

## SHORT NOTE

# An observation of a juvenile feeding an injured adult in pūkeko (*Porphyrio melanotus melanotus*)

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Altruism is defined as a behaviour which increases the fitness of recipients while decreasing that of the performer (Hamilton 1964). Inclusive fitness theory states that such behaviours are likely to have evolved primarily between closely related kin (Hamilton 1964; Trivers 1971; Gardner *et al.* 2011), or individuals with shared reproductive interest (Dyble *et al.* 2018). Altruistic behaviours are generally poorly understood, with the sole exception of humans (Warneken & Tomasello 2009). Indeed, there is considerable debate about the evolution of altruism in nonhuman species; however, there is growing evidence that this mechanism is phylogenetically ancient (see de Waal 2008).

Cooperatively breeding species display some of the most conspicuous examples of altruism (Koenig & Dickinson 2016). In some of these species, “helpers” appear to discriminate kin from non-kin and adjust the amount of help in response

to the degree of relatedness. Avian examples of this include long-tailed tits (*Aegithalos caudatus*; Leedale *et al.* 2018), chestnut-crowned babbler (*Pomatostomus ruficeps*; Browning *et al.* 2012), and bell miners (*Manorina melanophrys*; Wright *et al.* 2010). However, there are also reports of altruistic behaviours in cooperatively breeding species (both avian and non-avian), where the helper does not appear to discriminate between recipients based on degree of relatedness; i.e. they are indiscriminate altruists, and will assist conspecifics regardless of relatedness (Wright *et al.* 1999; Legge 2000; Canestrari *et al.* 2005; Vitikainen *et al.* 2017; Duncan *et al.* 2019). However, in most of these studies (6 of 7) the altruistic behaviours are directed towards the care of young, not adult group members. If an individual spontaneously helps another individual in distress by responding to its begging or distress signals this is interpreted as potential “directed altruism” (de Waal, 2008). Furthermore, if this behaviour is directed towards an individual regardless of their relation to the performer then it is considered “indiscriminate altruism” (Duncan *et al.* 2019).

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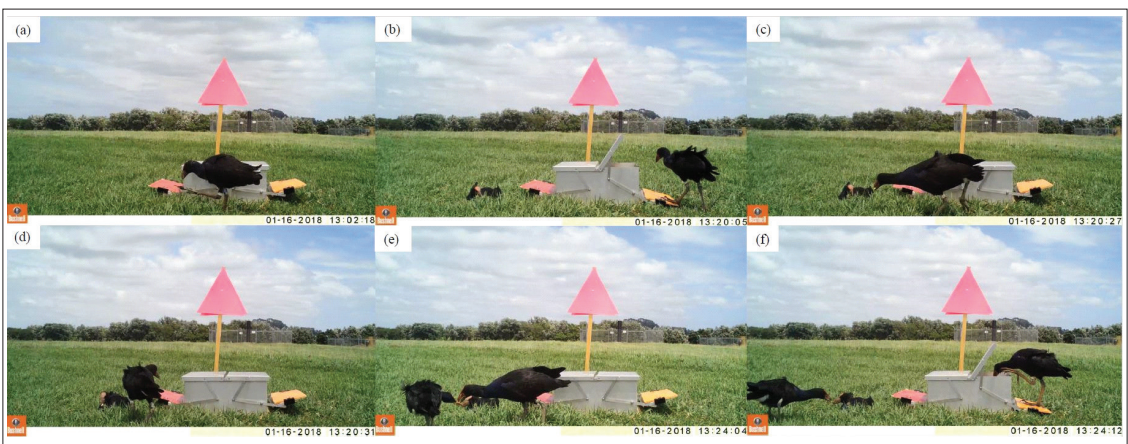
Pūkeko (*Porphyrio melanotus melanotus*) often live in cooperatively breeding and polygynandrous groups and defend a shared territory (Craig 1980a). If there are multiple breeding females present in a pūkeko group they may all lay in a single nest, a phenomenon known as joint-laying (Craig 1980; Vehrencamp & Quinn 2004; Sweeney *et al.* 2022), or closely adjacent “satellite” nests. Adults form mixed-sex dominance hierarchies (Craig 1980). Males are typically dominant over females; breeding males are highest ranked, breeding females and non-breeding males are of comparable rank, and non-breeding females typically rank lowest (Jamieson & Craig 1987; Dey *et al.* 2014). North Island populations are large, sedentary, comprised of related members, and defend territories year-round (Craig & Jamieson 1988; Craig & Jamieson 1990; Lambert *et al.* 1994; Jamieson 1997).

From September 2017 – October 2020 we monitored a pūkeko population at Watercare Coastal Walkway, Māngere, New Zealand (36.95052°S, 174.76543°E). Captured birds were individually banded with unique colour combinations on both legs. During experimental trials, double-sided, step-activated Chooketeria feeders (Chooketeria Ltd, NZ) were placed in territories and behaviour was recorded using Bushnell HD aggressor trail cameras with 0.2-second trigger speed, 0.5s recovery rate, and an extended nighttime photo range (Bushnell Corporation, USA). One side of the feeder was empty, while the other contained a food incentive of cracked and whole maize (*Zea mays*). Groups

were trained to use the feeders (Fig. 1). While visually distinguishing sex was not possible due to low sexual dimorphism, it was possible to distinguish adults (>1 year old) from the current year’s juveniles. Juvenile beaks and frontal shields gradually turn from black to red over the span of approximately nine months (Craig & Jamieson 1990).

In January 2018, when the observations presented below were made, the focal group consisted of five banded adults, three unbanded adults, and one juvenile, all of unknown sexes. In early January 2018, the beta male, Bird A (Table 1), became tangled in what appeared to be fishing line on its right foot. The second and third digits became tied closely together. When first observed, Bird A walked with only a slight limp. We made several unsuccessful attempts to recapture the individual to remove the line. Over the following couple of weeks, Bird A developed a more pronounced limp and appeared to become weaker (less dominant/aggressive behaviours were observed, APS *pers. obs.*). On 16 January 2018 a series of video clips were captured at one of the feeders showing another subordinate male from the group (Bird B) repeatedly feeding Bird A.

In the video recording, Bird A initially approached the feeder alone and went to the left (empty) side. It used its uninjured foot to activate the step, open the lid and peer in for ~10 seconds. It moved ~15 cm away from the feeder, stood for several minutes with the injured right foot held up, then sat down and remained sitting for nine



**Figure 1.** Photo series illustrating potential directed altruism in pūkeko (*Porphyrio melanotus melanotus*), note date-time stamp for sequence of events. Panels: (a) Bird A approaches feeder holding one foot up (the digits were wrapped in twine); (b) Bird A resting to the left of the Chooketeria feeder (this side of the feeder was empty), while Bird B opens the right-hand side of the feeder (full of maize) with its foot, (c) Bird B carries a piece of maize to Bird A; (d) Bird A accepts the maize, (e) Bird B passes another piece of maize to Bird C (a juvenile); (f) Bird C attempts to feed Bird A with the maize while Bird B retrieves another piece.

minutes. Bird B then approached the opposite (full) side of the feeder, opened the lid, retrieved a piece of corn, carried it ~1 metre to the other side of the feeder to where Bird A was sitting and fed Bird A (Fig. 1). There was no clear beak movement observed, and no sound recordings were taken, so it was not possible to establish if Bird A was vocalising (e.g. begging). However, Bird A appeared to be resting and uninterested in what Bird B was doing. Soft

communication calls have been recorded between adult pūkeko at nests during the wider study (APS *pers. obs.*), so it is plausible that Bird A was communicating without it being detectable in the footage (i.e. no clear beak movement).

Bird B repeated this process (opened feeder on opposite side, retrieved piece of corn, carried and fed it to Bird A) six more times before pausing to feed an unbanded juvenile (Bird C) that appeared. Bird

**Table 1.** Demographics of individual pūkeko (*Porphyrio melanotus melanotus*) involved in potential altruistic behaviour including adult males and single juvenile from a single social group. The juvenile was never successfully caught and remains the only unbanded individual in the group. Bird A was the recipient of feeding behaviours from Bird B & C.

ID	Age	Sex	Rank	Mass (g)*	Shield Length (mm)*	Shield Width (mm)* †
A	Adult	Male	Beta	1,050	70.2	26.8
B	Adult	Male	Subordinate	1,310	71.5	26.8
C	Juvenile	Unknown	Unknown	Unknown	Unknown	Unknown
D	Adult	Male	Alpha	1,210	77.1	28.8
E	Adult	Male	Subordinate	1,320	74.3	28.3

\* = measurements taken 12 weeks before footage of all birds except Bird E which was 6 six months later.

† = previous studies have shown shield width is highly correlated with dominance rank and therefore considered the most accurate indicator.

C was the only juvenile raised by this group in the months preceding this event and therefore easily identifiable due to its behaviour and darkened beak colour. Bird B fed Bird A four more times, before twice passing a piece of corn to the juvenile, which then offered it to Bird A, in a feeding chain. The juvenile offered food twice (Bird A refused both times; Fig. 1). Bird B then attempted to feed Bird A again. During one of these attempts Bird B spent ~25 seconds breaking up the maize to offer smaller pieces, while Bird A refused the food. In total, Bird B opened the feeder and brought corn to Bird A 19 times over a period of 10 minutes. A final (20<sup>th</sup>) successful food offer was captured 40 minutes after the initial attempt. Bird A accepted the food offering 17 times, it rejected food three times.

In pūkeko, the red frontal shield is correlated with dominance and used as a status signal (Dey *et al.* 2014; Dey & Quinn 2014). In addition, shield width is highly correlated with the overall area of the shield (Dey *et al.* 2017). As part of a broader study, we measured the shields of captured pūkeko from the longest point from the tip of the beak to the highest point of the shield, as well as the widest point across the shield. Upon initial capture in October 2017, 12 weeks before the footage was taken, Bird A had a shield width of 26.8 mm and

Bird B also had a shield width of 26.8 mm (Table 1). A third male, Bird D, had a shield width of 28.8 mm and was regarded as the alpha male (APS *pers. obs.*). A fourth adult male (Bird E) was not captured and measured until 6 months after this footage; however, it was assumed to be a subordinate male at the time of these observations. Even though Bird A and Bird B had equal shield widths (and Bird B had a higher mass; Table 1), Bird A was considered the beta male in the group based on observations of received aggressive behaviours from Bird D, and the aggressive behaviours displayed towards Bird B.

Birds were sexed almost three years after these observations were made and we were surprised to learn that both birds involved in this dynamic were adult males. It was originally assumed by the authors that the observed pair interactions were between the beta male and a dominant female, based on behavioural observations due to the level of interaction observed between them, here and at other times; however, it was between two lower (than alpha) ranking males. The degree of relatedness between the birds is unknown, but given the low dispersal and high site fidelity of North Island pūkeko (Craig & Jamieson 1988), it is likely that they are at least distantly related.

Because Bird A is a beta male (i.e. contributes to the maintenance of the group territory), its survival is beneficial for the entire group. However, this is the first known instance of a lower ranking male assisting a higher-ranking male within the same social group. If Bird A were to succumb to its injuries, Bird B would have been the likely successor.

In contrast to the reproductive success of dominant females, neither dominance nor copulations appear to be predictors of male reproductive success in pūkeko (Lambert *et al.* 1994). Territory size and quality are related to the number of breeding males present in a group (Craig & Jamieson 1990). Therefore, the cost of losing a male (from a territory defence perspective), as well as no apparent direct reproductive costs (in terms of access to females), may have been key driver in motivating Bird B to assist Bird A. Furthermore, indiscriminate altruism may be a product of high relatedness in a group (Duncan *et al.* 2019), as occurs when dispersal levels are low. Pūkeko differ from most avian species as both sexes can be highly philopatric and North Island populations in particular have very low dispersal (Craig & Jamieson 1988).

In addition, as noted above, it is plausible that Bird A was emitting begging calls. This possibility, coupled with how low it was to the ground, may have stimulated an innate response in Bird B. This seems unlikely, however, given that pūkeko are territorial and can vocally distinguish between kin, neighbours, and strangers (Clapperton & Jenkins 1984; Clapperton 1987). It is more likely that Bird B recognised Bird A, as well as its dominance rank, even if Bird A was emitting begging calls. It was also unusual for a juvenile to attempt to feed an adult. While many other occurrences of adult-adult feeding were observed during this study (although all other instances involved both adult birds feeding at the open feeder and passing maize between them), none involved juvenile-adult feeding or juvenile-juvenile feeding. It is difficult to speculate on what elicited this behaviour. To the best of our knowledge, this is the first example of potential altruistic behaviour between adult birds in a rail species. While this was an anecdotal observation, it indicates the potential for future altruism/reciprocity studies to consider this highly flexible and successful species as a model.

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#### LITERATURE CITED

- Browning, L.E.; Patrick, S.C.; Rollins, L.A.; Griffith, S.C.; Russell, A.F. 2012. Kin selection, not group augmentation, predicts helping in an obligate cooperatively breeding bird. *Proceedings of the Royal Society B: Biological Sciences* 279(1743): 3861–3869.
- Canestrari, D.; Marcos, J.; Baglione, V. 2005. Effect of parentage and relatedness on the individual contribution to cooperative chick care in carrion crows *Corvus corone corone*. *Behavioral Ecology and Sociobiology* 57(5): 422–428.
- Clapperton, B.K. 1987. Individual recognition by voice in the pukeko, *Porphyrio porphyrio melanotus* (Aves: Rallidae). *New Zealand Journal of Zoology* 14(1): 11–18.
- Clapperton, B.K.; Jenkins, P.F. 1984. Vocal repertoire of the pukeko (Aves: Rallidae). *New Zealand Journal of Zoology* 11(1): 71–84.
- Craig, J.L. 1980. Pair and group breeding behaviour of a communal gallinule, the pukeko, *Porphyrio p. melanotus*. *Animal Behaviour* 28(2): 593–603.
- Craig, J.L.; Jamieson, I.G. 1988. Incestuous mating in a communal bird: a family affair. *The American Naturalist* 131(1): 58–70.
- Craig, J.L.; Jamieson, I.G. 1990. Pukeko: different approaches and some different answers. Pp. 385–412 In Stacey P.B.; Koenig, W.D. (eds). *Cooperative breeding in birds: longterm studies of ecology and behavior*. Cambridge, England, Cambridge University Press.
- de Waal, F.B.M. 2008. Putting the altruism back into altruism: the evolution of empathy. *Annual Review of Psychology* 59(1): 279–300.
- Dey, C.J.; Dale, J.; Quinn, J.S. 2014. Manipulating the appearance of a badge of status causes changes in true badge expression. *Proceedings of the Royal Society B: Biological Sciences* 281(1775): 20132680.
- Dey, C.J.; Quinn, J.S. 2014. Individual attributes and self-organizational processes affect dominance network structure in pukeko. *Behavioral Ecology* 25(6): 1402–1408.
- Dey, C.J.; Quinn, J.S.; King, A.; Hiscox, J.; Dale, J. 2017. A bare-part ornament is a stronger predictor of dominance than plumage ornamentation in the cooperatively breeding Australian swamphen. *The Auk* 134(2): 317–329.
- Duncan, C.; Gaynor, D.; Clutton-Brock, T.H.; Dyble, M. 2019. The evolution of indiscriminate altruism in a cooperatively breeding mammal. *The American Naturalist* 193(6): 841–851.
- Dyble, M.; Gardner, A.; Vinicius, L.; Migliano, A.B. 2018. Inclusive fitness for in-laws. *Biology Letters*

- 14(10): 20180515.
- Gardner, A.; West, S.A.; Wild, G. 2011. The genetical theory of kin selection. *Journal of Evolutionary Biology* 24(5): 1020–1043.
- Hamilton, W.D. 1964. The genetical evolution of social behaviour. II. *Journal of Theoretical Biology* 7(1): 17–52.
- Jamieson, I.G. 1997. Testing reproductive skew models in a communally breeding bird, the pukeko, *Porphyrio porphyrio*. *Proceedings of the Royal Society of London B: Biological Sciences* 264(1380): 335–340.
- Jamieson, I.G.; Craig, J.L. 1987. Dominance and mating in a communal polygynandrous bird: cooperation or indifference towards mating competitors? *Ethology* 75(4): 317–327.
- Koenig, W.D.; Dickinson, J.L. (eds.). 2016. *Cooperative breeding in vertebrates: studies of ecology, evolution, and behavior*. Cambridge, England, Cambridge University Press.
- Lambert, D.M.; Millar, C.D.; Jack, K.; Anderson, S.; Craig, J.L. 1994. Single- and multilocus DNA fingerprinting of communally breeding pukeko: do copulations or dominance ensure reproductive success? *Proceedings of the National Academy of Sciences* 91(20): 9641–9645.
- Leedale, A.E.; Sharp, S.P.; Simeoni, M.; Robinson, E.J.H.; Hatchwell, B.J. 2018. Fine-scale genetic structure and helping decisions in a cooperatively breeding bird. *Molecular Ecology* 27(7): 1714–1726.
- Legge, S. 2000. Helper contributions in the cooperatively breeding laughing kookaburra: feeding young is no laughing matter. *Animal Behaviour* 59(5): 1009–1018.
- Sweeney, A.P.; Haerewa, N.L.; Cain, K.E. 2022. Observations of satellite nesting and nocturnal incubation behaviours in pukeko (*Porphyrio porphyrio melanotus*). *Notornis* 69: 199–204.
- Trivers, R.L. 1971. The evolution of reciprocal altruism. *The Quarterly Review of Biology* 46(1): 35–57.
- Vehrencamp, S.L. 2000. Evolutionary routes to joint-female nesting in birds. *Behavioral Ecology* 11(3): 334–344.
- Vehrencamp, S.L.; Quinn, J.S. 2004. Joint laying systems. Pp. 177–196 In: W. D. Koenig & J. L. Dickinson (eds). *Ecology and evolution of cooperative breeding in birds*. Cambridge, England, Cambridge University Press.
- Vitikainen, E.I.K.; Marshall, H.H.; Thompson, F.J.; Sanderson, J.L.; Bell, M.B.V.; Gilchrist, J.S.; Hodge, S.J.; Nichols, H.J.; Cant, M.A. 2017. Biased escorts: offspring sex, not relatedness explains alloparental care patterns in a cooperative breeder. *Proceedings of the Royal Society B: Biological Sciences* 284(1854): 20162384.
- Warneken, F.; Tomasello, M. 2009. The roots of human altruism. *British Journal of Psychology* 100(3): 455–471.
- Wright, J.; McDonald, P.G.; Te Marvelde, L.; Kazem, A.J.N.; Bishop, C.M. 2010. Helping effort increases with relatedness in bell miners, but ‘unrelated’ helpers of both sexes still provide substantial care. *Proceedings of the Royal Society B: Biological Sciences* 277(1680): 437–445.
- Wright, J.; Parker, P.G.; Lundy, K.J. 1999. Relatedness and chick-feeding effort in the cooperatively breeding Arabian babbler. *Animal Behaviour* 58(4): 779–785.

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