in probe hole.

Foraging microhabitat variables

Kiwi foraged in a variety of different microhabitat types within forest and pasture habitats. We classified these as: litter (leaf litter away from tree trunks); tree roots (within one kiwi body length of a tree trunk, or where roots emerged from the soil); logs (fallen logs/branches), supplejack tangles (*Ripogonum scandens* – a liana, with stems that form dense tangles close to the ground and that kiwi forage beneath); and fallen epiphytes; as well as banks, ditches, creek edges, swamp edges, grass roots, and bare ground. We extracted data from the video recordings on how long kiwi foraged in each of these microhabitat types. We did not collect data on the availability of each microhabitat within the study site, as availability, especially of ephemeral features such as fallen epiphytes, varied from month to month or even day to day after wind (pers. obs.). Our results therefore detail only the microhabitat types used by kiwi and provide no information on microhabitat choice or avoidance.
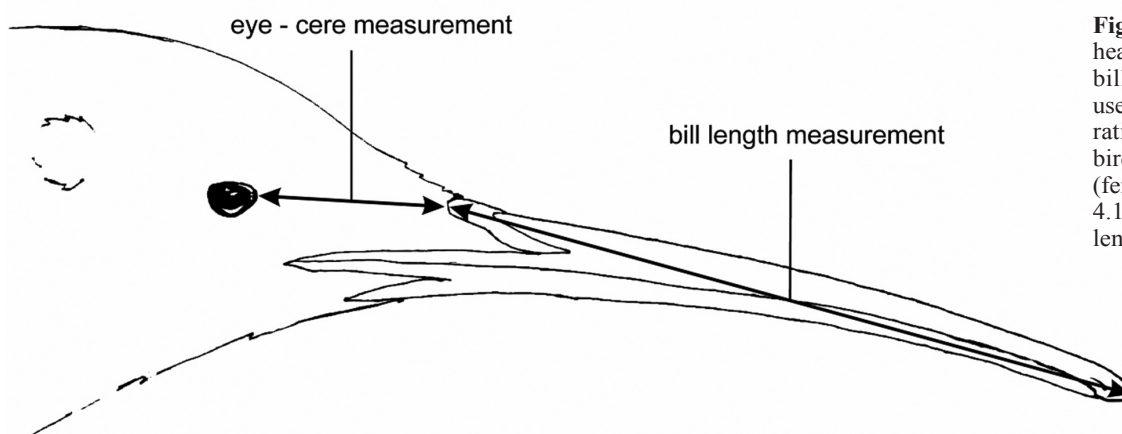

Figure 2. Diagram of a kiwi head showing eye – cere and bill length measurements used to calculate a bill length ratio for sexing untagged birds from video recordings (females: bill length ratio ≥ 4.15; males/juveniles: bill length ratio < 4.15).

Table 1. Ethogram of kiwi behaviours, including the aspects recorded and analysed and the percent of video sequences (*n* = 25) in which the behaviour occurred (% occurrence). The percent of time spent in each behaviour state was also recorded and used in analyses. One copulation sequence, one calling sequence and one fight sequence were recorded during the course of the study but were not included in the data analyses.

Behaviour state	Action	Description	% occurrence	Fine-scale aspects recorded and used in analyses
Foraging / orientation	Tap	Bill-tip sensory pad pressed briefly to the ground ahead. Kiwi tap the ground both while foraging and while walking.	100	− Tap frequency min^{-1} − Tap duration (s) − Ratio of taps to probes
Foraging	Rapid tap	Series of very short, rapid taps of the bill to the ground in a small area, bill not lifted far from the ground between taps; prey capture may follow.	60	− Rapid tap frequency min^{-1}: each back-to-back series of taps counted as one event. − Prey captures min^{-1}
	Soil probe	Bill inserted into soil substrate, depth ranges from bill-tip only, to entire bill and part of face. Head and bill may be repositioned via partial withdrawal of bill; vigorous rocking movement of whole body from legs sometimes occurs; bird may walk around bill during probe resulting in rotation of the bill within the ground; prey capture may follow. The conical probe holes left by deeper probes result from the rocking and rotation of the bill during probing.	88	− Depth of probes relative to bill length (see scale in Methods) − Probing frequency min^{-1} (total of soil & surface) − Duration of successful probes (s) − Duration of unsuccessful probes (s) − Percent of probes into soil
	'Surface' probe	Bill inserted into litter layer or matted grass roots in manner of a soil probe but angle often shallower. Bill may be shoved forward in the litter resulting in litter being shunted along, sometimes accompanied by the bird stepping forward. Head and bill movement and changes of angle may be apparent, but stepping around the probe and rocking of body not normally seen. Prey capture may follow.	96	− Percent of probes into litter/matted grass roots − Prey captures min^{-1} − Percent of captures in litter/ matted grass roots − Percent of captures in soil
	Bill hover	Looks like tapping but bill does not contact ground, rather hovers above; usually occurs in a short back-to-back sequence. May be used for obtaining information about scents on the ground left by prey, other species or conspecifics.	24	− Bill hover frequency min^{-1}
	Squeaky beak	Non-vocal squeaking noise produced while probing, apparently as the bill is removed from the substrate	Unknown	− Not recorded as detection dependent on distance to bird
Prey handling	Withdraw	Measured from the beginning of bill withdrawal from soil/litter after a successful probe / lifted from surface after successful rapid tap, until beginning of first swallowing movement	96	− Prey handling duration (sum of duration of withdrawal, swallow and latency) (s) − Number of bill flicks per capture
	Swallow	Rapid flicking/jerking of head and bill to toss the prey back within the bill ('bill flicking'). We sometimes observed prey-positioning movements during which the lower bill moved sideways independently of the upper bill.	96	
	Latency	Measured from the end of final bill flick in the swallowing sequence to beginning of next activity (e.g. start of next probe)	96	
Walking	Walk	Walking	100	− Percent of time walking
Escape	Run	Running	20	− Percent of time running
	Jump	Escape behaviour when startled, also used to get down banks and off logs	8	− Jumps min^{-1}
Comfort	Preen	Running bill through feathers; sometimes results in consumption of ectoparasites through conspicuous swallowing movements of head and bill	32	− Percent of time preening

Behaviour state	Action	Description	% occurrence	Fine-scale aspects recorded and used in analyses
	Scratch	Scratching of body, head and neck with foot	32	− Scratching bouts min^{-1}
	Shake	Puffing of body feathers followed by vigorous shake. Separate head and bill shake sometimes follows on from body shake, or can occur independently.	40	− Shakes min^{-1}
	Leaf toss	Rapid shaking of the head from side to side to clear bill of leaf litter speared during probing. Can involve opening and shutting of beak.	52	− Leaf toss min^{-1}
	Defecation	Defecation	8	− Defecation min^{-1}
Vigilance	Freeze	Freezes in position following disturbance	12	− Freeze min^{-1}
	Head lift	Head lifted above the level of the back and bill held horizontally, often in response to a noise audible to the observer. Can involve several back-to-back head lifts.	100	− Headlifts min^{-1}
	Olfactory search ('sniffing')	Stereotyped upright body posture, head and bill repeatedly drawn upwards and backwards in a series of audible 'sniffs'. Described in detail by Castro et al. (2010).	88	− 'Sniffs' min^{-1} towards observer − 'Sniffs' min^{-1} other directions
Investigation of obstacles	Bill reach	Reach forward with head and bill, tapping to investigate difficult terrain	24	− Bill reaches min^{-1}
Social / courtship	Call	Standing bird lifts head and neck and calls in a series of bars which involve wide opening of beak and lifting of upper bill to vertical while producing each bar	n/a	
	Grunting	Vocalisation made by birds in close proximity while engaged in other behaviours, e.g. foraging. On one occasion preceded copulation (see below)	n/a	
	Mewing	Vocalisation heard during pre-copulation grunting	n/a	
	Feather probing	Probing of the feathers of the other bird with the bill during courtship	n/a	
	Copulation	Female crouches on ground, male mounts briefly. In the sequence recorded, male's parted feathers offered a clear view of his uropygial gland prior to mounting. After (during?) copulation he fell backwards from the female onto his back on the ground. Copulation was followed by the male chasing the female with his beak inserted among her back feathers (both birds running).	n/a	
	Chasing	Chase post-copulation or during/after fighting	n/a	
	Fighting	Kicking and chasing accompanied by growling vocalisations	n/a	

Statistical analyses

Morphometric variables

Morphometric variables were normally distributed (Anderson–Darling tests, all $P > 0.10$) and were compared between male and female kiwi using two-tailed independent t-tests.

Footage length and behaviour data

Footage length and most behaviour data were not normally distributed (Anderson–Darling tests $P < 0.1$) and attempts at transforming the data did not redress these non-normal distributions. We therefore used non-parametric Wilcoxon rank sum W- tests to compare footage length and behaviours between sexes, seasons and habitat types. We used Wilcoxon signed-rank tests to compare related behaviours (e.g. the durations of successful versus unsuccessful probes). Both tests are reported in Results using the statistic W.

Size of behavioural repertoire was normally distributed (Anderson–Darling test, $P = 0.26$) and was compared between sexes, seasons and habitats using two-tailed t-tests. Shannon–Wiener diversity indices were calculated for behavioural repertoires of female and male/juvenile kiwi; kiwi video-recorded during 'summer' and 'winter'; and kiwi video-recorded in pasture and forest habitats. The Shannon–Wiener Index takes into account both the number of different behaviours used by kiwi (n, size of repertoire) and also the 'evenness' of use (i.e. how commonly each behaviour was observed). For calculating this index, behaviours were scored as present or absent in each video recording. The number of different behaviours performed by each bird could then be counted.

Likewise the number of times each behaviour occurred in birds foraging in pasture, for example, could then be found by summing the number of birds in pasture that displayed each behaviour. The equation of the index is as follows: $H' = (n \log n - \sum f_i \log f_i) / n$, where n = total repertoire size across each group of kiwi (e.g. those observed in pasture as opposed to forest), f_i = number of kiwi within each group observed performing behaviour i (Zar 1999). Indices were compared using Hutchison's t-test, following Zar (1999).

Foraging microhabitat use

Diversity of foraging microhabitat use within forest habitats was compared between sexes and seasons using Shannon–Wiener diversity indices followed by Hutchison's t-test. The proportion of time spent foraging in each microhabitat type was compared between sexes and seasons using Mann–Whitney U tests.

Most analyses were carried out in Minitab 15 except for Shannon–Wiener indices, which were calculated in Microsoft Excel. Data are presented as means ± SD or medians and interquartile ranges (IQR), as appropriate. Results were considered significant when $P < 0.05$.

Results

Kiwi morphometrics

Female kiwi were significantly larger than males (Table 2) in terms of weight ($t_{13, 17} = 2.83$, $P = 0.010$), tarsus width ($t_{13, 17} = 2.66$, $P = 0.015$), and bill length ($t_{13,17} = 10.63$, $P = 0.000$). Female bills were on average 30% longer than male bills and there was no overlap in bill length between the sexes.

Video recordings: sample size and length of observations

Ninety-six (73 summer; 23 winter) separate kiwi observations, including multiple sightings of the same individuals, were made, and over 8 hours (500 min) of video footage were obtained. The bias towards observations made in summer was despite one more winter (6) than summer (5) trips being made to the study site. Kiwi were observed in both pasture (19% of observations in summer when long grass made viewing kiwi difficult, 26% in winter) and forest (81% summer, 74% winter) habitats throughout the year.

After controlling for video quality and removing duplicate footage of individuals, ~6 hours of footage of 25 individual kiwi remained. Video-recording length ranged from 3.6 to 31.6 min (median = 13.4, IQR = 9.9 min). The sample included 12 adult females and 13 males or juveniles, 17 summer and 8 winter, and 19 forest and 6 pasture observations. There was no significant difference in video-recording length with sex, season, or habitat type (W = 185, 204 and 249, respectively;

all $P > 0.05$). Approximately equal numbers of male/juvenile and female kiwi were video-recorded in summer ($n = 9$ and 8, respectively) and winter ($n = 4$ and 4 respectively) and in forest ($n = 9$ and 10, respectively). More male/juvenile than females were recorded in pasture ($n = 6$ and 2 respectively). *Sample sizes given here apply to statistical tests throughout the Results*. Figure 1 shows the approximate locations where the sequences used in the analyses were obtained.

Behaviours observed and time budgets

Kiwi behavioural repertoire included behaviours related specifically to foraging and prey handling (9 behaviours), vigilance (3), social and courtship interaction with other kiwi (7), walking and escape (3), comfort (5) and investigation of terrain (1 behaviour) (see Table 1 for the ethogram). One behaviour, tapping the ground ahead with the bill tip, was displayed by both walking and foraging kiwi and may serve a dual purposes of prey detection and orientation. Social and courtship behaviours were observed rarely. One fight between two male kiwi, one female call, and one courtship–copulation sequence including female and male calls were video-recorded. Due to small sample size these behaviours are described but not used in analyses.

The median percent of total observation time spent in each of the behaviour states, foraging (74.3 %, IQR = 24.1), walking (10.8 %, IQR = 18.4), vigilant (4.3 %, IQR = 8.1), comfort (0.2 %, IQR = 2.5), escape, and investigation of obstacles (both medians and IQR 0%), did not differ significantly between kiwi sexes, seasons, or habitat types (W = 151–253, all $P > 0.05$).

Foraging behaviour

The most commonly observed behaviours used while foraging were tapping the ground ahead (100% of kiwi) and probing (Table 1; 100% of kiwi). The median ratio of taps to probes was 1.36 : 1 (IQR = 0.99 : 1). Rarer foraging behaviours included 'rapid tapping', which appeared to be an attempt to pick up prey items found on the surface (60% of kiwi) and 'bill hovering' where the bill tip was held close to the ground and moved back and forth with a motion similar to tapping (24% of kiwi; Table 1). In high quality footage, we were able to observe that foraging kiwi held their facial bristle feathers forward, forming a 'net' around the bill that contacted the surface of the leaf litter as the bird probed.

Kiwi never displayed pecking, or other obviously visually guided foraging behaviours. Several times kiwi ignored potential prey that walked past their bill tips as they probed, and on at least one occasion a rapid tap sequence was unsuccessful due to the prey item escaping from under the bill tip. The kiwi searched for this lost prey by tapping with the bill and did

Table 2. Size differences between male and female kiwi, Ponui Island, 2007–08.

	Males (n = 17)		Females (n = 13)	
	Mean ± SD	Range	Mean ± SD	Range
Weight (g)	1926 ± 221	1400–2350	2223 ± 326	1550–2775
Tarsus width (mm)	11.9 ± 0.7	10.8 – 13.1	12.7 ± 0.9	10.9 – 14.2
Bill length (mm)	92.3 ± 3.2	88.1 – 98.5	120.4 ± 8.3	108.0 – 136.2

not seem able to see it, although it continued to be visible to the observer. Kiwi did not glean prey items from vegetation surfaces, a possibility raised by Reid et al. (1982).

Foraging kiwi probed at a median rate of 10.03 probes per minute (IQR = 5.3 probes min^{-1}). Probes were into leaf litter (forested habitats) or matted grass roots (pasture habitats) (96% of kiwi; 57.7% of probes) and into soil substrates (88% of kiwi; both habitat types, 42.3% of probes). There were no differences between males/juveniles and females, or between seasons, in the percent use of these probing substrates (W = 139–230; all $P > 0.05$). Successful probes (resulting in prey capture) were longer in duration than unsuccessful probes (median 6.38 s, IQR = 4.05 s vs median 2.63 s, IQR = 1.30 s, respectively; Wilcoxon paired-sample test $Z = 295$, $P < 0.001$). Some soil probes included a non-vocal squeaking noise as the bill was withdrawn from the substrate.

Probing depth relative to total bill length varied with sex: male/juvenile kiwi used a significantly greater proportion of their bill length on average when foraging in leaf litter than females (W = 194.0, $P = 0.012$). The average proportion of bill length inserted during soil probes was similar for male/juvenile and female kiwi (W = 120.0, $P = 0.503$). However, a greater percent of male/juvenile than female soil probes used the full length of the bill or more (e.g. a part of the face inserted into the probe hole), (male/juvenile, 37.5%; female, 18.2% of probes; W = 207, $P = 0.041$).

Prey capture and handling

We observed 413 prey captures during the course of the study (median 9 captures per kiwi, IQR = 17). The majority of these followed probing into litter (19.6%), matted grass roots (14.3%), or soil (47.5%); although 11 prey items (2.7%) were captured directly from the surface using rapid tapping. The foraging strata could not be identified for 16.0% of prey captures, due to poor video quality. Prey capture rate was higher in pasture (median 5.08 captures min^{-1}, IQR = 5.06, $n = 6$) than in forest (median 1.25 captures min^{-1}, IQR = 0.83, $n = 19$) (W = 119.0; $P = 0.010$). Prey capture rate was also higher in winter (median 2.12 captures min^{-1}, IQR = 3.87, $n = 8$) than in summer (median 1.24 captures min^{-1}, IQR = 0.74, $n = 17$), although this only tended towards significance (W = 190.0; $P = 0.076$).

We divided the kiwi prey handling sequence into three parts: withdrawal of the bill from the substrate; swallowing; and latency, which was measured from the end of swallowing to the beginning of the next activity (e.g. a new probe). Median handling times were 1.67 s (IQR = 0.85) and did not vary significantly with sex, season or habitat (W = 162.5, 222, 221 respectively; all $P > 0.05$). Kiwi took a median of 1.95 bill flicks (Table 1) to swallow each prey item (IQR = 0.75). The number of bill flicks per prey item did not differ with sex, season or habitat (W = 138.5, 192.5, 239, respectively; all $P > 0.05$).

Walking and investigating terrain

Kiwi spent a median 11.3% of observation time walking or investigating obstacles such as steep banks and fallen logs in their path (IQR = 18.3). When investigating an obstacle, kiwi stretched their neck and reached forward with their bill repeatedly to touch the obstacle's surface. The bird then either clambered over the obstacle or walked around it.

While walking, as when foraging, kiwi continually tapped the ground ahead with the bill tip. This behaviour was not seen in birds that were running, or accelerating from a walk to a run. Kiwi tapped with greater frequency when walking in forested habitats (median 35.4 taps min^{-1}, IQR = 38.8) than when walking in open pasture (median 12.4 taps min^{-1}, IQR = 16.4; W = 285, $P = 0.017$).

Vigilance and escape behaviours

All video-recorded kiwi displayed some vigilance behaviour, ranging from 0.3 to 24.4% of total observation time (median 4.3%, IQR = 8.4). All kiwi displayed 'head lift' behaviour (Table 1), which was usually presented in response to a noise audible to the observer. Kiwi also commonly displayed olfactory search behaviour ('sniffing', 88% of kiwi; Table 1); often but not exclusively following head lifts (42% of the time). Olfactory search behaviour (OSB) was directed towards the observer (55.6% of OSBs) or towards odour sources other than the observer (when identifiable, other kiwi, on one occasion another kiwi's nest) (44.4% of OSBs). There was a near-significant increase in the frequency of OSB towards sources other than the observer in winter (W = 191; $P = 0.086$). Kiwi sometimes also 'froze' in response to particularly loud or sudden disturbances nearby (observed on three occasions, 12% of video sequences).

Escape behaviours following a disturbance included running away, either out of sight of the observer or a short distance prior to resuming foraging (20% of kiwi); or jumping out of the way (two kiwi, both in winter). On one occasion a kiwi leapt away from a twig that sprang from the leaf litter and hit the bird as it trod on it. No differences in vigilance or escape behaviours between sexes or in different habitats were observed (W = 170–241, all $P > 0.05$).

Comfort behaviours

Comfort behaviours exhibited by kiwi included dislodging dead leaves that they had speared with their beaks during probing ('leaf toss': forested habitats, 52% of kiwi), shaking, preening and scratching, and defecation. We observed kiwi defecations more frequently during winter than summer (W = 198, $P = 0.040$). We found no other differences in comfort behaviour with sex, season or habitat.

Behavioural repertoire diversity

Kiwi behavioural repertoire was larger in winter (11.63 ± 2.07 behaviours per observation) than in summer (9.29 ± 1.65 behaviours per observation) ($t = -2.80$, d.f. = 11, $P = 0.017$). Repertoire diversity also increased in winter (Shannon–Weiner H' winter = 1.239; H' summer = 1.127; Hutchison's $t_{0.05(2), 198} = -3.219$, $P < 0.002$). The behaviours that increased most in frequency in winter were OSBs towards odour sources other than the observer, and the rarely observed behaviours defecation and jumping.

Behavioural repertoire size and diversity were similar between male/juvenile and female kiwi, and between pasture and forested habitats (sexes: $t = -0.67$, d.f. = 22, $P = 0.509$; Hutchison's $t_{0.05(2), 896} = -0.615$, $P > 0.50$; habitats: $t = 0.83$, d.f. = 7, $P = 0.432$; Hutchison's $t_{0.05(2), 94} = 1.548$, $P > 0.10$).

Foraging microhabitat use

Within forested habitats, kiwi used a more diverse range of microhabitats in winter than in summer (H' winter = 0.812; H' summer = 0.667; Hutchison's $t_{0.05(2), 827} = -6.992$, $P < 0.001$) (Fig. 3). Kiwi observed in summer spent the majority of their foraging time in open litter, tree roots or fallen log substrates
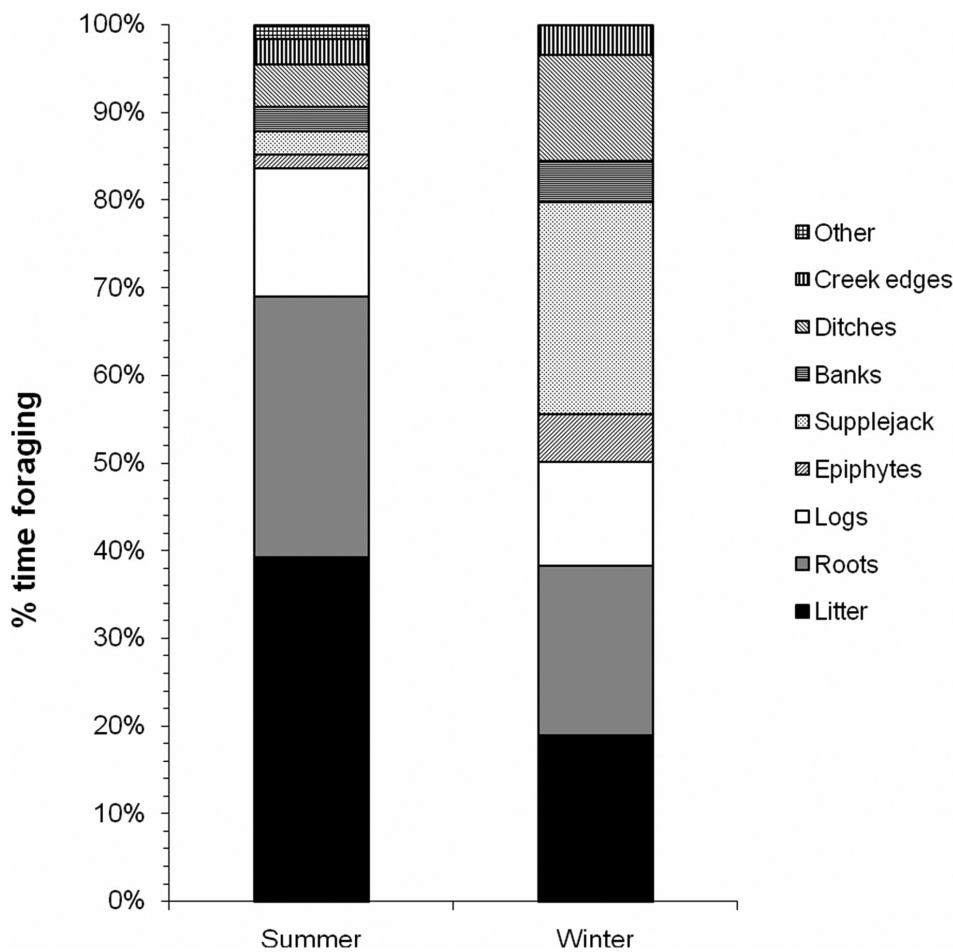
Figure 3. Foraging microhabitat use by kiwi in forested habitats in summer versus winter. Category 'Other' includes swamp edges, bare ground and grass roots. Summer n = 17, winter n = 8.

(median 86.8%, IQR = 43.3). In winter, birds spent a median 43.6 % of their foraging time in these three habitats, a near-significant decrease (IQR = 55.1; W = 159.0; P = 0.087). Supplejack tangles, ditches, banks, creek edges and fallen epiphytes together were used significantly more in winter than in summer, accounting for a median of 56.4% of time foraging in winter (IQR = 55.1; W = 116.0; P = 0.030).

There were no differences in microhabitat use or diversity of use related to sex: W = 65–90, all P > 0.05; Shannon–Weiner H' male/juvenile = 0.796, H' female = 0.779; Hutchison's $t_{0.05(2), 965}$ = 0.784, P > 0.20.

Discussion

We have described the nocturnal behaviour of wild brown kiwi from direct observation for the first time. We found that kiwi spent the majority (c. 75%) of their time foraging, and only c. 25% on other activities, including comfort, walking and vigilance behaviours. Direct social and breeding interactions between individuals were observed rarely. Our fine-scale data on kiwi behaviour allowed us to draw inferences about the sensory systems used by brown kiwi, examine their foraging success in native versus exotic vegetation patches, to test for seasonal differences in fine-scale behaviours and microhabitat use, and to raise questions about the extent to which they behaviourally partition their foraging niche.

Senses

Vision

Kiwi visual fields and brain visual processing areas are greatly reduced when compared to known nocturnal and flightless birds of comparable size (Martin et al. 2007). Kiwi are unlikely to guide their beak using visual cues because their bill tip falls outside their visual field (Martin et al. 2007). In keeping with this, we observed no behaviours in kiwi that appeared to be visually guided. Kiwi did not peck at food items in the manner of visually guided foragers (e.g. short-billed shorebirds; Barbosa & Moreno 1999) but captured prey by probing or by tapping repeatedly at prey items on the surface they appeared to have located by touch or smell.

Touch

Enlarged centres in the kiwi brain for the relay and processing of tactile information suggest that touch-related senses are important (Martin et al. 2007). Kiwi possess an organ in the bill tip that is sensitive to vibration (Cunningham et al. 2007) and trials in captivity show that they use remote touch, a sense mediated by this organ, together with olfaction to find buried prey (Cunningham et al. 2009). We observed behaviours that provide evidence kiwi also use tactile cues in exploration and navigation. Kiwi in difficult terrain used 'bill reach' behaviours, presumably to investigate the topography ahead. Kiwi employed similar tapping behaviours both when foraging and when walking. The frequency of taps per minute when walking

in forest habitats, where they were likely to encounter more obstacles like tree trunks and undergrowth, was significantly higher than when walking in open pasture. This provides support for the idea that kiwi use their sensitive bill tip to assess obstacles in their path. Our observations are in keeping with earlier observers' comments that the kiwi bill is also used similarly to 'a blind man's walking stick' (e.g. Haeusler 1923). Kiwi nostrils are placed at the tip of the bill and therefore it is likely the birds gain olfactory as well as tactile information when performing tapping and bill-reach behaviours. The information from both senses could be integrated to create a more complete picture of the environment.

Brown kiwi facial bristle feathers are long (Baker et al. 1995) and often held back away from the beak when the birds are handled (authors' pers. obs.). Kiwi bristle feather follicles are surrounded by Herbst corpuscles suggesting that they have a tactile function (Cunningham et al. 2010). We observed kiwi holding their bristle feathers forward during foraging, forming a 'net' around the bill that contacted the leaf litter during probing. It is therefore possible that the bristle feathers have a tactile function in prey-detection. However, on at least one occasion we observed a prey item walk through the bristle feather net apparently without being perceived by the kiwi. A second possibility is that kiwi use their bristle feathers to gauge distance to the ground or ground evenness.

Olfaction

Kiwi possess a large olfactory chamber and olfactory bulb, which, together with the positioning of the nostrils, suggest specialisation (Bang 1971; Martin et al. 2007). Kiwi are known to use olfaction for foraging (Wenzel 1968, 1971; Cunningham et al. 2009) and could potentially also use olfaction for a variety of other purposes (Jenkins 2001; Castro et al. 2010). We observed kiwi using stereotyped OSB as described by Castro et al. (2010) on numerous occasions (88% of video sequences). Kiwi directed OSBs towards observers and in directions other than the observer, often in directions in which other kiwi could be heard. Our observations corroborate Castro et al.'s (2010) contention that odour is used by kiwi in environmental exploration and social interactions. We also observed a new behaviour that seems likely to be related to olfaction: bill hovering. When performing this behaviour, kiwi move the beak back and forth close to the ground without contacting it. We classified this behaviour as a foraging behaviour, but kiwi may use it to detect scents other than prey odour close to the ground.

Hearing

Trials in captivity showed that kiwi do not seem to use auditory cues to locate buried prey (Cunningham et al. 2009). Other auditory foragers, like American robins (*Turdus migratorius*) and Australian magpies (*Gymnorhina tibicen*), distinctively cock their heads towards source of sound (Floyd & Woodland 1981; Montgomerie & Weatherhead 1997). We observed no such overt behaviour related to auditory prey detection in our study, although this does not preclude kiwi using this sense when foraging. We recorded behaviours related to hearing in other parts of kiwi life – 'head lifts' are likely to be auditory-related behaviour as they often occurred in response to the observer, or a kiwi other than the focal individual, making a sound. Kiwi have a cochlea structure similar in some aspects to barn owls (*Tyto alba* – auditory specialists) and hearing range shifted to higher frequencies (Corfield 2009). Corfield (2009)

suggests this range shift would be ideal for hearing invertebrate rustlings in leaf litter. We suggest kiwi's high frequency hearing may also be used in detection of conspecific footsteps on leaf litter, or similar disturbances in the environment.

Foraging success in native versus exotic vegetation patches

Kiwi foraged in native forest and exotic pasture habitats throughout the year. The majority of observations (76%) were made in forest habitats. This likely reflects both the longer walking routes and the easier detection of kiwi in forest where their footsteps on leaf litter could be clearly heard.

Prey capture rate was significantly higher in pasture than in forest. Previous studies of kiwi living in areas including both exotic and native vegetation patches have concluded that native vegetation is preferred by kiwi (Taborsky & Taborsky 1995) and has higher soil invertebrate availability than exotic vegetation (Colbourne & Kleinpaste 1983). These studies (Colbourne & Kleinpaste 1983; Taborsky & Taborsky 1995) also found that kiwi territories encompassing fragments of native vegetation were smaller than those that did not, suggesting that native vegetation increases territory quality. Our observation of higher foraging success in exotic pasture is therefore in direct contrast with previous work. Most pasture observations were near a forest edge and higher invertebrate diversity due to edge effects could help explain high prey-capture rates in this habitat type (see review Didham 1997). Black field crickets (*Teleogryllis commodus*) were seasonally abundant in the pasture in summer (pers. obs.), and earthworms could be found in higher abundance in pasture than within the forest year round (Shapiro 2005). The forest fragment itself was unfenced, and regularly used by livestock (sheep, cattle and donkeys) browsing and trampling (pers. obs.). Recent research shows that, in New Zealand, forest fragments accessible to livestock have 10- to 100-fold lower densities of leaf litter invertebrate species compared with forest reserves from which livestock are excluded (Didham et al. 2009). Forest leaf litter was an important foraging stratum for kiwi in this study (almost 20% of prey captured came from litter). Therefore, the impact of livestock may depress kiwi prey capture rates in our forest fragment, helping explain the differences between our study and those of others.

Seasonal differences in behaviour and microhabitat use

Kiwi experienced near-significantly higher foraging success and significantly higher behavioural repertoire size and diversity in winter than in summer. Repertoire size and diversity increases were mainly due to an increase in OSB in directions other than the observer, and in rarely observed behaviours such as defecation and jumping. Non-observer-related OSBs may have a social function (when the odour source is another kiwi) or a function in assessing the environment (see also Castro et al. 2010). Higher defecation rates may also have a social context – kiwi leaving odorous signals aimed at conspecifics. These results suggest that kiwi might be experiencing reduced foraging pressure in winter and this, combined with the beginning of the breeding season, might explain the greater behavioural diversity observed, particularly in terms of odour-sensing behaviours.

Kiwi used a greater diversity of microhabitat types within native forest habitat in the winter. As we did not collect data on microhabitat availability we cannot examine whether a wider variety of microhabitats were selected by kiwi in winter,

or whether more microhabitat types were simply available. For example, softer, damper soil in winter may have made some microhabitats such as banks more attractive to kiwi in winter and fallen epiphytes may have been more available after winter storms.

Foraging niche partitioning

Taborsky and Taborsky (1991, 1992) showed that home ranges of mainland brown kiwi pairs overlapped only partially (60–70%), which potentially reduces foraging competition between pair members via spatial habitat partitioning. On Ponui Island, the kiwi population is dense and home ranges of multiple birds overlap more (B. Zeisemann, Massey University, pers. comm.). We therefore expected to find behavioural and foraging microhabitat differences between large (female) and small (male and juvenile) kiwi that could reduce intraspecific competition – such as are found in other species with sexual bill-length dimorphism (e.g. western sandpipers, *Calidris mauri*, Fernández & Lank 2008; green woodhoopoes, *Phoeniculus purpureus*, Radford & du Plessis 2003; bar-tailed godwits, *Limosa lapponica*, Zharikov & Skilleter 2002).

Male/juvenile and female Ponui Island kiwi showed no separation in foraging substrate, microhabitat or habitat use, or any behaviour related to foraging except for probing depth. When probing into leaf litter or matted grass roots, male/juvenile kiwi used a greater average proportion of their bill length than females, presumably allowing them to reach the same depth. This implies kiwi were foraging in direct competition within 'surface' substrates. When probing into soil, however, all kiwi inserted the same average proportion of the bill. Female kiwi at our study site had bills 30% longer on average than those of males, and therefore probed 30% deeper on average than males. Males and juveniles probed to the full length of their bills 37.5% of the time, but would still be in competition with females at this depth. Significantly fewer (18.2%) of female soil probes used the full length of the bill, reaching soil strata completely unavailable to males.

As well as accessing different soil depth strata, kiwi on Ponui Island might use further mechanisms to reduce intraspecific competition that we could not detect with our sampling method. For example, in most cases the definition of our video footage was too low to allow us to identify prey items captured by kiwi. Diet studies suggest kiwi are generalists that take prey in proportion to their availability (e.g. Kleinpaste 1990; Miles 1995); however, it is currently unknown whether sexes specialise on different types of prey. Further, we could not distinguish untagged juvenile females from untagged males in our study. If foraging differences exist between the sexes that are independent of size and bill length, we would not have been able to detect these. Direct observation of tagged kiwi of known sex and age using higher definition video cameras may help discover whether behavioural and dietary differences exist between these groups.

Limitations of direct observation

The direct observation technique used in this study is ideal for collecting fine-scale behavioural data. However, direct observation is subject to a number of limitations. For example, we were unable to record kiwi in densely vegetated areas such as swamps and scrubby ridges due to the difficulty of observing or approaching the birds in such areas. We also recorded more kiwi in summer than winter, despite equal or greater sampling effort in winter. This suggests kiwi are harder

to detect in winter, perhaps because they were using swamps and ridges more often or because dampened leaf litter muffled their movements. Further, in winter, breeding males spend time incubating eggs and are therefore unavailable to view.

We made every effort not to disturb the birds we recorded. Even so 64% of kiwi displayed vigilance behaviour (OSBs) directed towards the observers, suggesting that kiwi behaviour may be affected to some degree by observer presence. Despite these limitations, direct observation remains the only way to collect the kind of fine-scale behavioural data presented here, and such data can offer valuable insights into the secret life of kiwi.

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