

SHORT NOTE

Evidence for a lack of egg recognition in the pukeko (*Porphyrio porphyrio melanotus*: Rallidae)

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In birds, brood parasitism (BP) can be an obligate or facultative reproductive strategy that occurs both between and within species (Lyon & Eadie 1991; Lyon 2007). 'Hosts' of such parasitic acts often incur severe fitness costs (Rothstein 1990). Thus, host species often develop defensive strategies that eliminate or mitigate the negative consequences associated with BP. A variety of such defenses are based on recognition and subsequent rejection of the parasitic eggs. In some cases, animals recognise their own eggs and can identify all eggs that differ sufficiently from their own eggs regardless of the frequency of foreign eggs (termed 'true egg recognition'; Rothstein 1975; Lyon 2007). Alternatively, some birds may simply reject any rare egg-type in the clutch (termed 'recognition by discordancy'; Rothstein 1975). The family Rallidae has received particular attention in the study of egg recognition. Several species in this family parasitise the nests of conspecifics, and despite the suggestion that recognising conspecific eggs is more difficult than recognising those laid by heterospecifics (see

Lyon 2007 for explanation), hosts are still able to recognise and reject foreign eggs (e.g., American coots, *Fulica americana*; Lyon 2003; red-knobbed coots, *F. cristata*, and lesser moorhens, *Gallinula angulata*; Jamieson *et al.* 2000).

In this paper we present the 1st reported instance of heterospecific BP on the pukeko (*Porphyrio porphyrio melanotus*). Unlike other confamilials, our observations suggest that pukeko hosts were unable to recognise a parasitic egg and continued incubating it as if it was their own. To further explore this apparent lack of egg recognition, we monitored the behaviour of 2 other pukeko groups following the experimental addition of heterospecific eggs. Finally, we discuss the consequences of a lack of egg recognition on pukeko social dynamics and highlight possible constraints on the evolution of egg recognition in this species.

On 9 Aug 2010, we discovered a pukeko nest containing 6 pukeko eggs and 1 duck egg (Fig. 1) under a small manuka (*Leptospermum scoparium*) tree at the Tawharanui Open Sanctuary, Auckland Region, New Zealand (36° 22' S, 174° 49' E). The duck egg was easily distinguishable due to its uniform white colour and relatively large size

(duck egg: 59.1 mm × 43.3 mm; pukeko eggs: 50.8 ± 0.4 mm × 37.0 ± 0.3 mm, mean ± SE). Of the duck species present at Tawharanui, only mallards (*Anas platyrhynchos*) have been reported as brood parasites of heterospecific hosts (Weller 1959; Lyon & Eadie 1991). Thus, we assumed a mallard laid the foreign egg in the pukeko nest. While mallards typically parasitise other waterfowl (Weller 1959), the pukeko nest we observed under a manuka tree was located in an atypical location (most pukeko nest in emergent vegetation over water or in a tussock; Craig 1980). It is possible the pukeko nest was parasitised through a misdirected attempt to parasitise a more traditional host (i.e., another anatid), which are more likely to nest in drier forest habitats.

Upon discovery, all eggs in the parasitised pukeko nest were warm to the touch. Floatation indicated the pukeko eggs ranged in age from ~4–10 days old when discovered (based on comparison with floated eggs of known age). The duck egg also upended when floated, suggesting that the embryo was developing (Miles & Bizeau 1983). During 7 subsequent visits to the nest from 11 to 30 Aug, a pukeko was always flushed from the nest. The eggs were also always warm on each visit, and the duck egg was not consistently located near the edge of the nest. Thus, it seemed the pukeko failed to recognise the foreign egg, and incubated the duck egg as if it was their own. An iButton temperature logger (Embedded Data Systems, Lawrenceburg, USA) placed in the nest from 12 to 20 Aug confirmed that incubation was consistent during this period. Refloatation of the eggs on 19 Aug indicated that both the pukeko eggs and duck egg were developing as expected.

On 31 Aug, the duck egg was no longer present and a search of the surrounding area did not yield the egg, any shell fragments, or a newly hatched duckling. As this date was near the expected hatching date for the duck egg (based on an incubation period of 25 days for mallards; Heather & Robertson 2005) it was presumed that the duck egg had either hatched and the duckling had been predated or had followed a pukeko away from the nest.

To further investigate the lack of egg discrimination by pukeko, 2 duck eggs, abandoned at other duck nests in Tawharanui, were added to 2 pukeko nests. One duck egg was added per nest. The pukeko nests contained 7 and 5 eggs, respectively. Both pukeko groups had completed egg-laying and were in the early stages of incubation. Each nest was monitored daily for 7 days following egg addition. In both nests, all eggs were warm at each visit and pukeko were observed incubating the mixed-clutches. Although neither duck egg appeared to be developing during this period, this



Fig. 1. Pukeko nest containing 6 pukeko eggs (spotted and laying around edge of clutch), and 1 duck egg (unspotted and laying at centre of clutch). Pukeko nest located at the Tawharanui Open Sanctuary.

was probably due to embryo mortality resulting from cold exposure during abandonment and not from a lack of incubation by the pukeko hosts.

Both the naturally parasitised nest and our 2 experiments suggest that pukeko are unable to recognise heterospecific eggs, or if they do, then they fail or are unable to eject foreign eggs from their clutches. Further support that pukeko lack egg recognition was found by Bunin & Jamieson (1996), who reported that pukeko readily incubated takahe (*Porphyrio mantelli*) eggs, although the latter are about 2.5 times larger than pukeko eggs. Recent experiments have demonstrated that pukeko will also incubate painted domestic chicken eggs (J.S. Quinn *et al.*, *pers. comm.*).

The apparent lack of egg recognition in pukeko is surprising, especially when considering that many individuals of this species breed in polygynandrous groups where multiple females will lay in a single nest (termed joint-laying; Vehrencamp & Quinn 2004). In such groups, per capita hatching success is low due to increased egg breakage in larger clutch sizes, and it seems likely that a dominant female pukeko would benefit from the ability to discriminate and remove the eggs of a subordinate (Quinn *et al.*, *pers. comm.*; see also, Vehrencamp 2000; Vehrencamp & Quinn 2004). Given that several confamilial species are able to recognise and remove or bury foreign eggs (see above), why have pukeko not similarly evolved this ability? One possibility is that there has not been sufficient time for egg recognition to evolve

in pukeko. Pukeko are thought to have colonised New Zealand from Australia only within the last 800 years (Millener 1981) and conspecifics in Australia have not been reported to exhibit joint-laying. This suggests that joint-laying has evolved relatively recently in New Zealand populations of the pukeko. Alternatively, it is possible that the addition of a second laying female to the group increases chick survival to maturity. In pukeko groups, territory size is correlated with the number of males present in a group (Craig & Jamieson 1990) and breeding success is largely dependent on territory quality (Craig 1980). If the addition of a second laying female to a group helps to recruit additional male co-breeders (thereby increasing territory quality) there may be little selective pressure to drive the evolution of egg recognition. Whether the lack of egg recognition in pukeko is a product of a time lag, or an adaptation to joint-laying is not clear and further work is needed. However, our results highlight the importance of understanding the constraints and abilities facing each individual in studies of cooperative breeding birds.

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