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Ospreys do not teach offspring how to kill prey at the nest

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Abstract

There is strong evidence for teaching in only a handful of species, most of which are cooperative breeders, leading some researchers to suggest that teaching may be more likely to evolve in such species. Alternatively, this initial distribution could be an artefact of the popularity and tractability of cooperative breeders as behavioural study systems. Therefore, establishing or refuting this potential evolutionary link requires researchers to assess potential cases of teaching in more non-cooperatively breeding species. We tested for teaching in the osprey (*Pandion haliaetus*), a non-cooperatively-breeding bird anecdotally reported to teach hunting skills to their offspring. We tested whether parents brought back more live prey to the nest as their offspring got older, allowing the latter to practice killing prey in a manner analogous to the progressive teaching seen in meerkats. We found the opposite trend to that predicted by the teaching hypothesis, indicating that ospreys do not teach their young at the nest.

Introduction

The capacity to learn from others by social learning is known to be widespread across the animal kingdom[1, 2]. However, for many years teaching- the active facilitation of learning in others, was considered to be a behaviour unique to humans. Early studies of animal teaching stressed the intention of the tutor to instruct the pupil as an important defining factor, effectively restricting teaching to humans [3]. The emphasis of such studies shifted when Caro and Hauser [4] adopted a functional perspective, defining teaching as follows:

37 "An individual actor A can be said to teach if it modifies its behaviour only in
38 the presence of a naïve observer, B, at some cost or at least without obtaining
39 an immediate benefit for itself. A's behaviour thereby encourages or punishes
40 B's behaviour, or provides B with experience, or sets an example for B. As a
41 result, B acquires knowledge, or learns a skill earlier in life or more rapidly or
42 efficiently than it might otherwise do so, or would not learn at all'' (p. 153).
43 The goal of Caro and Hauser's definition is to identify behaviour that has the
44 evolutionary function of promoting learning in others, and is generally accepted by
45 those studying potential cases of teaching in animals [e.g. 5].
46 There are only a handful of species exhibiting behaviour which convincingly
47 meets all of Caro and Hauser's criteria, including tandem running ants, *Temnothorax*
48 *albipennis* [6]; honeybees, *Apis spp.* (see [3, 7] for debate on this); pied babblers,
49 *Turdoides bicolor* [8]; and superb fairy-wrens, *Malurus cyaneus* [9]. Of particular
50 relevance to the study presented here is the teaching behaviour seen in meerkats,
51 *Suricata suricatta* [10]. Adults bringing back prey to pups do so in way that gives the
52 pups the opportunity to practise their hunting skills on dangerous prey (scorpions).
53 When the pups are very young, they are provisioned with dead scorpions, but as
54 they age they are presented first with disabled (sting removed) and later with intact
55 scorpions. Thus pups are provided with prey of increasing difficulty as their hunting
56 skills develop- a process that has been termed 'progressive teaching' [11].
57 A number of researchers have used evolutionary theory to explain the
58 taxonomic distribution of teaching and elucidate the circumstances under which it
59 evolves [3, 11, 12]. Since teaching is a cooperative behaviour [5], it is likely that kin

selection [13] plays a role, though this is unlikely to be the whole story. A mathematical model [12] found that teaching only has a selective advantage within a narrow range of pre-existing learning levels. If the probability of individuals learning through asocial or social learning is too high then there is no need for teaching to evolve, too low, and there is insufficient information in the population to be taught to others.

Most of the species for which there is evidence of teaching are cooperative breeders (including all those listed above), leading some researchers to tentatively suggest a link between teaching and cooperative breeding (see [5, 11, 12] for a discussion of the possible evolutionary link). However, this taxonomic distribution may be misleading, since it is based on only a handful of species, which do not constitute strong evidence that an underlying pattern exists [14]. Furthermore, the observed pattern may be biased if it is easier to obtain evidence for teaching in cooperative breeders [5], maybe due to their popularity and tractability as study systems. This possibility is supported by suggestive evidence of teaching in a number of non-cooperative breeders [4, 11], including progressive teaching of hunting skills similar to that seen in meerkats, in non-cooperatively breeding felids [4, 15]. Therefore, in order to critically assess the potential link between cooperative breeding and teaching, it is necessary to examine many more potential cases of teaching in non-cooperative breeders.

Another taxonomic group for there are anecdotal reports of teaching are avian raptors (order Accipitriformes)[4] few of which are frequent cooperative breeders. In particular, adult ospreys (*Pandion haliaetus*) have been observed

dropping caught fish (their primary prey) allowing their young to dive and catch the prey, perhaps allowing the young to practise their hunting skills [4, 16]. Such behaviour is difficult to study systematically as it would involve observing a large number of ospreys over a wide area within a short window of time. However, we reasoned that if there is selection for teaching in ospreys, we might also expect to see progressive teaching, of a form similar to that seen in meerkats, at the nest. We hypothesised that adult ospreys would bring back a larger proportion of live prey to the nest as their offspring get older, allowing them to practise killing prey. We were able to collect data on osprey behaviour at the nest via live-streaming and publically available webcams, allowing us to test the hypothesis. A positive result would not constitute a strong case of teaching, since not all of Caro and Hauser's [4] criteria would have been assessed. Nonetheless, a positive result would be sufficient to highlight a highly plausible case worthy of further investigation. Furthermore, a strong negative result (significant opposite trend) would be sufficient to rule out the possibility that osprey teach their young to kill prey at the nest in a manner analogous to meerkats.

Methods

We used public-access websites with live-streaming webcams to observe ospreys at their nests. Webcams were selected if they monitored nests that were currently in use by a nesting pair with one or more chicks, gave a consistent view of the main body of the nest, and gave a good quality picture. Young were an average of 16.1 days old (S.D. = 6.3) at the start of the study. Twelve cameras were chosen: eight in the UK and four

in the USA (see Table S1 in the Supplementary Material). From June 11th to September 5th, 2016, we observed the webcams from approximately 12:00 (GMT) until 22:00 on 70/87 days. Six webcams were observed concurrently, with each set of six (Nests 1-6 and 7-12 in Table S1) observed on alternate days. We recorded all events where an osprey was seen bringing prey to the nest and recorded a) whether the prey appeared alive or dead at the time of arrival at the nest (see Supplementary Material); and b) whether the other, non-delivering parent was present at the nest. By the end of the observation period, all but one of the chicks had survived, successfully fledged, and nearly all birds had left the nest to migrate.

We fitted Generalised Linear Mixed Models (GLMMs), in order to test whether chick age had an effect on a) the proportion of prey brought to the nest alive and b) the probability the other parent was present at the nest when prey was delivered. We used a binomial error structure and a logit link function, with 'pair' as a random effect on both intercept and slope (see Supplementary Material). We used the lme4 [17] package in the R statistical environment [18].

Results

356 feeding events were recorded (29.6 per pair ± 13.2 SD)[19]. The proportion of prey brought back to the nest alive decreased with chick age (GLMM, Wald test: $z = 2.67$, $p = 0.0076$; see Fig. 1a), contrary to the predictions of the teaching hypothesis. The odds of prey being brought back alive reduced by an estimated factor of 0.934 (95% C.I. = 0.889 – 0.982) for every increase of one day in chick age. When prey was alive on arrival at the nest, it was always killed by the parents, never the offspring,

129 also contrary to the expectations of the teaching hypothesis. We conclude that
130 progressive teaching of the handling of difficult prey, as seen in meerkats [10] does
131 not occur during the nesting period of ospreys.

132 We found that prey was more likely to be brought back alive when the other
133 parent was present at the nest (19/264 events) than when it was not (0/92) (Fisher's
134 exact test: p= 0.0052; odds ratio= 0, 95% C.I.= [0,0.587]). As in previous studies [e.g.
135 20], there was a clear tendency for the other non-delivering (probably female) parent
136 to remain in the nest for feeding events until chicks reach a certain age (~ 44 - 66
137 days), after which they are generally not present at all (GLMM, Wald test: $z = 7.938$, $p < 0.001$, see Fig. 1b). Since the female feeds pieces of prey to the young until they
139 fledge [20] , the male can deliver some live prey to the nest prior to fledging, because
140 the female is present to handle and kill the prey. Combined, these two effects explain
141 the decreasing trend in the proportion of live prey as chicks get older.

142

143 **Discussion**

144 There is potential for teaching to occur during other stages of osprey
145 development. Meinertzhagen [16] reported that osprey chicks were encouraged to
146 fly from the nest in order to claim fish from their parents. However, such behaviour
147 was not recorded in this study, nor in Bustamante's [21] study using live
148 observation from a hide. Adult ospreys have also been reported to drop fish from
149 flight allowing their young to dive and catch the prey [4, 16]. This behaviour might
150 enable young ospreys to practise diving at prey without having to locate prey
151 themselves, allowing them to learn the behaviour faster, and thus could qualify as

152 teaching. Intuitively, the feet-first diving ospreys use to catch fish seems likely to be
153 the most difficult motor skill for them to learn in order to hunt effectively. This
154 means diving is probably the component of hunting behaviour that would benefit
155 most from parental teaching. In our study, we only observed behaviour at the nest
156 due to the accessibility of online webcams monitoring the nests- assessing potential
157 teaching away from the nest is significantly more challenging.
158 Nonetheless, if there is selection for ospreys to teach, the question remains as
159 to why progressive teaching does not occur at the nest. When prey was delivered to
160 the nest alive, it was always killed before presentation to the offspring, suggesting
161 handling live prey once caught is a difficult skill to master. Progressive teaching
162 similar to that seen in meerkats [10] would seem an effective method of maximizing
163 offspring survival. It is possible that the benefits to the parents of teaching in
164 general do not outweigh the costs (e.g. energetic costs of flying with live prey) and
165 there is no selection for teaching. Alternatively, it may be that nestlings are not
166 sufficiently physically developed to handle live prey, making teaching at the nest
167 ineffective, with teaching occurring only later in development.
168 We aimed to assess whether teaching occurs in a non-cooperatively breeding
169 species, in which teaching might plausibly occur. We were able to collect sufficient
170 data to show that ospreys do not teach at the nest in a manner analogous to
171 meerkats, contrary to what might be expected if there is selection for teaching in
172 ospreys. Whilst we cannot conclusively conclude that ospreys do not teach their
173 young at all, it remains the case that strong cases of teaching are disproportionately
174 more common in co-operatively breeding species. However, further studies of

potential cases of teaching are required for researchers to fully understand the factors driving the evolution of teaching.

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Data Accessibility

https://doi.org/10.5518/193 [19]

Author Contributions

MH collected the data, MH and WH both planned the study, analysed the data and wrote the manuscript. Both authors agree to be held accountable for the content of this paper and approved the final version of the manuscript.

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Competing Interests

We have no competing interests

Ethical statement

Observations were made remotely via pre-existing and publically available webcams, therefore no birds were disturbed or harmed as a result of the study.

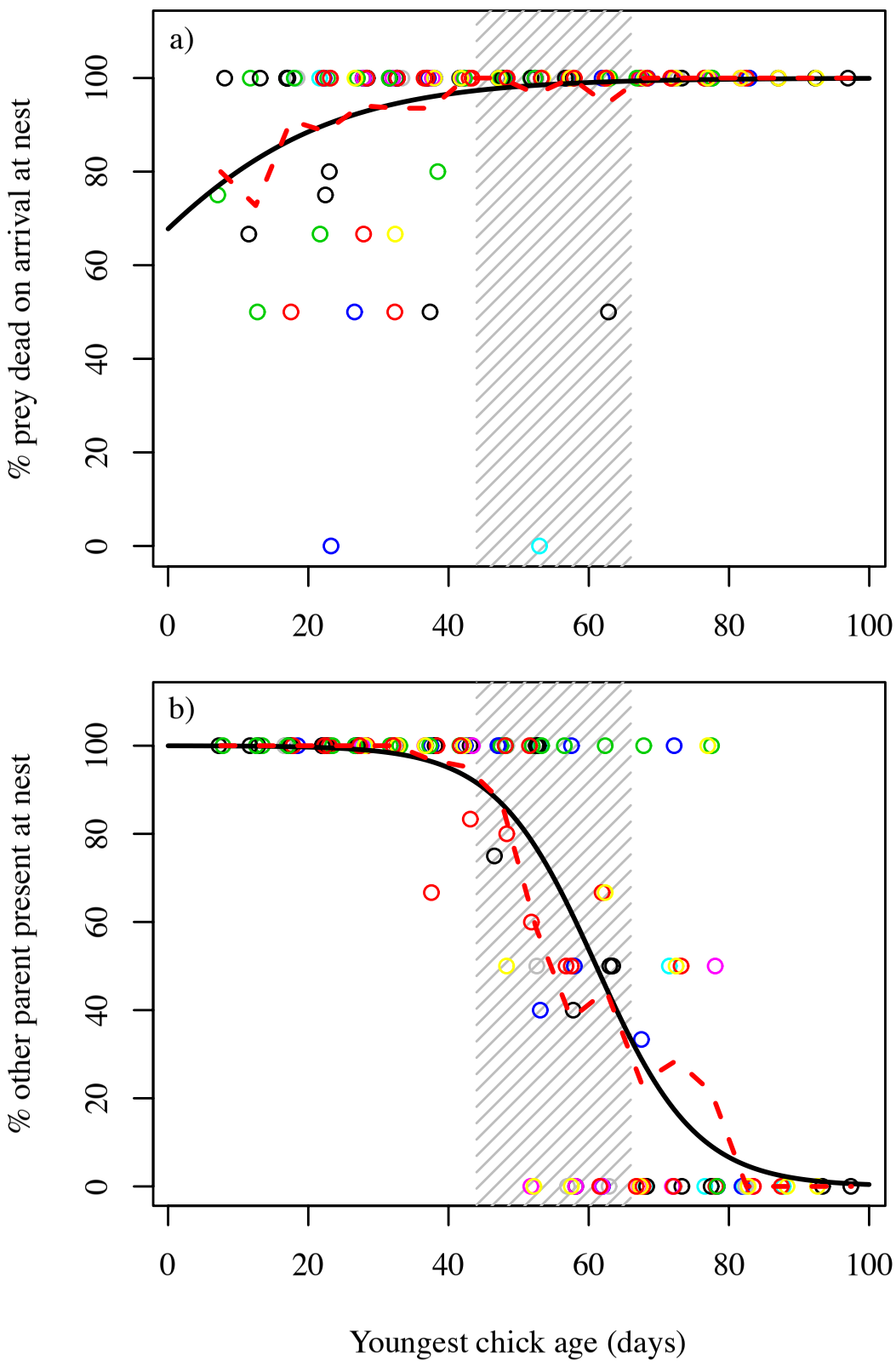
a)
% prey dead on arrival at nest
0
20
40
60
80
100
b)
% other parent present at nest
0
20
40
60
80
100
Youngest chick age (days)

Figure 1. a) The percentage of prey brought back to the nest dead; and b) the percentage of prey delivery events for which the other parent was present at the nest, as a function of chick age. Each point shows data summed across a 5-day interval for a single pair, with each pair represented by a different colour. Dashed red lines show the average across all pairs, and solid black lines show the fitted GLMM. The shaded area shows the range of days at which the last chick fledged.