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Short Communication

Factors influencing the behavioural development of juvenile New Zealand Falcons (*Falco novaeseelandiae*)

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Abstract. Adult raptors are thought to train their progeny in flight and hunting techniques during the period of dependence after fledging. Parental teaching is poorly understood but its effects may impinge on the success of reintroduction projects where juveniles are released into areas without adults, as is commonly done with raptors. We compared behavioural development over the first 4 weeks after fledging in wild-reared juvenile New Zealand Falcons (*Falco novaeseelandiae*) with that of juvenile Falcons recently hack-released as part of a conservation initiative. Juveniles with parents spent nearly half as much time perching, spent twice as much time playing, and chased conspecifics five-times more often than juveniles without parents. Juveniles with siblings chased conspecifics 60 times more often, and engaged in twice as much play behaviour compared with juveniles without siblings. We suggest that, provided juvenile New Zealand Falcons are hack-released in groups, reintroduction of this threatened species without adults does not have a major effect on the behavioural development of individuals, although ongoing monitoring to corroborate these results with a larger sample size is recommended.

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Introduction

In addition to learning through direct experience with food items (Pietrewicz and Kamil 1979), foraging skills may be acquired through observation of siblings and parents (Edwards 1989; Lickliter *et al*. 1993; Ricklefs 2004) and, in altricial birds, learning from conspecifics may play a vital role in development (Lickliter *et al*. 1993). The period of dependence after fledging, if any, is an important, but understudied, stage in the development of young birds. During this period, non-precocial birds rely on their parents for some or all of their food, while simultaneously developing the flight, foraging and social skills necessary for independent survival (Weathers and Sullivan 1989; Heinsohn 1991; Wheelwright and Templeton 2003). Upon reaching independence, young birds from many species suffer high mortality rates, and the behavioural development achieved during the period of dependence after fledging likely plays a role in the severity of these mortality rates (Heinsohn 1991).

Reintroductions are a popular tool in threatened-species conservation but often have low rates of success (Fischer and Lindenmayer 2000). There are indications that a lack of behavioural development, related to reduced exposure to parents, siblings or natural conditions, has led to lower survival in captive-reared and released individuals compared with wild-reared individuals, as found in Aplomado Falcons (*Falco femoralis*; Brown *et al*. 2006).

Commonly, as part of translocation programs, raptors are released using a method known as 'hacking', whereby juvenile birds are released in small groups from artificial nests at approximately the time they would normally fledge from a natural nest (Sherrod *et al*. 1982). The period of dependence after fledging in hacked individuals is particularly important, because these juveniles must be fed by humans to survive. This has potential implications for the development of vital behaviours such as flight and hunting, because adult birds are thought to participate in training of young birds by hunting within view of the nest and through aerial food-passes, sometimes of live prey (Newton 1979; Weathers and Sullivan 1989; Kitowski 2005).

With the exception of a few studies, the role of conspecifics on the development of behaviour in birds is an overlooked topic (Lickliter *et al*. 1993), yet horizontal transmission of learned skills between siblings may influence the speed of behavioural development (Ricklefs 2004; Kitowski 2005, 2009). In birds of prey, the importance of horizontal transmission of flight and hunting skills is little known, although in Western Ospreys (*Pandion haliaetus*), siblings developed complex hunting behaviour faster than single juveniles (Edwards 1989).

A reintroduction project of the threatened New Zealand Falcon (*Falco novaeseelandiae*) provided us with the opportunity to examine the effects of parental and sibling presence on the behavioural development of young Falcons in the post-fledging dependence period. We compared the behaviour of wild-reared Falcons with that of recently released Falcons to determine the time spent engaged in several behaviours relevant to survival until independence, such as perching, flight, play and hunting (Edwards 1989; Negro *et al*. 1996; Kitowski 2009).

Methods

We spent 181 h observing 22 juvenile New Zealand Falcons during the critical 4 weeks immediately after fledging (juvenile age 5–9 weeks). Our sample size was restricted owing to the threatened status of this species and the small number of release sites used. Observations were made at four natural nests with parents (henceforth 'wild-reared' juveniles), and at six release sites where no parents were present (henceforth 'released' juveniles). Released juveniles were 'soft' released by the hacking method (see Sherrod *et al*. 1982). Seventeen of the 22 juveniles observed were individually marked with bands or radio-telemetry tags. Wild-reared and released juveniles were either single birds, or part of a cohort of two or three siblings. One nest contained a wild-reared juvenile that did not have siblings, and five juveniles were released as single birds.

Released juveniles were similar in age to those that were wild-reared, but may have been up to 5 days older. Each site was visited weekly for 3 h for the 4 weeks immediately after natural fledging or release. We observed 16 juveniles in their first week after fledging, when 6 weeks old (six of which were wild-reared), 21 juveniles when 7 and 8 weeks old (10 of which were wild-reared) and 17 juveniles when 9 weeks old (six of which were wild-reared).

Using focal animal sampling, we noted the duration of each behaviour that lasted >30 s. Treating juvenile identification as the unit of replication, the mean observation time per session was 141.1 ± 7.75 min (±s.e.), and did not differ significantly for the groups with or without siblings or parents (paired *t*-tests, all $P > 0.10$). Focal Falcons could be *perching* off the ground, *walking on the ground* or *flying*. We also noted if juveniles were taking part in *play behaviour*, which was characterised by individuals (either alone or with siblings) partaking in behaviour with no apparent adaptive gain (Bekoff and Allen 1997), such as pouncing on objects or siblings, grabbing at objects or siblings with their talons, and running and rapidly flapping their wings.

Distance (m) of each flight (*flight-distance*), as well as the accuracy and difficulty of each landing attempt, was estimated. *Landing difficulty* was classified by the size and stability of perches on a scale of 1 to 5, with 1 representing the most stable perches. *Landing accuracy*, and the accuracy of *food-passes* from adult Falcons to juveniles was classified on a similar scale (Supplementary material). We also noted if flights involved a *chase* of either a sibling or adult Falcon. If a juvenile took flight in pursuit of a heterospecific, these were considered as *hunting flights*.

The time spent engaged in each behaviour divided by the observation time for each focal individual was used to calculate proportional data for standardisation. The frequency of flights and hunting attempts that each individual made per minute of observation time per week was also calculated. Data were modelled using generalised linear mixed effects models (GLMM) in the lme4 package (Bates *et al*. 2008) in *R* (*v*.2.7.2; R Core Development Team 2008). Some data were transformed before analysis to meet assumptions of the model (Supplementary material). For models fitted using Gaussian errors a Markov Chain Monte Carlo (MCMC) resampling method with 10 000 simulations was used to estimate *P* values for the fixed effects, carried out using the 'pvals.fnc' function in the languageR package in *R* (Baayen 2008).

We nested juvenile identification within nest or release-site and included these terms as random effects to control for non-independence of samples from the same juvenile or from juveniles at the same site. Age (in weeks), presence of siblings, presence of parents, sex and habitat type (sites were in either unmanaged hills or managed vineyards) were included as categorical fixed effects in the models. We included interaction terms between two of the fixed effects in the models, and determined the most appropriate interaction term based on model fit (measured using the Akaike Information Criterion (AIC)). Models were simplified by removing non-significant interaction terms followed by main effects until model fit was maximised. Where relevant, we present the mean (±s.e.) for untransformed data (as a measure of effect size). Simplified model estimates are included in Supplementary material.

Results

Immediately after fledging (Week 6), released juveniles spent a significantly greater proportion of observation time perching (0.87 ± 0.05) than wild-reared juveniles (0.45 ± 0.11; $t = 2.82$, $P = 0.03$). In Weeks 7, 8 and 9 there was no change in the time that released juveniles spent perching ($t < 1.9$, $P > 0.1$ for all), whereas over this same period wild-reared juveniles had a significant tendency to increase the time they spent perching ($t > 2.6$, $P < 0.02$ for all; Fig. 1). Immediately after fledging there was a non-significant tendency for juveniles with siblings ($t = 1.84$, $P = 0.07$) and wild-reared juveniles ($t = 2.00$, $P = 0.09$) to spend more time walking on the ground compared with single and released juveniles respectively. In Week 7, wild-reared juveniles decreased the time spent on the ground ($t > 2.10$, $P < 0.04$ for all), whereas released juveniles increased the time on the ground ($t = 2.16$, $P = 0.04$), resulting in both released and wild-reared juveniles spending a similar proportion of time on the ground in Weeks 8 and 9 (Fig. 1).

Juveniles with siblings spent a greater proportion of the day (0.04 ± 0.007) engaged in play than single juveniles (0.02 ± 0.012; $t = 2.19$, $P = 0.03$). Parental presence was associated with a non-significant tendency to spend a greater proportion of the day (0.05 ± 0.01) engaged in play compared with no parents (0.03 ± 0.01; $t = 1.90$, $P = 0.06$).

Age was also positively correlated with frequency of flights. At 6 weeks, juveniles flew a mean of 0.08 ± 0.02 flights min^{-1} and at 7 weeks they flew 0.11 ± 0.02 flights min^{-1}, although this difference was not significant ($t = 1.32$, $P_{MCMC} = 0.22$). Compared with age 6 weeks, juveniles flew significantly more often in Week 8 (0.21 ± 0.03 flights min^{-1}; $t = 3.741$, $P_{MCMC} < 0.001$) and in Week 9 (0.219 ± 0.056; $t = 3.94$, $P_{MCMC} < 0.001$). Additionally, the presence of siblings had a non-significant tendency to increase the mean number of flights observed ($t = 2.75$, $P_{MCMC} = 0.08$).

Mean flight-distance (m) was also positively affected by age, but this varied with habitat type. In Weeks 6 (13.36 ± 2.9 m) and 7 (39.1 ± 16.9 m) there was no significant change in the mean flight-distance (all $t < 1.5$, all $P_{MCMC} > 0.15$). In Week 8 and then Week 9, juveniles significantly increased their mean flight-distances in unmanaged hill habitats (Week 8: 109.8 ± 30.2 m, $t = 4.70$, $P_{MCMC} < 0.001$; Week 9: 146.92 ± 13.9, $t = 6.76$, P_{MCMC} 0.001) and in vineyards, although the increase was not as steep in vineyards (Week 8: 47.3 ± 6.1, $t = -2.48$, $P_{MCMC} = 0.01$; Week 9: 87.1 ± 19.2, $t = -3.32$, $P_{MCMC} = 0.002$). Landing accuracy was only influenced by juvenile age, with an increase in accuracy across each week ($t > 2.7$, $P_{MCMC} < 0.008$ for all), but all other factors (sex, habitat type, presence of parents or siblings) were removed from the reduced model. Similarly, landing difficulty did not change with any of our variables, including age, and remained constant at a mean difficulty of 2.55 ± 0.06.

Holding all other variables constant, a greater proportion of the observed flights consisted of chases for birds that had siblings

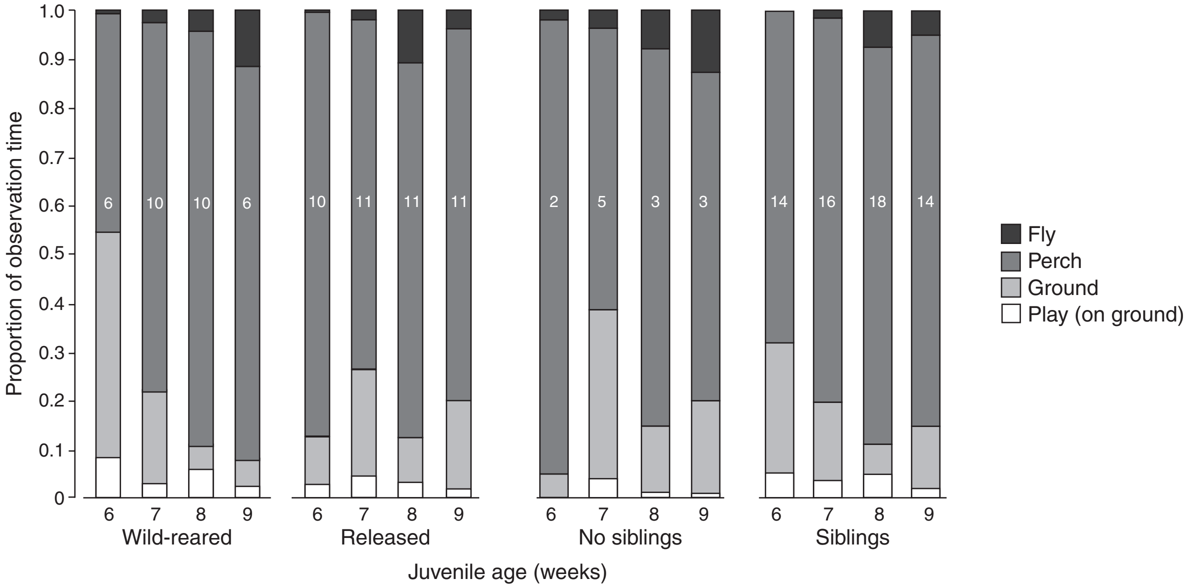

Fig. 1. Mean proportion of observation time that juvenile New Zealand Falcons spent walking on the ground (Ground), perched off the ground (Perch), or flying (Fly). Playing (Play) generally took place on the ground so has been indicated as time spent on the ground. Juveniles were either wild-reared and raised by adult Falcons, or were released and reared without parents. Juveniles were also either raised alone (No siblings) or with siblings (Siblings). Numbers within each column represent sample sizes.

compared with single birds ($Z = 4.21$, $P < 0.001$) and for wild-reared juveniles compared with released juveniles ($Z = 3.64$, $P < 0.001$). The proportion of chasing flights increased with age ($Z > 3.2$, $P < 0.002$ for all). Model estimates indicated that over Weeks 7, 8 and 9, the slope for the relationship between age and proportion of flights that were chases decreased for wild-reared juveniles compared with released juveniles ($Z > 3.00$, $P < 0.003$ for all), although the proportion of flights that were chases was still higher for wild-reared birds.

We observed 75 hunting attempts by juveniles, none of which was successful. Comparing juveniles with and without siblings or parents we found that wild-reared juveniles with siblings hunted the least (0.003 ± 0.001; $t = -3.23$, $P_{MCMC} = 0.002$); released individuals without siblings hunted slightly more often (0.005 ± 0.004; $t = 2.65$, $P_{MCMC} = 0.01$); released individuals with siblings had a non-significant tendency to hunt more often (0.009 ± 0.002; $t = 1.48$, $P = 0.08$); and the one wild-reared juvenile without siblings had a non-significant tendency to hunt the most often (0.023 ± 0.009; $t = 2.65$, $P = 0.21$). We observed 19 food-passes between adult and juvenile Falcons. Although the accuracy of food-passes seemed to improve with age, the sample size was too small for statistical analysis. In Week 6, we only observed one food-pass (with an accuracy score of 2); in Week 7, we observed two passes (mean accuracy 2.75 ± 0.75); in Week 8 we observed six passes (3.22 ± 0.58); and in Week 9 we observed three food-passes (4.33 ± 0.67).

Discussion

In social animals, solitary conditions in the early stages of life can have negative effects on development (Lévy *et al.* 2003) and hunting skills (Edwards 1989). Our results suggest that, in the New Zealand Falcon, the presence of both parents and siblings is likely to result in the fastest development of important flight and foraging behaviours. However, our results should be taken with caution as, owing to the threatened status of this species, we had only small sample sizes.

In the New Zealand Falcon, food-passes from parents, chases of conspecifics and play behaviour are all likely to provide experience needed for the hunting of prey later in life (Negro *et al.* 1996; Kitowski 2009). We did not find any obvious trends in the frequency of hunting attempts and the conditions in which juveniles were raised, but wild-reared juveniles without siblings and released juveniles with siblings appeared to hunt more often than the other two groups. The reasons for this are not clear and may be a reflection of sample size, and it is likely that with a larger sample size our results that were close to a probability of 0.05 would become significant.

The importance of sibling presence on the behavioural development of raptors is not well known. Juveniles of many species, including American Kestrels (*Falco sparverius*; Negro *et al.* 1996), stay close to one another in the early stages of the period of dependence after fledging and increase distance between siblings as they approach independence. Although this is sometimes considered in light of potential competition among broodmates, there may be evolutionary benefits to remaining nearer to siblings in the early stages of development. For example, socially reared precocial birds retain better species-specific visual imprinting capabilities compared with individuals reared in solitary conditions (Lickliter *et al.* 1993). The few studies that have examined the effect of sibling presence on the development of hunting in raptors have shown that individuals with siblings develop vital foraging behaviours faster than single individuals (Edwards 1989). We observed single juveniles often perching or standing on the ground for long lengths of time, suggesting that single juveniles flew less often than those with siblings.

Sibling presence also triggered more play behaviour in young New Zealand Falcons. In raptors, play behaviour is associated with the skill each species requires to hunt their prey: in species that actively pursue prey, such as falcons, play is more frequent than in food generalist or scavenger species (Ricklefs 2004; Kitowski 2005). Therefore, increased incidence of play in juveniles with siblings is likely to have implications for hunting skills later in life.

The ability of translocated individuals to display natural behaviour can influence the success of reintroduction projects (Blumstein and Fernández-Juricic 2004) and is vital when animals are reintroduced into anthropogenic landscapes. Wild-reared individuals often display higher survival rates than released individuals (Brown *et al*. 2006; Reid *et al*. 2010) but this trend can be mitigated by pre-release conditioning. Further research is needed into the optimal pre-release and release conditions to optimise the survival and recruitment of released individuals.

Our results support the notion that in New Zealand Falcons, and possibly in other raptors, interactions with conspecifics in the period of dependence after fledging leads to faster development of flight and hunting behaviours, and is likely to result in greater social development. Released individuals that go on to breed have been shown to have higher rates of attendance at nests, and provide their chicks with more food and with a similar diet compared with wild-reared New Zealand Falcons (Kross *et al*. 2012, in press), supporting the idea that released individuals can develop the hunting and social skills needed to reproduce successfully.

Supplementary material

Further information on our observation methods, our data analysis and a table including a summary of the variables retained in the models for measured behaviours are included in the supplementary material (see http://www.publish.csiro.au/?act=view_file&file_id=MU12020_AC.pdf).

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