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SHORT NOTE

Observations of satellite nesting and nocturnal incubation behaviours in pūkeko (*Porphyrio melanotus melanotus*)

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Pūkeko (*Porphyrio melanotus melanotus*) range throughout Aotearoa New Zealand, and although their breeding systems can vary greatly, they generally live in polygynandrous groups, especially in the northern portions of their distribution (Jamieson 1997, 1999). These groups are comprised of highly philopatric kin which form mixed-sex dominance hierarchies (Craig 1980b). North Island populations consist of large, sedentary, closely related groups which defend territories year-round. There is also low adult mortality, limited juvenile dispersal, and high female reproductive skew (Craig & Jamieson 1988, 1990; Lambert *et al.* 1994; Jamieson 1997). Pūkeko are typically cooperative breeders, which occurs in only ~3–4% of avian species (Arnold & Owens 1999; Jetz & Rubenstein 2011). When there is more than one reproductive male and female in a group, chicks are always of mixed parentage (Lambert *et al.* 1994). While other life-history attributes vary widely, cooperatively breeding birds all share one important feature; males make a large contribution to incubation and care of the young (Vehrencamp & Quinn 2004).

In many cooperative breeders, there is a single breeding pair or female. However, in pūkeko there are sometimes multiple breeding females present. When this occurs, all females generally lay in a single nest, a phenomenon known as joint-laying (Craig 1980b; Vehrencamp & Quinn 2004). Conspecifics in Australia have not been reported to exhibit joint-laying, which suggests that joint-laying may have developed relatively recently in New Zealand populations (Dey & O'Connor 2010). The dominant female's fitness is reduced when joint-nesting occurs due to egg breakage and low hatch rates (Craig & Jamieson 1990; Vehrencamp 2000). Despite this, currently there is no evidence of intentional egg breakage or rejection in pūkeko (Jamieson 1997; Quinn *et al.* 2012). Current thought is that because males invest heavily in incubation, and renesting can occur rapidly, there is a risk that males will abandon nests that have reduced egg numbers due to egg-breaking or rejection. Thus, the heavy male investment may suppress female-female competition and allow joint-laying to occur, despite the fact that dominant female breeders experience a reproductive cost when a subordinate female also breeds (Quinn *et al.* 2012; Dey *et al.* 2014b).

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Figure 1. Photographs illustrating observations from text. **A)** Females have consistent and unique colouring/patterns on eggs. The image shows seven eggs from two different females within the same joint nest. **B)** Example of a main nest and "satellite" nest; this satellite nest included a well-formed bowl using collected materials; some satellite nests used little or no collected material. **C)** Screenshot from footage captured on a trail camera. In this image six eggs are visible in the main nest (on the left) and three in the satellite nest (on the right). In later footage from the same day there were five eggs in the main nest and four in the satellite nest. The bird in the image is moving the eggs around in the satellite nest. Unfortunately, footage of the egg being moved between nests was not captured. **D)** Screenshot from trail camera footage demonstrating simultaneous incubation of satellite nest. **E)** Trail camera footage from nocturnal incubation changeover. The departing bird's bands are visible.

Male pūkeko increase fitness by having a male cobreeder present (regardless of breeding female numbers) because they can defend higher quality territories and breeding success is largely dependent on territory quality (Craig 1980b; Vehrencamp 2000). A breeding female benefits from more than one breeding male present in the group due to access to higher quality territories, and likewise males benefit from more than one breeding female present as it increases their potential reproductive success (Quinn *et al.* 2012). Subordinate females benefit by being able to breed on a high-quality territory. Therefore, there is a conflict of interest between the dominant female and subordinate females and males. This conflict appears to resolve in favour of the males and subordinate females (Vehrencamp & Quinn 2004). Dominant females lay more eggs than subordinate females, especially in the first clutch of the season, and also achieve more copulations (Craig 1974; Craig & Jamieson 1990). This appears to result in the production of more offspring for the dominant females. However, in contrast, neither dominance nor copulations are predictors of male reproductive success in pūkeko (Lambert *et al.* 1994).

Pūkeko nests are built in tufts of vegetation, with species such as *Juncus*, *Carex* or *Typha* grasses typically favoured (Dey *et al.* 2014a). Typically, longer foliage is beaten down and intertwined to form the base of the nest and surrounding vegetation may also be incorporated, sometimes as a loose canopy (Haselmayer 2000). The pūkeko rely on the low vegetation to camouflage nests and precocial chicks. Females produce eggs with colouring and patterns that are unique to the individual bird and consistent over time (Craig 1974; 1980a). The morphological features of eggs are distinct enough to allow for accurate visual interpretation of maternity within a joint-nest (Haselmayer 2000; Quinn *et al.* 2012; Dey *et al.* 2014; Fig. 1A). Despite this clear individuality, pūkeko appear to lack egg recognition; females do not respond to their eggs being experimentally removed, or even the presence of a heterospecific egg in a nest (Dey & O'Connor 2010; Quinn *et al.* 2012). Non-breeding "helpers" of both sexes, never partake in courting or copulations but do assist in rearing chicks (Jamieson *et al.* 1994). On the North Island, laying can occur in any month, with a peak during August–November (Dey & Jamieson 2013). Clutch size is typically 4–6 eggs per female. As such, when multiple females contribute to a single nest the total clutch size can be as high as 18 eggs (Dey & Jamieson 2013). In the North Island, all individual pūkeko that copulate subsequently assist in incubating the eggs (Craig & Jamieson 1990). Hatching is asynchronous and chicks are precocial and capable of leaving the nest within hours; however, they generally remain on the nest for a day or two while other eggs hatch (Craig & Jamieson 1990). Mortality is high during this initial period; reproductive success is ~20%, despite egg loss being low (Craig 1974).

For over three years (September 2017 – October 2020) we monitored a pūkeko population as part of a larger project in Auckland, New Zealand (36.95052°S, 174.76543°E). During experimental trials, Bushnell HD aggressor trail cameras (Bushnell Corporation, USA) were placed in territories of chosen groups and behaviour was recorded. Breeding behaviour was observed in the main study population over three breeding seasons. Nests were located, marked with a GPS point and a flagging stake (50 cm from nest), and were monitored until either, 1) abandonment/predation/destruction, or 2) hatching completion. Eggs were labelled using a marker pen with numbers to indicate their laying order, as well as either "A" (main) or "B" (satellite, see below) to indicate the nest in which they were laid. Many of the monitored groups contained individuals that were banded with unique colour bands for accurate identification. Regular census counts and *ad libitum* observations occurred throughout the study period. Here we report on some observations of breeding behaviour from this population of North Island pūkeko.

Satellite nests

While describing how pūkeko often build "trial" nests prior to the onset of laying, Craig (1980b) stated that eggs were observed laid in two nests 3 m apart in a pair's territory (but only one nest was incubated). Further, Craig (1980b) describes how all nests within and surrounding the study area were single-bowled but noted "multiple-bowled nests, each containing eggs and incubated simultaneously, were found in other habitats". It is unclear how close these multiple-bowled nests were to each other, but the pair's territory nests 3 m apart were not described as multiple-bowled, so it is likely less than 3 m. The observation of pūkeko laying in separate nests was a regular occurrence at our study site. For example, in the breeding season 2018/2019 (the season when nests were mostly intensely monitored), of the 31 nests monitored in the area, over a quarter (n = 8) were double nests, or "satellite" nests (Fig. 1B, C), which are likely the same as Craig's (1980b) multiple-bowl nests. These satellite nests had several factors in common; they ranged approximately 20–80 cm apart from the main nest, the main (original) nest always contained more eggs than the satellite nest, the satellite nest was formed several days after the main nest, eggs were almost always (seven out of eight nests) moved between the nests during the incubation period, and nests were not exclusive to a laying female (i.e. there was always a mix of multiple female eggs in both nests). Nests were frequently observed being incubated simultaneously (Fig. 1D), but this was not always the case; often only one nest was incubated at a time. We suggest that one driver for the formation of a satellite nest might be the expulsion of an egg from a nest, either during incubation changeover or during egg rearrangement by the incubating bird. While pūkeko will typically roll a displaced egg back into the main nest (APS *pers. obs.*), sometimes, because of vegetation and/or elevation, this was not possible. In these instances, often the egg is abandoned or predated within days. However, for reasons unclear, a new nest may sometimes be formed around the displaced egg by a member of the group. This visual signal of a nest structure may then elicit incubating behaviour in more adults. Further, if the main nest is occupied when a female is ready to lay, the presence of a satellite nest may trigger the female to lay there instead, and this in turn may induce further satellite nest egg laying. On two occasions we potentially witnessed this sequence of events. On each occasion, we noted a singular displaced egg approximately 30 cm from a nest (it was confirmed to be from the original nest and not a newly laid egg because of its label). On examination of the nest 24–48 hours later, a loose nest structure had been formed around the displaced egg. A further 24–48 hours later, a second (newly laid/unlabelled) egg appeared in the satellite nest. One of the described nests is shown three days after the initial expulsion of an egg from the main nest (Fig. 1B) after a newly laid egg appeared next to it.

Movement of eggs and nests

When well-hidden in vegetation, nests were marked with metal stakes (1 m tall, 1 cm diameter) to make monitoring easier. Stakes were inserted into the ground close to the outer edge of the nest and they never appeared to affect the birds or influence nest abandonment. On one occasion in mid-August 2018 a nest was constructed in a large tuft of cow parsley (*Anthriscus sylvestris*). The nest site was marked with a stake and noted to be orientated on the northern side of the main stalk of the cow parsley. However, several days later on the 14 August 2018, the nest and labelled eggs within it (n = 8) had moved to the southern side of the cow parsley approximately 50 cm from the original site and flagging stake. There was little evidence of the original nest (all materials had been moved to the new location). It is unclear what stimulated this behaviour. It occurred immediately after the presence of the marking stake, but this pūkeko group had previous nests that had also been marked with a stake and were not moved. Furthermore, three days later (17 August 2018) a satellite nest was created next to the main nest and the eight eggs were found in each of the two nests (five in the main nest and three in the satellite). The satellite eggs were relabelled to indicate they were now in a second nest. A further eight days later (25 August 2018) only a single nest and six eggs remained; three from the main nest and three from the satellite nest were found together. The nest eventually failed with no successful hatching. This was the only observed instance of an entire nest and eggs being moved to a new location, before being turned into satellite nests and then finally reverting to a single nest again.

What was far more frequently observed in this study was the movement of individual eggs between nests. Frequently, eggs labelled in one nest were noted in a different nest on a subsequent day, and often back in their original nest again on later visit. Of the 13 satellites nests monitored, 12 had eggs moved between nests at least once. The thirteenth satellite nest had only one egg in the nest and neither that egg nor eggs from original nest moved between the two nests. The other 12 nests all had multiple eggs in both nests. Total clutch size (i.e. both nests combined) ranged 5–15 eggs. The number of eggs moved at each nest check ranged between 1–5 (in both directions- as in sometimes 1 egg was moved from nest A to B, but also 2 from B to A).

We hypothesise that a driver for this behaviour is that while the satellite nests were often incubated simultaneously by two members of the group, there were also many instances when only one nest was incubated. A female ready to lay may interpret a satellite nest as a suitable location. However, a bird returning to the nest to incubate may conclude that satellite eggs are displaced eggs. Given that the individual incubating one nest would have a clear view of the second nest (if it was unattended) this may initiate an attempt to move the eggs back into the nest it is currently incubating (see Fig. 1C where a single bird is incubating the satellite nest and appears to move an egg from the main nest). Why this behaviour would not lead to all eggs being moved back into a single nest remains unclear. Perhaps it is too difficult to move multiple eggs in a row, or perhaps a second bird would arrive and commence incubation of the second nest, hence only one or two eggs would ever be moved at a time. Unfortunately, no footage of the movement of eggs between nests was ever captured. Only one satellite nest was suitable for a trail camera because the sudden die back of vegetation exposed the nest pair. Despite roughly nine days of trail camera monitoring (motion triggered 10 second video recording with a 10 second delay between activation), resulting in over 13 hours of footage of this satellite nest, and evidence of eggs being moved between the nests, no instance of moving eggs was filmed.

Nocturnal incubation

Craig (1980b) reported that incubation is shared by breeding males and females, and that it is exclusively done by males at night. This was confirmed by an automatic camera set at night; "in all territories, males sat at dusk and were relieved immediately before dawn by a female" (Craig 1980b). Day shifts of incubation were reported as being approximately three hours in length (Craig 1980b). However, in this study, birds were observed changing incubation shifts 1–10 times during the night, via trail camera (4 of 6 nests monitored).

We were able to monitor one single-bowl nest by motion-activated camera for a period of 37 days (30 August – 6 October 2019). Some nights contained no footage (e.g. batteries depleted). However, on nights when footage was captured (n = 25), nocturnal incubation changeovers were recorded 100% of the time. After 37 days, we terminated the monitoring; hatching typically occurs 23–27 days after incubation commences (Craig 1980b) and the nest was assumed failed.

A typical changeover sequence involved the following series of events: 1) The replacement incubator approaches the nest and interacts with the sitting bird; 2) low vocalisations were detected during these interactions (acoustic recording was used on a small portion of video recordings); 3) After ~10–20 seconds of vocalising, the incubating bird leaves the nest and the replacement begins incubating, competing the exchange. In one specific sequence, two birds were observed joint-incubating (both sitting on the nest) for 3.5 hours (0226 h – 0554 h) until one finally moved away. In another sequence, over the course of a night (8 September 2019) there were ten nocturnal incubation changeovers, including five changes in just over one hour (0336 h – 0449 h). At least three different birds contributed to these night shifts; one banded and two unbanded individuals (Fig 1E). This indicates that, 1) nocturnal incubation is not solely the dominant male's role in this population, and, 2) no individual bird completes an entire nocturnal incubation shift, instead there were regular changeovers in every observed nest.

There is considerable intra-population behavioural variation and plasticity in reproductive systems and breeding behaviours in pūkeko. For example, they show considerable inter-population variability in mating systems including monogamous, polyandrous, and polygynous (Jamieson 1997, 1999). Craig's (1980b) study was carried out near Palmerston North on the North Island and this geographical variation (and the potential difference in group structure it infers) may be an explanation why changeovers were not documented in either of the study populations monitored. However, the extent to which variation in mating systems may impact the nocturnal incubating behaviour in pūkeko remains unclear. It is also unclear what distance the rest of the group are from the nest during nocturnal periods. As the camera is set up close to the nest (~1 m), birds are only visible when on or immediately behind the nest. Whether these regular nocturnal changeovers have any impact of hatching success – and just how widespread the behaviour is within the species – would be a direction for future study.

A final possibility is that such night-time variation in behaviours is common among bird species more generally. If so, we may be missing a fair amount of variability in behaviour by assuming nothing changes overnight. Craig (1980b) used an automatic camera, which has limitations relative to continuous filming and infrared recording. He observed no nocturnal incubation changeover sequences and concluded that one bird incubates throughout the night. It is possible that Craig's technology meant a limited ability to detect changeovers. However, he still observed the same bird on the nest at dusk and dawn (all birds were banded/marked), which we rarely observed. This implies at least some intra-population behavioural variation and flexibility in this species' incubation behaviour. Pūkeko are generally considered to be diurnal birds; however, using our cameras set up on feeders, we frequently observed pūkeko foraging and moving throughout the night even away from nests. Though this field site is within the Auckland region, it is relatively dark (McNaughton *et al.* 2022), thus it is unclear whether this activity is due to artificial light at night or natural behaviour variation. These findings add to accumulating evidence that many species are more active at night than previously assumed and engaged in activities we are oblivious to without research (Gaston 2019). How many other behaviours might we be missing by assuming all activities occurs in the daylight hours for diurnal species?

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