Original Article

The cost of teaching embryos in superb fairy-wrens

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There is growing empirical support for teaching in nonhuman animals. To unravel the evolutionary dynamics of teaching, we need to understand its costs and benefits. In superb fairy-wrens (*Malurus cyaneus*), females teach their embryos by calling to them: embryos learn a vocal password, and hatchlings incorporate the learned vocal password into their begging calls to solicit parental feeding. The more a female teaches (higher call rate), the better the embryos learn (greater call similarity), leading to more food provisioning by parents. Given these direct benefits, we would expect all female fairy-wrens to call often to maximize embryonic learning in their genetic progeny, yet they do not. Teaching the password carries a severe cost: nest predation was higher at both natural and artificial nests that had more incubation calls. At artificial nests, predation was 8-fold higher for high incubation call rate (30 calls per hour) and 5-fold higher for low incubation call rate (15 calls per hour) compared with nests without any incubation calls. At natural nests, nests that were depredated during incubation had higher incubation call rate (18.3 calls per hour) than nests that survived (11.4 calls per hour). Mother fairy-wrens must trade-off the costs of calling and the benefits of learning to optimize fitness benefits of teaching.

Key words: **embryonic learning, *Malurus cyaneus*, teaching.**

INTRODUCTION

Over the last decade, there has been increasing research on teaching in animals leading to growing empirical support. Teaching is a specialized form of cooperation, whereby knowledgeable individuals facilitate learning in naive individuals (Galef et al. 2005; Thornton and Raihani 2008). Outside the controlled environment of the laboratory, it is difficult to show that purported acts of teaching cause new or accelerated learning by pupils (Galef et al. 2005; Thornton and McAuliffe 2006). But in the Australian superb fairy-wren (*Malurus cyaneus*), a recent study showed a correlation between exposure to teaching and copy accuracy by the pupil (Colombelli-Négrel et al. 2012). Specifically, by learning a vocal password from the mothers as embryos, nestling fairy-wrens produce a call that elicits more feedings from the parents, whereas the parents often do not waste investment in feeding foreign, brood parasitic Horsfield's bronze cuckoo (*Chalcites basalis*) young in the nest. But fairy-wrens do not always have a high incubation call rate—despite possible benefits of embryonic vocal learning (Kleindorfer et al. 2014). Seminal studies by Mery and colleagues showed that there can be costs to learning (Mery and Kawecki 2005). Here, we ask if there are costs to teaching that could explain why teaching effort is not maximized in the fairy-wren system.

Caro and Hauser (1992) functionally defined teaching using 3 observable criteria: 1) a teacher modifies its behavior in the presence of a pupil; 2) the teacher incurs some cost or at least does not obtain an immediate benefit to itself; and 3) the recipient of the teaching acquires new skills or information to its benefit. This operational definition of teaching allows researchers to separate active teaching from inadvertent social learning in which learning can occur as a by-product through observation of another individual's behavior (Hoppitt and Laland 2013). Hoppitt et al. (2008) applied the Caro and Hauser definition to published examples of teaching and learning, and concluded that teaching occurs across a much wider range of taxonomic groups than previously suspected. In their review they found strong evidence for all 3 criteria from insects to mammals. Here, we assess if "mother to neonate communication" in fairy-wrens meets the full definition of teaching by testing if there is a cost of teaching to explain the dynamic variation of teaching effort seen in the wild.

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In line with this, brood parasite–host systems offer another possibility to examine aspects of animal teaching and learning. For example, in birds, brood parasites lay their eggs in the nests of hosts. From the hosts' perspective, there are a range of defense mechanisms to thwart brood parasites, including the rejection or abandonment of foreign eggs and chicks, or front line defenses such as socially learned mobbing of cuckoos to altogether prevent parasitic egg laying (Feeney and Langmore 2013; Feeney et al. 2013). But each of these defense tactics carries the costly risk of recognition errors (Grim 2007; Trnka et al. 2012; Langmore 2013) which could be reduced through teaching and learning. Superb fairy-wrens and their brood parasite are a particularly good model system to investigate this aspect because 1) female superb fairy-wrens actively teach their embryos a vocal password within an incubation call that the hatchlings must emulate in their begging call in order to be fed at high rates, as previous experimental study showed lower food provisioning by parents at nests with low call similarity in chicks (Colombelli-Négrel et al. 2012). The more often the female calls to the embryo the higher the call similarity after hatching (Colombelli-Négrel et al. 2012; Kleindorfer et al. 2014). 2) In the superb fairy-wren we experimentally showed that the begging calls of cross-fostered fairy-wrens are learned rather than innate, because the begging call element more closely resembled the vocal password (element of the incubation call) of their foster mother rather than their genetic mother (Colombelli-Négrel et al. 2012). 3) Embryos of the fairy-wrens' primary brood parasite, Horsfield's bronze cuckoo, have a shorter incubation duration, are hence exposed to the fairy-wren incubation calls for less time, and they also have lower call similarity after hatching (Colombelli-Négrel et al. 2012). And 4) adult fairy-wrens respond to adult cuckoo calls according to the risk of brood parasitism (Kleindorfer et al. 2013). The finding of increased alarm calls and defense behavior by fairy-wrens in response to acoustical cues of different brood parasites in their territory indicates that host fairy-wrens modify their behavior toward cuckoo species, including their investment in teaching effort of embryos (Kleindorfer et al. 2014).

The superb fairy-wren and Horsfield's bronze cuckoo system satisfies 2 of 3 teaching criteria (Caro and Hauser 1992). First, female fairy-wrens increase their teaching effort (call rate) when the naive pupils (the embryos) are more developed, during late-stage incubation (criterion 1; Colombelli-Négrel et al. 2012). Second, learning has fitness benefits because parents feed hatchlings more when they have more accurately learned the vocal password and incorporated it into their begging call compared with hatchlings with lower call similarity, which may include cuckoos (criterion 3). But if teaching is only beneficial, then why is it not more prevalent? The fact that fairy-wren mothers modify teaching effort according to the risk of brood parasitism (e.g., cuckoo presence) (Kleindorfer et al. 2014) suggests that mother to embryo communication may bear costs. One potential cost of acoustic education of embryos in the nest could be that the sound of the incubation call can attract predators and lead to increased nest predation. There is ample evidence from studies of nestling begging calls that vocalization behavior increases predation risk (Haskell 1994; Briskie et al. 1999) and that parental calling (but not visual displays) attracts neighbors and predators (Grim 2008). Consequently, female investment into incubation call production may be the result of a trade-off between benefits from teaching and increased predation risk.

Here, we use observational and experimental approaches to test whether superb fairy-wrens incur a fitness cost from teaching embryos (criterion 2). At natural nests, we recorded incubation calls by female fairy-wrens and compared incubation call rate with nest predation across study years. At artificial nests, we experimentally broadcast incubation calls at different rates and compared predation at nests that differed in number of incubation calls per hour. Finally, we discuss possible evolutionary outcomes when teaching mothers are faced with conditions of high predation and brood parasitism risk.

MATERIALS AND METHODS

Study sites and species

We monitored superb fairy-wren nests and recorded female incubation calls and nest predation during the fairy-wrens' peak breeding period from September to January in the years 2007, 2009–2012. We conducted experimental trials in 2013 to test if artificial nests with incubation calls had a higher proportion of depredated nests outcome than artificial nests without incubation calls. The 2 study sites were in South Australia at: 1) Cleland Wildlife Sanctuary (34°58′S, 138°41′E), 25 kms SE of Adelaide; and 2) Newland Head Conservation Park (35°37′S, 138°29′E), a coastal area 15 kms SW of Victor Harbor on the Fleurieu Peninsula.

Nest predation

Between 2007 and 2009–2012, we located 138 nests and monitored them every 3 days for nesting outcome (fledging, predation, abandonment) (Table 1). For this study, we only test incubation call rate in relation to nesting outcome for nests that were observed during the incubation phase ($n = 42$ nests with incubation call rate and predation outcome). Predation was scored if eggs were missing from the nest between the nest content examinations every 3 days.

Recording incubation call rate across years

Between 2007 and 2009–2012, we recorded 428 female incubation calls from 42 nests. The methods to record the in-nest vocalizations between 2007, 2009–2011 are given in Colombelli-Négrel et al. (2012). In 2012, we recorded all vocalizations at the nest for 2h on days 10–11 of incubation using a Zoom Handy Recorder H4n (Zoom Corporation, Tokyo, Japan); sound files were recorded as broadcast wave files at 48kHz sampling rate, 24-bit depth. We transcribed each recorded vocalization to an Apple MacPro (Apple Corporation, Sydney, Australia) for editing with Amadeus Pro 1.5 (Hairersoft Inc., Kenilworth, UK). For this study, we analyzed the number of incubation calls per hour (call rate) in relation to

Table 1

Incubation call rate and predation outcome differ across years

Study site and year	Number of incubation calls per hour ($n = 42$)	Nest predation ($n = 138$)
Newland Head		
2007	13.9 ± 4.8	57% (8/14)
2009	23.3 ± 5.6	83% (5/6)
2011	10.9 ± 1.1	56% (18/32)
2012	9.8 ± 3.6	53% (10/19)
Cleland		
2011	17.6 ± 0.2	40% (8/20)
2012	10 ± 1.4	34% (16/47)

Annual differences in number of incubation calls per hour (mean ± standard error) and nest predation (%) are shown for Newland Head Conservation Park and Cleland Conservation Park in South Australia.

predation outcome. We compared call rate per female based on 2 h of recording for 2 consecutive days per female.

Broadcast of incubation calls at artificial nests

In October and November 2013, we broadcast incubation calls at artificial nests to test whether incubation calls elevate predation risk. We used domed woven nests baited with a single domestic Japanese quail (*Coturnix japonica*) and for 5 h (0600 to 1100) at every nest including control nests, we placed a battery powered amplified speaker connected to an Apple iPod (Apple Inc., Sydney, Australia). The experiment was repeated every day for 3 days. Three days is the average number of days a female calls to a late-stage embryos in the nest (females call to cuckoo eggs for ~2 days and to wren eggs for ~4 days). After the 5 h we checked every nest for predation and collected the playback equipment. The nests were placed 30–50 cm above the ground every 100 m along 5 transects at Newland Head Conservation Park. At every second nest, we broadcast a female incubation call. Each transect had 20 nests for a total of 100 nests: 30 nests with a high call rate (30 incubation calls per hour), 20 nests with a low call rate (15 incubation calls per hour), and 50 control nests with no incubation call. The natural range in mean incubation call rate across years in South Australia was 10–23 incubation calls per hour (Table 1). The playback stimuli were the incubation calls of 4 fairy-wrens that had been recorded in 2009. We normalized the playbacks at −6 dB and saved them as uncompressed 24-bit 48 kHz broadcast wave files using Amadeus Pro 1.5.

To test if nest concealment due to vegetation cover differed between experimental (47), control (50), and wild (22) nests, we compared the proportion of the nest that was concealed by vegetation between the 3 treatment groups. None of the nest-site vegetation scores differed significantly across the 3 groups: vegetation cover 1 m in front of the nest (Anova: $F = 1.322$, df = 2, $P = 0.270$), vegetation cover 1 m to the left of the nest ($F = 2.110$, df = 2, $P = 0.110$), vegetation cover 1 m to the right of the nest ($F = 1.139$, df = 2, $P = 0.323$), or nest height (cm) measured from the ground to the entrance hole ($F = 2.056$, df = 2, $P = 0.138$). None of the pairwise post-hoc comparisons was significantly different for vegetation cover between experimental, control, and natural nests.

Ethics statement

This study on wild superb fairy-wrens was approved by the Animal Welfare Committee of Flinders University (E234-236) and supported by a scientific permit to conduct the research (Z24699 4).

Statistical analysis

Data were analyzed with SPSS 20 for Windows (SPSS Inc., Chicago, IL). We used multivariate analysis of variance (MANOVA) to analyze incubation call rate and annual predation per year with study site as a random factor. We used binary logistic regression to test if number of incubation calls per hour per nest was correlated with predation outcome (survived, predated) at natural nests, and a chi-squared test for the effect of incubation call rate on predation outcome at artificial nests.

RESULTS

Both nest predation and number of incubation calls per hour differed significantly across study years in South Australia (MANOVA: predation outcome: $F_{3,41} = 231.77$, $P < 0.001$; call rate: $F_{1,41} = 3.82$, $P = 0.018$). The range in percentage of depredated nests was 34–83% across study years, and the range in mean number of incubation calls per hour was 10–23 (Table 1). To test if incubation call rate increased with the risk of predation at natural nests, we examined predation outcome during the incubation phase (survived, depredated) against the number of incubation calls per hour. Nest predation was significantly higher when females produced more incubation calls per hour (binary logistic regression: odds = 0.35, $P = 0.023$, $n = 42$; Figure 1). Mean number of incubation calls per hour at nests that survived was 11.4 ± 1.4 ($n = 33$) compared with 18.3 ± 2.5 at nests that were depredated ($n = 9$) (Figure 1).

Experimental incubation calls and predation outcome

At experimental nests, nest predation was higher when incubation call rate was higher ($\chi^2 = 30.39$, df = 2.100, $P < 0.001$; Figure 2). Of the 30 nests with high incubation call rate, 20 were depredated (67%). Of the 20 nests with low incubation call rate, 8 were depredated (40%). Of the 50 control nests, 4 were depredated (8%). Thus, predation was 8-fold higher at nests with high incubation call rate (8% vs. 67%), and 5-fold higher at nests with low incubation call rate (8% vs. 40%). In most cases, the predation events occurred during the 5-h playback trial (during 18/20 cases for high incubation call rate, 4/8 cases for low incubation call rate, and 0/4 cases for no incubation calls) ($\chi^2 = 7.1$, df = 1.36, $P = 0.008$).

DISCUSSION

We have previously shown that superb fairy-wren embryos learn a vocal password by listening to their mother's incubation call and base their begging calls on the unique vocal password taught to them by the female (Colombelli-Négrel et al. 2012). One function of this teaching and learning is for parents to recognize host hatchlings and expose intruder cuckoo chicks that use call matching after hatching rather than call learning before hatching to emulate the host begging call (Langmore et al. 2008; Colombelli-Négrel et al. 2012). We previously used an experimental approach to show that
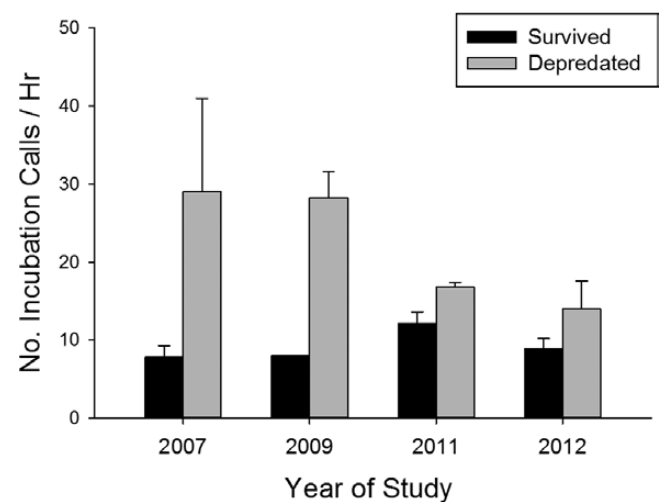

Figure 1
More predation at natural nests with many incubation calls. Nest predation at natural nests is shown in relation to female teaching effort (number of incubation calls) by superb fairy-wren females ($n = 42$ nests). Nest predation was higher at nests with many incubation calls (mean ± standard error). The data are pooled for nests from Newland Head Conservation Park and Cleland Conservation Park, South Australia (Table 1).
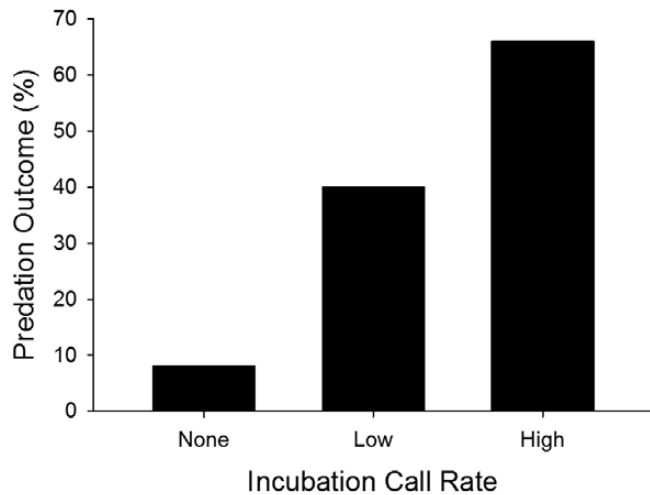
Figure 2
More predation at artificial nests with many incubation calls. Artificial nests were baited with quail eggs and each nest had an iPod and speaker for 5 h. There were 3 treatment groups: 1) no incubation calls (playback equipment present but inactive, $n = 50$); 2) low incubation call rate (15 calls per hour, $n = 20$); or 3) high incubation call rate (30 calls per hour, $n = 30$).

females increased their teaching effort (call rate and vocal password rate) when they heard a cuckoo calling near the nest (Kleindorfer et al. 2014). Here, we show that teaching in this system also carries a potentially high cost as the risk of predation was much higher when there were many incubation calls at both natural and artificial nests. Across years, predation was higher when incubation call rates were higher. At depredated natural nests females produced ~20 incubation calls (18.3) per hour, whereas at nests that survived females produced ~10 incubation calls (11.4) per hour. In experimental nests, predation was 8 times more likely if females had high incubation call rate (30 calls per hour) compared with nests without incubation calls, whereas nests with low incubation call rate (15 calls per hour) were 5 times more likely to be predated. Notably, most predation at artificial nests occurred during the 5-h experimental broadcast (see also Grim 2008). Thus, call rate, and not some other nest-site feature, was the primary cue used by a predator to locate the nest.

Female incubation calling and embryonic learning in the superb fairy-wren system now satisfies all 3 criteria for the operational definition of teaching: 1) modified behavior by the teacher in the presence of a naive observer; 2) a cost to the teacher; and 3) a benefit to the pupil (Caro and Hauser 1992). These findings of teaching and learning in the superb fairy-wren should spur more comparative and field research into the evolution of teaching and learning. For example, females that invest in their offspring via teaching may also have invested other nutrients or resources to promote condition-dependent song learning (Buchanan 2000, 2011; Nowicki et al. 2002a, 2002b; Gil et al. 2006), as has been found in the maternal effects on the learning of song and human language in embryos and neonates (Qvarnström and Price 2001; Spencer et al. 2003; Lipkind et al. 2013). Thus, teaching might be an important but greatly ignored aspect of maternal investment (Fox and Mousseau 1998).

Socially Cued Anticipatory Plasticity is the term given to behavioral plasticity in response to environmental and social cues that alter an individual's morphology, behavior, or life-history strategy (Kasumovic and Brooks 2011). Teaching is one social mechanism that facilitates learning and phenotypic change associated with learning (Hoppitt and Laland 2013). There is growing evidence

across taxa from insects to birds and primates that animals teach, and evidence that teachers modify their behavior according to prevailing social and environmental conditions (e.g., Kleindorfer et al. 2014). In this manner, teaching is a social learning mechanism to facilitate the transfer of essential skills from teacher to the next generation (Feeney and Langmore 2013; Hoppitt and Laland 2013). Although many studies focus on the benefits of teaching and learning, this study shows the costs of teaching in the superb fairy-wren system.

Given we have shown teaching has high costs we conclude that teachers should be selected to evaluate the costs and benefits of teaching in dynamic environments. The costs of teaching include mortality risk to adults and/or offspring, such as predation of adults and/or chicks, or brood parasite-induced mortality of chicks (Wyllie 1981; Thornton and Raihani 2008; Anderson et al. 2009; Colombelli-Négrel and Kleindorfer 2009; Fogarty et al. 2011). The benefits of teaching may be different for the teacher (in relation to parent–offspring relatedness) and pupil (impact of learning for survival and/or reproductive success). We suggest that across study populations, and other species of cuckoo hosts, fairy-wrens may strategically adjust their teaching effort (call rate and/or vocal password rate). The following predictions can be formulated: 1) low teaching effort (low call rate) in areas with high predation risk; 2) high teaching effort (high call rate and/or vocal password rate) in areas with high brood parasite risk; and 3) evolutionary adaptations toward making teaching more efficient in systems where both predation and parasite risk is high or in areas where cuckoos are also nest predators. A solution to this dilemma could be to increase the password rate (begging call element within the incubation call) while decreasing call rate and/or call complexity.

Thus, the adaptive interplay between teaching and learning generates testable predictions for other systems with mother to egg teaching. There are 28 species of wrens in the Maluridae, of which 4/4 species of fairy-wren studied to date have female incubation calls (Colombelli-Négrel D et al. unpublished data). When extrapair copulations are frequent, as often occurs in the Maluridae (Cockburn et al. 2013), we also predict different evolutionary selection on putative mothers and fathers. In these circumstances, males and females have different certainty of relatedness to their brood and hence should evaluate the costs and benefits of teaching differently.

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