



Hatching order affects offspring growth, survival and adult dominance in the joint-laying Pukeko *Porphyrio melanotus melanotus*

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In birds with asynchronous hatching, hatching order is an important factor in determining offspring phenotype. Many previous studies have demonstrated that later-hatched offspring show reduced growth and survival during development. However, few studies have followed individuals from hatching to adulthood to test whether the effects of hatching order persist into later life. Here, we explore patterns of hatching order and fitness-related traits in the Pukeko *Porphyrio melanotus melanotus*, a cooperatively breeding bird that lives in stable social groups that form linear dominance hierarchies. Pukeko groups sometimes contain two breeding females that lay eggs in the same nest (joint-laying). Thus, competition between nest-mates can influence the relative fitness of each laying female. We show that in both single-clutch and joint-clutch nests, earlier-hatched Pukeko chicks grow faster and survive better than later-hatched brood-mates. Moreover, earlier-hatched chicks achieve higher dominance ranks as adults, making this study one of the first to find a relationship between hatching order and adult dominance in wild birds. Finally, we show that in groups with two breeding females, the chicks of the primary female hatch earlier than the chicks of the secondary female. As a result, the offspring of the primary female may be at a competitive advantage, which could have important implications for social dynamics in this species.

Keywords: carryover effects, cooperative breeding, hatching asynchrony, hierarchy, nestling, sibling competition.

Hatching asynchrony is widespread among birds (Magrath 1990) and occurs as a result of incubation being initiated before laying of the clutch is complete. In general, hatching asynchrony is thought to be adaptive because the formation of size hierarchies within the brood is beneficial to parents. Although the adaptive value of hatching asynchrony is likely to differ between species due to biological and ecological idiosyncrasies (Magrath 1990, Stenning 1996), the most common explanations are that size hierarchies facilitate brood reduction in unfavourable environmental conditions (e.g. Ricklefs 1965), provide insurance against the failure of core offspring (e.g. Mock &

Forbes 1995, Forbes *et al.* 1997) and improve the efficiency of raising the brood by reducing competition among nestlings (e.g. Mock & Ploger 1987). Alternatively, hatching asynchrony may simply be a by-product of selection to initiate incubation prior to clutch completion (e.g. to minimize nest predation; Clark & Wilson 1981), and may not be directly due to selection on offspring size hierarchies.

Regardless of the ultimate factors favouring hatching asynchrony, there is strong empirical evidence that hatching order affects offspring phenotype. Typically, later-hatched chicks show reduced growth (Stokland & Amundsen 1988, Rosivall *et al.* 2005) and survival (Magrath 1990, Viñuela 2000) as they are unable to compete with older brood-mates for resources (e.g. Mock 1984, Bryant

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& Tatner 1990, Legge 2000). Yet, although many studies have investigated the influence of hatching asynchrony on offspring phenotype, there is limited empirical evidence on whether hatching order effects persist into adulthood, especially in the wild. In captive studies, some species can partially or completely overcome early life challenges (such as late hatching) through compensatory growth or other forms of developmental plasticity (Hector & Nakagawa 2012). Additionally, a series of recent studies on Blue-footed Boobies *Sula nebouxii* have demonstrated that while later-hatched chicks experience increased aggression, food deprivation and chronically increased levels of stress hormones during development, they do not suffer increased mortality (Drummond *et al.* 2011) or reduced body size (Carmona-Isunza *et al.* 2013), nor do they show different levels of aggression when defending their own nest as adults (Sánchez-Macouzet & Drummond 2011) when compared with earlier-hatched chicks. However, offspring produced in the first 3 years of life by adults who were raised as junior (later-hatched) chicks were less likely to recruit into the breeding population than were the offspring of former senior chicks, suggesting that the costs of hatching order are passed on to subsequent generations (Drummond & Rodríguez 2013). How hatching asynchrony affects adult phenotypes in other wild birds remains unclear, and further studies are needed to assess whether the patterns observed in Blue-footed Boobies are more general.

If hatching order effects persist into adulthood, they could be an important source of inter-individual variation in fitness-related traits such as social dominance. There is good empirical evidence that dominance influences reproductive success (Ellis 1995) and survival in different taxa (e.g. Kikkawa 1980, Thomas *et al.* 2003, Koenig *et al.* 2011). Dominance relationships usually form as a result of repeated interactions among individuals that vary in their resource-holding potential (i.e. the ability of an animal to win an all-out fight), and researchers have found predictable correlations between dominance rank and body size (McElligott *et al.* 2001, McCauley 2010, Reddon *et al.* 2011), body condition (Huang *et al.* 2011) and measures of strength (Sneddon *et al.* 2000, Husak *et al.* 2006). Because these physical traits can be influenced by conditions during growth (e.g. Cooch *et al.* 1991, Searcy *et al.* 2004), it is important to understand how hatching order influences

development and adult phenotype if we are to gain a comprehensive understanding of the causes and consequences of dominance in animal societies.

Cooperatively breeding birds provide an interesting system in which to investigate asynchronous hatching. In many such species, offspring show a high degree of natal philopatry, which provides a convenient opportunity to track individuals from hatching to adulthood and to assess the effects of hatching order at multiple time points. Furthermore, in some cooperative breeders, group offspring have mixed parentage, which can increase within-brood competition due to low relatedness among brood members (Briskie *et al.* 1994, Mock & Parker 1998). For example, in some cooperatively breeding birds, multiple females contribute eggs to a single nest and contribute to parental care (joint-laying; Vehrencamp 2000, Vehrencamp & Quinn 2004). In many joint-laying species, females employ behavioural strategies such as egg tossing or egg burial (i.e. burying eggs in the nest structure) to avoid having their eggs hatch later than those of other females and to reduce the number of competitors within the group nest (e.g. Mumme *et al.* 1983, Schmaltz *et al.* 2008, Riehl 2010). Similar strategies are observed in communally breeding species from other taxa, which perform infanticide or eviction, or alter gestation periods to avoid the negative consequences of among-female reproductive asynchrony (Ims 1990, Poikonen *et al.* 2008, Hodge *et al.* 2011). Although these competitive reproductive behaviours have been well documented, the consequences of hatching asynchrony are poorly understood for almost all joint-laying birds.

Here, we explore the effects of hatching order on offspring growth, survival and competitive ability during adulthood in the joint-laying Pukeko *Porphyrio melanotus melanotus*. Although mated Pukeko pairs can breed successfully, it is more common for groups of 3–12 individuals to defend a shared territory and raise the group offspring cooperatively (Craig 1980a). Such groups usually contain multiple breeding males and one or two breeding females who mate promiscuously, as well as non-breeding helpers of both sexes. Adult Pukeko form a linear dominance hierarchy (Jamieson & Craig 1987, C.J. Dey unpubl. data), with breeding males being the highest-ranked individuals, breeding females and non-breeding males having intermediate ranks, and non-breeding females

being the lowest ranked. When there are multiple breeding females in a group, the dominant female is involved in more copulations, and usually lays more eggs than the subordinate breeding female (Craig 1980b, Jamieson & Craig 1987), and dominance status determines the order of replacement of breeding females by non-breeding helpers (Jamieson & Craig 1987). The dominant breeding male is more likely to perform nocturnal incubation than other males (Craig 1980a) but it is unclear whether there is a relationship between dominance status and paternity in this species (Jamieson *et al.* 1994, Jamieson 1997).

Incubation of Pukeko nests begins part way through the laying period, and thus hatching is asynchronous (Craig 1980a). Pukeko offspring are nidifugous, leaving the nest after 3–4 days, but are fed by adults for up to 2 months (Dey & Jamieson 2013). Offspring fledge at 2–3 months old and groups frequently fledge multiple chicks from a nest. On the North Island of New Zealand, where this study was performed, Pukeko are highly philopatric and offspring of both sexes typically inherit breeding positions within their natal group rather than dispersing to join other groups (Craig & Jamieson 1988; C.J. Dey unpubl. data). As a result, nest-mates are often in competition for breeding positions when they reach adulthood. We investigated the consequence of hatching order on fitness-related traits by testing three predictions: (1) that earlier-hatched offspring would show increased growth during development relative to later-hatched nest-mates, (2) that earlier-hatched offspring would show reduced mortality during development relative to later-hatched nest-mates and (3) that earlier-hatched offspring would be socially dominant over later-hatched nest-mates in adulthood. To control for the possibility that egg size might influence offspring traits we also assessed how egg size varied across the hatching period. Finally, we explored patterns of hatching order in joint-clutch nests to begin to understand how hatching asynchrony might affect female reproductive success in this species.

METHODS

Field methods

We conducted this study at Tawharanui Regional Park (36°22'S, 174°49'E) on the North Island of New Zealand. During the 2010 breeding season

(July–December), we located Pukeko nests by searching suitable nesting habitat (among *Juncus*, *Carex* or *Typha* grasses). Although Pukeko groups can breed several times per year, only the first reproductive attempt by each social group was considered in this study. In total, we collected data from 32 social groups (20 single-clutch and 12 joint-clutch nests) for this study. However, not all data were available for each nest and thus sample sizes differ among analyses.

At each nest, we measured length and width of all eggs, marked them with a non-toxic marker and floated them in warm water to estimate the date they were laid (Hays & LeCroy 1971). In nests with known initiation dates, flotation scores are highly correlated with egg age (Dey *et al.* 2014a). We visited nests daily during the laying and hatching periods, and every 3rd day between those periods. During the hatching period, we recorded the hatching date of each chick and fitted each hatchling with one coloured plastic leg band and one metal ring (with a unique number), both containing soft foam to allow for leg growth.

To determine whether hatching order affects offspring growth (prediction 1), we recaptured as many chicks as possible between the age of 10 and 59 days. Chicks were captured by hand or using funnel traps baited with corn (which was consumed almost entirely by accompanying adult birds). Upon recapture, we measured the length of each chick's left tarsus and fitted it with a further three coloured plastic leg bands to create a unique ring combination for each individual. In total, 64 chicks from 24 nests were recaptured in this manner.

To determine whether hatching order influences offspring survival (prediction 2), we surveyed the social groups in which we had monitored nests at 60 days after the completion of hatching and again in January 2012 (15–17 months after hatching). At this age, Pukeko are sexually mature but are typically non-breeding helpers within their natal groups. At Tawharanui, Pukeko are highly philopatric (consistent with other North Island sites; e.g. Craig & Jamieson 1988) and no offspring were found in groups other than their natal group. Moreover, long-distance dispersal by Pukeko is extremely rare (Craig & Jamieson 1988). Thus, we assumed that individuals that were not located in their natal group were dead. Groups were surveyed using spotting scopes or binoculars from portable hides positioned on hilltops. We performed two

30-min surveys at each time point (i.e. at 60 days and in January 2012) to ensure that all individuals in each group were identified. In total, 30 social groups (with 68 surviving and 53 dead offspring) were observed at 60 days after hatching and 28 social groups (with 34 surviving and 79 dead offspring) were observed in January 2012.

To test whether hatching order influences social dominance in adult Pukeko (prediction 3), we performed detailed behavioural observations on eight social groups that had multiple chicks that hatched in 2010 and that survived until January 2012 (a total of 23 chicks survived in these groups). Observations were made in January and February 2012 and consisted of one 30-min observation per day for a period of 5 days (following the methods in Jamieson & Craig 1987 and Dey *et al.* 2014b). The observer placed approximately 50 g of dried corn in the territory of the group of interest immediately prior to each observation period in order to increase the frequency of dominance interactions. Pukeko are accustomed to human presence at this site and quickly resumed normal behaviours after this disturbance. The observer then recorded all dominance interactions (physical aggression as well as dominant and submissive postures; Craig 1977) from a camouflaged hide. We only recorded interactions that occurred between the surviving young because not all other group members were ringed. Observers were blind to the hatching order of the individuals and all observations were conducted between 06:30 and 10:00 h.

To assess how hatching order might differentially affect the reproductive output of dominant and subordinate female Pukeko, we examined patterns of hatching in joint-clutch nests (12 nests). The eggs of individual female Pukeko are identifiable, as each female lays eggs with a unique colour, shape, size and spotting pattern (Craig 1980a, Jamieson 1997, Quinn *et al.* 2012). We assigned each egg to either the 'A' clutch (i.e. the first egg type laid; assumed to be the dominant female's clutch) or the 'B' clutch (i.e. the clutch that was initiated second) and recorded the hatching date of each egg. Eggs from both the A and the B clutch often hatched on the same day, and so while we were able to assess differences in hatching order between the dominant and subordinate female, as well as assess the consequences of hatching order for chicks, we were not always able to determine the maternity of each chick. Thus, we did not perform analyses of the direct

relationship between maternal status and growth, survival or dominance.

Statistical analysis

All analyses were conducted using R version 3.0.1 (R Core Team 2013). *A priori*, we restricted all models to include only the variables of interest and essential covariates, as our sample size did not allow for complex models. To determine whether our data met the assumptions of each model, we visually inspected diagnostic plots including residuals vs. fitted and quantile–quantile plots. Generalized linear mixed models (GLMMs) were also checked for overdispersion. To assess the effect of hatching order on various measures of offspring fitness, we calculated a 'hatch order' value for each chick from each nest by ranking the hatching sequence for each nest. When multiple individuals hatched on the same day, they were given equal hatch order values. For example, if three chicks hatched on day 1 they would all receive a hatch order value of 2 (the mean of rank 1, 2 and 3). The next chick to hatch would receive a hatch order value of 4. Hatch order values ranged from 1 to 8 in this study and these data were treated as continuous in all models.

To assess whether hatching order influences offspring growth within the first 60 days of hatching we used a linear mixed-effects model (LMM) implemented in the 'nlme' package in R (Pinheiro *et al.* 2013). In this model, tarsus length was used as the response variable, social group was included as a random intercept, and both chick age (days since hatching) and hatch order were included as fixed effects.

To test the effect of hatching order on offspring survival, we performed two separate binomial family GLMMs with logit link functions. In these models we used a binary score of whether an individual survived to 60 days or until January 2012 as the response variable. In each model, we included social group as a random intercept and hatch order as the sole fixed effect. Models were fitted with Laplace approximation in the 'lme4' package (Bates *et al.* 2013), as suggested by Bolker *et al.* (2009), when the expected number of survivals and deaths are fewer than five for each social group.

To test the effects of hatching order on social dominance, we calculated dominance scores using all of the dominance interactions pooled across the

five observation periods. We used the dominance scoring method outlined in David (1987), which incorporates the number of animals that an individual directly dominates, while also considering the dominance status of the focal individual's opponents. Thus, individuals can receive high scores if they are dominant over many individuals or if they dominate individuals who are dominant over many other individuals. All types of dominance interactions (physical aggression and dominant/subordinate postures) were included in this analysis and received equal weight. Next, we rank-transformed the dominance scores to produce a dominance rank for each individual (with 1 being the highest ranked) and used these ranks as the response variable in a cumulative link mixed model (CLMM) which analyses ordinal response variables while allowing for random factors. This model was implemented using the 'ordinal' package in R (Christensen 2012). We included social group as a random effect and hatch order as the sole fixed effect in this model.

To examine how egg size varied with hatching order we calculated egg volume using the equation $\text{volume} = 0.51 \times \text{length} \times (\text{width}^2)$ (Hoyt 1979). Volume was then used as the response variable in an LMM, which included nest as a random intercept and both hatch order and female status (primary or secondary) as fixed effects. This analysis included data from all eggs that hatched in this study (124 eggs from 32 nests).

To assess whether the dominant female's offspring hatched earlier than the subordinate female's offspring in joint-clutch nests, we performed an LMM with hatch order as the response variable. In this model, social group was included as a random factor and maternity (i.e. A or B clutch) was included as the sole fixed effect.

RESULTS

After controlling for age (LMM: $n = 64$ offspring from 24 nests; estimate = 1.31, 95% CI = (1.15, 1.46), $t_{1,38} = 17.21$, $P < 0.0001$), hatching order predicted chick size within 60 days of hatching, with earlier-hatched chicks being larger than later-hatched chicks (estimate = -1.34, 95% CI = (-2.60, -0.08), $t_{1,38} = -2.16$, $P = 0.038$). Additionally, earlier-hatched chicks were more likely to survive to 60 days of age (GLMM: $n = 121$ offspring from 30 nests; estimate = -0.53, 95% CI = (-0.84, -0.23),

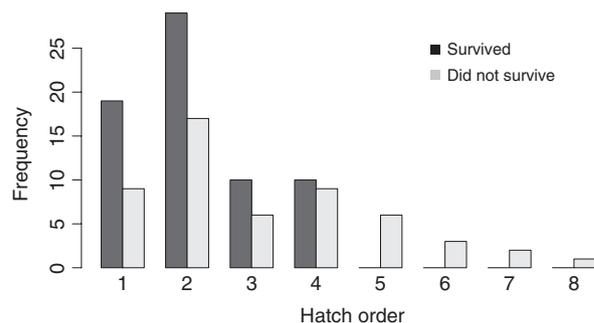


Figure 1. Frequency histogram of offspring survival to 60 days after hatching in relation to hatch order. The frequency histogram shows individuals that survived (dark bars) vs. individuals that did not survive (light bars) for each hatch order value (rounded to the nearest integer). See text for details of statistical analysis.

$z_1 = -3.46$, $P < 0.001$; Fig. 1) and until January 2012 (GLMM: $n = 113$ offspring from 28 nests; estimate = -0.65, 95% CI = (-1.10, -0.20), $z_1 = -2.82$, $P = 0.005$). As adults, individuals that hatched earlier within their broods were more likely to be socially dominant than later-hatching individuals (CLMM: $n = 23$ offspring from eight nests; estimate = 1.92, 95% CI = (0.72, 3.12), $z_3 = 3.129$, $P = 0.002$; Fig. 2). These relationships were not due to large hatching spreads in joint-clutch nests because models conducted with only

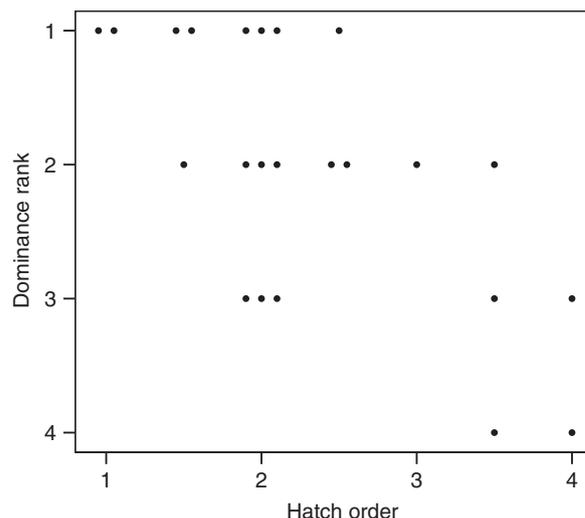


Figure 2. Relative adult dominance ranks (1 = most dominant) of brood-mates vs. hatch order (1 = first-hatched) of each individual within their brood. Overlapping data points are offset by 0.05 units on the x-axis. See text for details of statistical analysis.

single clutch nests included yielded qualitatively similar and statistically significant results. Furthermore, these relationships were not explained by differences in egg size because earlier-hatched eggs were not significantly larger than later-hatched eggs (LMM: $n = 124$ eggs from 30 nests; estimate = 87.00, 95% CI = (-162.45, 336.46), $t_{1,92} = 0.69$, $P = 0.49$), nor were the eggs of secondary females smaller than the eggs of primary females (estimate (secondary) = -553.93, 95% CI = (-1557.2, 449.86), $t_{1,92} = -1.09$, $P = 0.28$). Finally, although there was considerable overlap in the age of chicks from each female in joint-clutch nests (Fig. 3), the primary female's offspring hatched earlier than those of the secondary female (LMM: $n = 60$ eggs from 12 nests; estimate = 1.27, 95% CI = (0.49, 2.09), $t_{1,47} = 3.11$, $P = 0.003$).

DISCUSSION

In many birds, hatching asynchrony leads to size hierarchies in the developing brood (Mock & Parker 1986, Stokland & Amundsen 1988, Rosivall *et al.* 2005). Here we show that earlier-hatched chicks are larger for their age and have higher survival rates than later-hatched brood-mates. Additionally, we found that hatching order effects persist into adulthood, as earlier-hatched chicks achieve higher adult dominance ranks within their social group. Previous studies have demonstrated that hatching order has effects on offspring pheno-

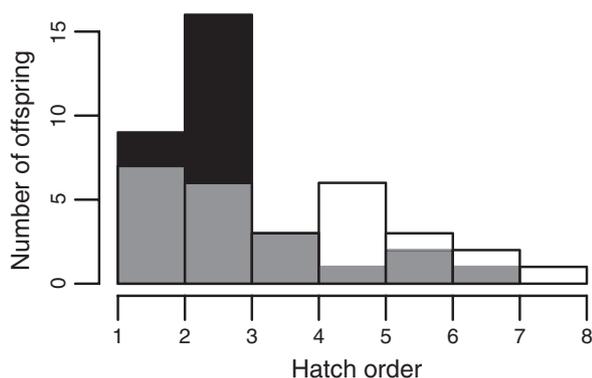


Figure 3. Hatching order histogram from joint-clutch nests. Data shown are hatch order values of offspring laid by the primary (black) and secondary (white) females, with grey shading representing the overlap between the histograms from each female type. Hatch order values are rounded to the nearest integer. See text for details of statistical analysis.

type in many birds (e.g. Zach 1982, Love *et al.* 2003) but ours is one of the first to follow wild birds from hatching to adulthood to determine how initial differences in competitive ability might influence adult traits. Our results are consistent with laboratory experiments in demonstrating that early life deficits (e.g. dietary restrictions, stress hormone treatments) can alter adult traits such as body size, sexual attractiveness, cognitive performance and dominance (Lindström 1999, Fisher *et al.* 2006, Royle *et al.* 2006). However, the manipulations performed in many experimental studies may impose challenges that are more severe than those faced in the wild (Drummond *et al.* 2011), and thus it is important to assess whether natural early life challenges also lead to these costs during adulthood.

The mechanism by which hatching order affects adult dominance in Pukeko remains unclear. It may be that earlier-hatched individuals achieve larger adult size due to increased food acquisition during growth. Pukeko chicks are led and fed by members of the social group after hatching, and larger chicks appear to receive more food from adult group members (C.J. Dey pers. obs.). Because adult body size is correlated with dominance in this species (Dey *et al.* 2014b), a bias in food acquisition during development could lead to hatch-order-mediated dominance hierarchies in adulthood. It is also possible that Pukeko chicks establish dominance hierarchies early in life through direct interactions with their brood-mates, and that these hierarchies persist into adulthood due to winner or loser effects (Drummond & Osorno 1992, Dugatkin 1997, Drummond & Canales 1998). Additionally, this study cannot eliminate the possibility that the relationship between hatching order and social dominance, body size or survival is due to a sex-ratio bias in hatching order in Pukeko nests. Because male Pukeko are generally larger and more dominant than females (Jamieson & Craig 1987, Dey *et al.* 2014b), a tendency for males to hatch earlier than females could confound apparent hatching order effects. However, a sex-ratio bias in hatching order would not be expected in Pukeko because males and females have about equal variance in lifetime inclusive fitness (Dey *et al.* 2012) and therefore there is no apparent advantage for breeding females to produce either sons or daughters earlier in the hatching sequence (Trivers & Willard 1973). Furthermore, a sex-ratio bias in hatching order

would itself suggest that there are some fitness consequences to hatching order *per se*, otherwise there would be no selective pressure to favour a sex-ratio bias. Finally, this study was restricted to observations of the first reproductive event of the year for each social group. The first reproductive event is the most likely to be successful and is therefore a more important fitness determinant than are later reproductive events (Craig 1980b). However, it is possible that the effects of hatching order may be different for later reproductive events, as there may be dependent offspring from previous nests competing for or providing parental or alloparental care. Future studies should determine offspring sex, observe interactions between nest-mates and manipulate hatching asynchrony in order to fully understand the causal relationships between hatching order and fitness-related traits in Pukeko.

The long-term effects of hatching asynchrony are particularly interesting in cooperatively breeding species because the group offspring may be of mixed parentage. As a result, there should be strong selection on traits involved in competition between brood-mates. Here, we show that in Pukeko groups with two breeding females, offspring of the dominant female hatch earlier than those of the subordinate female. Although we could not directly determine the maternity of each offspring (because multiple offspring often hatched on a single day), it is likely that this systematic difference in hatching order influences the relative competitive ability of the offspring from each breeding female. This could have important implications for social dynamics in this species, because subordinate individuals may be disadvantaged in terms of both breeding opportunities and the likelihood of success of their surviving offspring. In general, joint-nesting in Pukeko is thought to be disadvantageous for dominant females because a lower percentage of eggs hatch in joint-clutch nests than in single-clutch nests (Vehrencamp & Quinn 2004, Quinn *et al.* 2012, Dey *et al.* 2014a). However, if the dominant female's offspring are able to out-compete those of the subordinate breeding female, the dominant female may not pay as severe a cost of joint-laying as previously inferred. Hatching asynchrony and the resultant effects on offspring competitive ability have been implicated as an important factor in the social dynamics of other joint-laying birds (e.g. Cariello *et al.* 2006, Schmaltz *et al.* 2008, Riehl 2010) but we are aware of only one other joint-laying species

in which this relationship has been directly studied. In the Acorn Woodpecker *Melanerpes formicivorus*, earlier-hatched chicks are larger and more competitive than their later-hatched brood-mates (Stanback 1994, Koenig *et al.* 2011). However, egg destruction by co-breeding females minimizes hatching asynchrony in this species (Mumme *et al.* 1988), and the effects of hatching order therefore probably do not influence the relative fitness of co-breeding females.

In addition to hatching (or birth) order, communally breeding animals could also influence offspring competitive ability by adaptively manipulating the growth environment through so-called 'maternal effects' (Russell & Lummaa 2009). For example, several studies have demonstrated that avian parents manipulate the size and content of their eggs better to match the phenotype of their offspring to the environment they will face (e.g. Groothuis *et al.* 2005) or to provide competitive advantages within the brood (Müller *et al.* 2007). Although few studies have investigated this phenomenon in joint-laying birds, in the crotophagine cuckoos, mothers are known to adjust both egg size (Riehl 2010) and yolk testosterone levels (Cariello *et al.* 2006, Schmaltz *et al.* 2008) to improve offspring competitiveness. While our data suggest that variation in egg size is not responsible for the patterns of growth, survival and dominance observed in the current study, it is possible that yolk hormone levels play a role. If females deposit higher levels of androgens in earlier-laid eggs, or if dominant females deposit more androgens than subordinate females, then earlier-hatched offspring may grow faster and achieve higher dominance ranks regardless of any hatching order effect *per se* (Schwabl 1997, Strasser & Schwabl 2004). Future studies investigating how yolk hormone deposition varies with laying order and maternity in Pukeko will be valuable in understanding the complex social dynamics of this species. However, even if females do invest more in early than late-laid eggs, hatching order will probably still have an important influence on offspring fitness given that hatching order has a stronger effect than yolk androgen levels on offspring fitness in other birds (Schwabl 1997, Eising *et al.* 2001, Groothuis *et al.* 2005).

In conclusion, Pukeko show persistent effects of hatching order on adult phenotype in wild, free-ranging individuals. Earlier-hatched chicks have benefits such as increased growth and survival as

juveniles, as well as higher social rank as adults. This pattern may increase the fitness of dominant females in joint-nests, as they are responsible for earlier-laid eggs. This research demonstrates that the timing of reproduction has profound impacts on offspring quality, and lends insight into the factors driving intragroup competition in a cooperative breeding system.

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